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## NATURAL HISTORY AND DIFFERENTIATION IN THE YELLOW-BELLIED SAPSUCKER

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### INTRODUCTION

The Yellow-bellied Sapsucker (*Sphyrapicus varius*) is a species of woodpecker subdivided into strongly characterized geographic races that are clearly distinguishable even in the field and which differ markedly in the extent of interbreeding where their ranges meet. The purpose of this investigation has been the analysis of the differentiation in the group as it approaches the species level.

Between some races of sapsuckers there is free interbreeding, whereas between others it is so rare that reproductive isolation is almost complete, even though physical and ecological barriers, if present, seem no greater than where intermixture takes place. The species is also peculiar in that sexual dimorphism in color is distinct in one race whereas it is completely lacking in another. Similarly, the races vary from highly migratory to practically sedentary. These rather unusual features, coupled with the fact that most of the zones of contact are limited and relatively accessible, make the Yellow-bellied Sapsuckers an excellent subject for the study of morphological variation in combination with field studies on the breeding behavior of the races at the points of junction. The latter topic was especially emphasized, for despite the fact that specimens showing intermediate characters have been known for almost a hundred years, no mixed pairs had ever been reported and no data published on the viability and fertility of the intermediates. I have also attempted, insofar as the meager evidence permits, to determine the genetic, environmental, and historical factors which may have influenced the evolution of the forms within this group.

### MATERIALS AND METHODS

To obtain data on breeding behavior in zones of contact and overlap, field trips were made to selected areas in northern California in 1948 and 1949 and to British Columbia in 1950. I spent five days, from May 20 to May 24, 1948, in the vicinity of Canby, Modoc County, California, and in 1949 stayed for about six and one-half weeks, from May 21 to July 4, at Crowder Flat, 38 miles northwest of Alturas, Modoc County, California. From April 27 to July 14, 1950, I visited various localities in British Columbia, spending most of the time in the region between Hope and Princeton and between Williams Lake and Quesnel. In these periods I was able to observe stages in the life history of the birds from pre-nesting territorial behavior through the emergence of the young from the nest. Sapsuckers were collected at all the localities mentioned except Manning Provincial Park in the Hope-Princeton area. They are deposited in the Museum of Vertebrate Zoology.

Additionally, specimens have been examined from the following institutions and collections: The Donald R. Dickey Collection and the Department of Zoology Collection, University of California, Los Angeles (UCLA); the Los Angeles County Museum, Los Angeles (LACM), through Mr. Kenneth E. Stager and Mr. William G. Reeder; the

Robert T. Moore Collection, Pasadena, California (RTM), through Dr. Moore and Dr. John Davis; the United States National Museum, Washington, D.C. (USNM), through Mr. H. G. Deignan; the Allan R. Phillips Collection, Tucson, Arizona (ARP), through Dr. Phillips. A total of approximately 1040 specimens was examined, mostly from the California institutions.

#### ACKNOWLEDGMENTS

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#### THE GENUS AND SPECIES

The genus *Sphyrapicus* differs strikingly from other genera of woodpeckers in its feeding habits and the associated structural modifications. Sapsuckers rarely if ever dig into infested trees for woodboring insects and larvae but feed to a considerable extent on the cambium and softer parts under the bark of trees and shrubs and on the sap as well. They do this by drilling rows of holes through the outer bark or by removing it over a long strip. The diet also includes fruits and berries and many insects; the latter may be caught on the wing or gathered from tree trunks, branches, and the sap workings. Detailed accounts are given in McAtee (1911), and Grinnell and Storer (1924).

In relation to these feeding habits, the tongue is brushy or bristled at the tip rather than barbed, and it is much less extensile than in other genera of woodpeckers. The hyoid elements are less elongated than in other picids and do not extend over the crown; the capital apertium is correspondingly small. For details of tongue structure and pterylosis see Lucas (1895), Coues (1903), and Burt (1929); for a complete listing of generic characters see Coues (1903) and Ridgway (1914).

The breeding range of the genus is restricted to North America north of México; some races migrate south of the border, and one goes as far as Panamá and the West Indies. Two species are currently recognized by most authors. *Sphyrapicus thyroideus* is a well-marked form divided into two subspecies, *S. t. thyroideus* and *S. t. nataliae*, and is of only incidental importance in this report. The other species, *Sphyrapicus varius*, is the one on which the present study is based.

*Sphyrapicus varius* is now considered by most authors to be a polytypic species comprising four well-characterized subspecies, although the group has frequently been divided into two species with each one including two races. Oberholser (1938) has proposed that the eastern form be split into northern and southern subspecies, *S. v. atrothorax*, and *S. v. varius*, respectively, on the basis of size; however, this procedure has not been followed by most taxonomists (Wetmore, 1940), and the question of its validity is outside the scope of the present study. In this paper I have followed the current nomenclature in recognizing four races of one species, for reasons which will be discussed

later. A synonymy of earlier names may be found in Ridgway (1914), and the basis for adoption of those presently in use may be found in Swarth (1912). The four races are *S. v. varius*, *S. v. nuchalis*, *S. v. daggetti*, and *S. v. ruber*.

Detailed descriptions of the forms may be found in Ridgway (1914), and descriptions of juvenal plumage and molt sequence appear in Bent (1939). The following accounts of the characteristics of the races have been condensed from these sources and have been modified from them by checking against large series of specimens.

#### SYNOPSIS OF RACES

##### *Sphyrapicus varius varius* (Linnaeus)

*Adult male*.—Forehead and crown bright poppy red or crimson, bordered posteriorly by an occipital crescent of glossy blue-black, extending laterally to above middle of eye; nape white or brownish white, rarely tinged lightly with red, laterally confluent with white postocular stripe; auricular region glossy black; a broad band of white originates at nasal tuft and extends between orbital and malar region to side of neck; malar stripe black, becoming narrow posteriorly where it joins a large patch of glossy blue-black, strongly convex posteriorly, extending across jugulum; chin and throat bright poppy red, like crown; median underparts and sides of jugulum white tinged with primrose yellow, more strongly so in fresh plumage; sides and flanks dull white or brownish white, broken by streaks and V-shaped markings of blackish; back and scapulars black heavily spotted with white, especially on sides of back; rump and upper tail coverts mostly black laterally, mostly white medially; wings black, with exposed portion of middle coverts and outer web of greater coverts except proximal ones white, forming a conspicuous longitudinal white patch along anterior part of wing; outer webs of primaries with large elongated spots of white, proximal portions of inner webs of primaries, including rudimentary outermost, with elongated white spots; secondaries and tertials much spotted with white on both webs distally; tail black, with inner web of middle pair of rectrices heavily barred with white or mostly white, the lateralmost with white spots on outer or both outer and inner webs in about half the cases.

*Adult female*.—Similar to adult male, but with a white instead of red chin and throat; red on crown varies from somewhat less posteriorly to lacking altogether; white spotting generally heavier, always present on one or both webs of outermost pair of rectrices.

*Juvenile* (sexes alike).—Wings and tail as in adults; back similar but washed with yellowish brown; sides and flanks similar, but more brownish; median underparts tinged with yellow; head region notably different from adults in that red and black areas are lacking; pileum sooty brown, each feather with a small, lighter-colored terminal or subterminal spot; auricular region and malar stripe brownish, the former with light shaft-streaks; stripes on sides of head dull white instead of clear white as in adult; chin dull white shading to pale buffy brown on throat; jugulum pale brown marked with fine crescentic bars of dusky, not strongly demarcated from adjacent areas.

The juvenal plumage is replaced gradually by protracted partial molt, at least of the body feathers. Red feathers may appear in the young males shortly after they leave the nest, and usually before any black feathers appear in the head region. Females may be much slower in acquiring the red crown. By late spring the adult plumage is almost always complete, but the black feathers of the jugulum may have light buffy edgings which disappear later through wear. In all the races the feathers of the jugulum appear to be the last to be replaced.

Adults have a prenuptial molt about the head and throat early in spring and a complete molt in late summer and fall (Bent, 1939). In fresh fall plumage, the lighter markings of the body are suffused with yellowish, and the belly is deeper yellow. A few narrow buffy edgings may be present on the feathers of the jugulum.

*Occurrence*.—*S. v. varius* breeds in deciduous or mixed deciduous and coniferous forest of eastern and northern parts of the continent, especially that including *Populus* (poplar, aspen, cottonwood, etc.) and *Betula* (birch). For geographic range see maps (figs. 1, 2).

In winter it occurs in a variety of forest associations from latitude 40° south to Panamá and the Greater Antilles. It is accidental in Greenland, Bermuda, Wyoming, Colorado, Arizona, and California. Wintering intermediates between this race and *S. v. nuchalis* have been taken at San Antonio, Bexar

County, Texas (USNM no. 112922) and 1 mile north of Tapalpa, Jalisco, México (RTM no. 27012).

Spring migration begins at least by the last week of March and may continue until the first week of May. Fall migration begins as early as the latter part of August and may continue into early November.

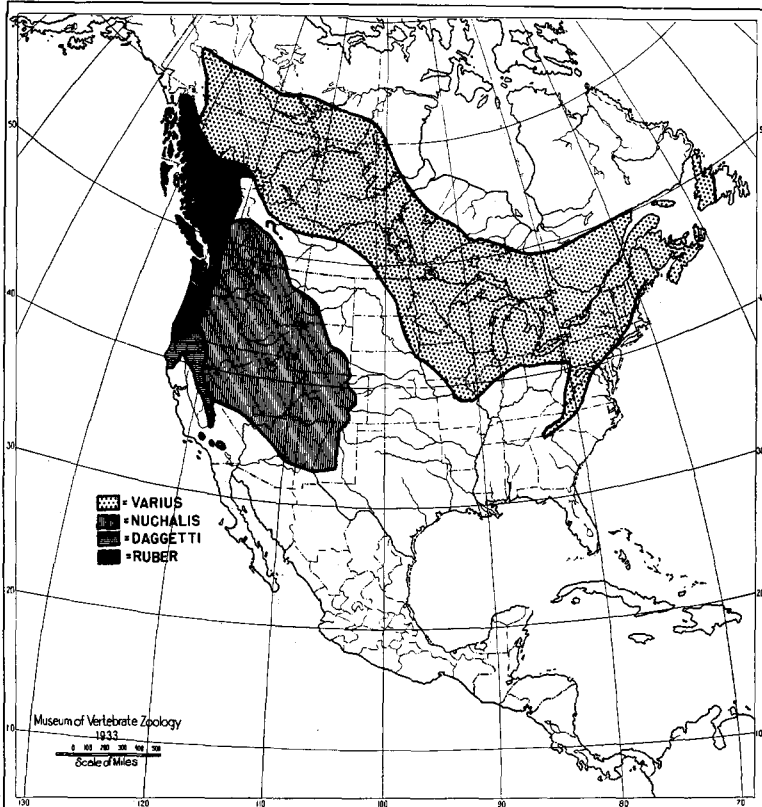


Fig. 1. Approximate outlines of breeding ranges of the four subspecies of Yellow-bellied Sapsucker (*Sphyrapicus varius*).

### *Sphyrapicus varius nuchalis* Baird

*Adult male*.—Similar to *S. v. varius*, but with much less white on back, this usually forming two definite but broken stripes laterally, converging posteriorly; nape red instead of white; red of throat more extensive, covering posterior portion of malar stripe and extreme upper part of jugulum; auricular region frequently tinged with red; white spots on outermost pair of rectrices almost always lacking; underparts usually less yellowish than in *S. v. varius*.

*Adult female*.—Similar to adult male, but chin and sometimes upper throat white, rarely almost completely red, the red not extending over malar stripe or tinging auricular region; facial striping may be less sharply defined than in male; white spots on outer web of outermost rectrix almost always present; crown always red, never largely or completely black as is sometimes true in *S. v. varius*.

*Juvenile*.—Similar to *S. v. varius*, but darker and less brown; pileum uniform sooty slate, unspotted, sometimes washed with brown; white of back less brownish; underparts less yellowish; dark markings of head more blackish; jugulum brownish gray, the dusky barring less apparent because of the darker background; chin and throat darker than in *S. v. varius*. Molt is apparently as in *S. v. varius*, but adult plumage is sometimes attained by late fall and always by early spring at the latest.

*Remarks*.—In very rare instances the red of the nape is lacking. An occasional juvenal *S. v. nuchalis*

is pale enough to be indistinguishable from a dark juvenal *S. v. varius*. An adult male from 17.5 miles south of Quesnel, British Columbia, lacks the white postocular stripe and is black in this area; another male from Alexandria, 28 miles south of Quesnel, has this white stripe reduced to a very narrow streak.

*Occurrence.*—*S. v. nuchalis* breeds primarily in forests containing aspen (*Populus tremuloides*) in pure stands or mixed with conifers; more rarely, it breeds in predominantly coniferous growth. It does not breed in oak (*Quercus*) woodland or mixed oak and pine forests. Its breeding range is primarily the Rocky Mountain region. It also breeds across southeastern British Columbia (chiefly east of the Fraser River) from the vicinity of Williams Lake south to the east slope of the Cascade Mountains and along the east side of this range to extreme northeastern California, between the Rocky Mountains and the Sierra-Cascade Range wherever suitable habitats are found, and at a few localities along the east slope of the Sierra Nevada in east-central California and extreme west-central Nevada.

*Nuchalis* winters in a variety of forest associations at low elevations in the southern part of its breeding range and farther south (see fig. 2). It is casual in Kansas, Nebraska, and Oklahoma and accidental in Guatemala. Wintering intermediates between this race and *S. v. daggetti* have been taken in Arizona, Sonora, southern California, and on Santa Cruz Island, California (LACM no. 2893), and a specimen from Crescent City, Del Norte County, California, taken November 29, 1915 (UCLA no. 24856) is almost certainly a *nuchalis* x *ruber* intermediate.

Spring migration begins at least by the last week of March and may continue until about the latter part of April. Fall migration probably begins about the first part of September and may continue throughout October.

#### *Sphyrapicus varius daggetti* Grinnell

*Adult male.*—Basically similar to *S. v. nuchalis*, but with much more red; nasal tufts and anterior and lower portion of lores dull yellowish white; posterior portion of lores and antero-inferior half of orbital ring black; frequently a small spot of white at upper posterior edge of ring; rest of head, neck, and chest bright red superficially, sometimes extending over breast and half-way down sides. The pattern of black and white markings on the head which is found in the two previously described races is still present, although much less distinct, on the subterminal parts of the feathers; the markings show faintly through the overlying red. White of back as in *S. v. nuchalis* or slightly less; abdomen yellowish white, more yellowish in fresh plumage; wings as in *S. v. nuchalis*, but white spots on rudimentary outermost primary frequently lacking; tail as in *S. v. nuchalis* but without white spots in outermost rectrices.

*Adult female.*—Like adult male, and indistinguishable in the field; rudimentary outermost primary usually with white spots; outermost pair of rectrices with white spots on outer web in about half the cases; white postocular spot of more frequent occurrence than in male.

*Juvenile.*—Somewhat similar to *S. v. nuchalis*, but head, neck, and breast much darker sooty, with no whitish markings except a dull white loreal streak and frequently a dull white postocular spot; dark barring on breast obscure; pileum, throat, and breast frequently washed with reddish. Molt into adult plumage seems to be completed at least by early spring and often by late fall. There is a complete molt in late summer and fall in the adults; no prenuptial molt is known.

*Occurrence.*—In all but the coastal part of its range, *S. v. daggetti* breeds primarily in an aspen-ponderosa pine (*Pinus ponderosa*) association; on the coast, it inhabits the predominantly coniferous forest of this humid region. Like *S. v. nuchalis*, *daggetti* does not breed in oak or oak-pine woodland. The breeding range of this race is primarily from the Cascade Mountains of southern Oregon (Klamath County) and the Sierra Nevada in California and Nevada west across northern California to the coast (fig. 1). In extreme southern Oregon it intergrades completely with *S. v. ruber*.

*S. v. daggetti* winters chiefly west of the Sierra Nevada in a variety of forest associations at low elevations throughout most of its breeding range, in suitable areas in the interior, along the entire coast of California, and south to about latitude 30° in Baja California. It is casual on the Santa Barbara Islands off the southern California coast and accidental in Arizona.

Migration in the spring and fall is not extensive, but the times of such movements are apparently similar to those of *S. v. nuchalis*, although probably of shorter duration.

*Remarks.*—The shade of red in the adults varies from dull in fresh fall plumage through bright red in the spring to an orange red, at least in part, in late summer before the annual molt. This color change is brought about by a process of wear which will be discussed briefly in a following section.



Fig. 2. Approximate outlines of winter ranges of the four subspecies of Yellow-bellied Sapsucker. The dark area in southern California represents overlapping of ranges of *nuchalis* and *daggetti*.

### *Sphyrapicus varius ruber* (Gmelin)

*Adults* (sexes alike).—Similar to *S. v. daggetti* but slightly larger and darker, red deeper and brighter, black more extensive; white of back usually restricted to two obscure and narrow broken stripes, frequently tinged with yellow; with very rare exceptions no white spots on rudimentary outermost primaries or on outermost pair of rectrices; white spots on other wing feathers fewer and smaller; red frequently more extensive, sometimes reaching down onto abdomen; median underparts deeper yellow than in *S. v. daggetti*; underlying black and white pattern of head and neck very obscure.

*Juvenile*.—Similar to *S. v. daggetti*, but much blacker, especially about head and neck; no trace of the striping present in *S. v. varius* and *S. v. nuchalis*. Molt into adult plumage is complete at least by early spring, usually by late fall or winter; other molts apparently as in *S. v. daggetti*.

*Remarks*.—In fresh fall plumage, the red is darker and duller than later in the year, as is true in *S. v. daggetti* but not in *S. v. varius* and *S. v. nuchalis*.

*Occurrence*.—*S. v. ruber* breeds in the humid coast forest of the Pacific Northwest from southeastern Alaska to southern Oregon. It also breeds in the mixed deciduous and coniferous forests along the west slope of the Cascade Range, occasionally east of it in Oregon (Deschutes County) and Washington (Yakima County), and in the central interior of British Columbia from Doch-da-on (=Dok-daon) Creek to the Peace River district (Tupper Creek) and south to Indianpoint Lake, the vicinity of Quesnel, and probably Lillooet.

This race winters in the coastal part of its breeding range, at least as far north as Prince of Wales Island, Alaska, and possibly even farther north.

Spring migration into the interior of British Columbia begins at least by the first week of April; the time of fall migration to the coast is not known.

A specimen from Arizona taken on October 27, 1932 (Godfrey, 1944) is close to typical *ruber* but appears to have traces of *nuchalis* characters in that it shows the underlying head and breast pattern more distinctly than is usual in *ruber*. This specimen is almost perfectly matched by one taken on November 24, 1926, at Tillamook, Oregon (UCLA no. 26441); both are probably *ruber* slightly approaching *nuchalis*. Such a mixed ancestry might account for the long migration of the Arizona bird, as *nuchalis* is of frequent occurrence as a migrant in the southwestern United States.

#### PIGMENTATION

One of the most noticeable features of the bright red feathers of sapsuckers and other woodpeckers is the polished, waxy luster and the loose, somewhat hairy texture. In such feathers the entire barbs or only their distal parts are enlarged both in length and diameter, devoid of barbules, and packed with pigment. This has been pointed out briefly and succinctly by Chandler (1916), and in detail by Frank (1939). In most cases the barbules are minute or absent even when the feather is just breaking out of its sheath, but in *Sphyrapicus varius daggetti* and *S. v. ruber* the red barbs bear numerous blackish barbules when freshly erupted. This causes the dullness of their red feathers in early fall which was mentioned in the foregoing descriptions of these races. The barbules are apparently fragile, for they soon wear off and leave the barbs with the gloss and loose texture which is present most of the year. Severe abrasion of the feathers during nesting activities results in a lightening of the red until it appears almost orange in some parts. In feathers which are parti-colored, or even in individual barbs which are part red and part black, the red area lacks barbules and the non-red region has them. Interestingly, the black malar feathers of the males of the Yellow-shafted Flicker (*Colaptes auratus*) have naked barbs distally and Test (1942) has shown they contain red pigment which is masked by black.

Another unusual aspect of red coloration in sapsuckers is that it is largely superficial in position; the red is present only as an extensive tipping to the feathers. When no red is present in the adult, as in some females of *S. v. varius*, this reveals the basic black and white pattern on which in other plumages red is superimposed. If red tips were added to the black feathers of the pileum of such an individual, proceeding from anterior to posterior, the other plumages of the adult female *S. v. varius* would be attained. If red tips were added to the white throat feathers, the plumage of the male *S. v. varius* would be approximated. Then, if the white nape and the black malar stripe and perhaps part of the auriculars were tipped with red, the plumage would resemble that of the male *S. v. nuchalis*. A little less red tipping on the face and throat would approach the pattern of the female *S. v. nuchalis*. If the entire head, neck, and upper breast were red-tipped and the underlying black and white pattern made duller and less well defined, the result would simulate *S. v. daggetti*. If the underlying pattern were still more obscured, the coloration would be like *S. v. ruber*. Or, to put it another way, if all the red tips were trimmed from any adult plumage of any race of *S. varius*, a pattern similar to that of a non-red female *S. v. varius* would be revealed.

Although the extremes in color are connected in a gradual transition in an appropriate series of specimens, as pointed out over seventy-five years ago by Baird, Brewer and Ridgway (1874), the color variation is not arranged along a smooth gradient. Variation in one race never produces an individual with all the characters of another, and it is only in specimens from the usually narrow zones of intergradation that the bridging of the gaps may be seen. The additional fact that the juveniles of each race are also distinct,

with patterns corresponding to those found in the adults, indicates that the color differences are deeply-rooted characteristics.

As red coloration in the sapsuckers is important both in sexual and racial distinctions, it may be useful at this point to review briefly the nature of this type of pigmentation. In birds, almost all the brilliant red, orange, and yellow pigments which have been chemically analyzed are found to be carotenoids. Turacin, the purplish red pigment found in the Musophagidae, is the only exception. Reddish brown or rusty colors are often referred to as red, especially in domestic fowl and laboratory animals, but these pigments are melanins and are not to be confused with the bright red carotenoids. A detailed discussion of the chemical nature of the carotenoids is presented by Bogert (1938); for present purposes it is sufficient to note that these pigments are polyene hydrocarbons, alcohols, and ketones. They may be extracted with fat solvents and hence are included among the lipochromes.

Carotenoids have been identified in various members of the Picidae by Brockmann and Völker (1934), Völker (1939), Test (1942), and Kritzler (1943). Although the red pigments of sapsuckers have never been analyzed to my knowledge, there is every reason to suppose that they too are carotenoids and probably are quite similar to those in the other woodpeckers.

Birds have never been shown to be capable of synthesizing the carotenoid pigments, and there is abundant evidence that they must be acquired from plant sources in the diet. On the whole, however, the process of carotenoid pigmentation from ingestion to deposition in the feather is poorly known.

Most woodpeckers show sexual dimorphism in color, and it is almost always manifested by the presence or greater extent of carotenoid color, especially red, in the male. *S. v. daggetti*, *S. v. ruber*, *Melanerpes erythrocephalus*, and *Asyndesmus lewis* are the only North American picids in which the plumage of the sexes is not distinguishable with certainty; *S. v. varius* and *S. v. nuchalis* fit the more usual pattern. The fact that in some picids carotenoid colors may appear in the adult males and juveniles of both sexes but not in the adult females suggests the influence of sex hormones, and it has been thought that carotenoid coloration in these species is correlated with a low concentration of estrogens. However, this seems to be disproven in the case of *Dendrocopos major* by the experiments of Nowikow (1939). He found that castration, ovariectomy, and injection of follicular hormones had no effect on the red in the plumage of juveniles or adults of either sex. It is likely that the same results would be obtained in other members of this closely-knit genus and in *Sphyrapicus varius* as well, since the sexes are alike in the early juvenal plumage of all four races and in the adults of two. With the exception of minor changes caused by wear, the sapsuckers show no seasonal differences in color such as are often found in birds with hormonal control of pigmentation. What evidence there is, as given above, suggests that in the sapsuckers the differences in carotenoid color between the sexes and the races are caused by genetic differences which are not influenced by the endocrine system.

Differences between the sexes and the races in melanin pigmentation are slight but follow the same trends as those in carotenoid pigmentation, that is, there is a progressive increase in extent of melanin pigmentation of the body, wings, and tail from *S. v. varius* to *S. v. nuchalis* to *S. v. daggetti*, and a progressive decrease in color difference between the sexes. In *S. v. ruber*, the sexes are equally dark. Although in these birds both pigment types vary similarly, it is probable that the melanins and carotenoids change independently of one another.

Consideration of albinistic woodpeckers indicates that the genetic factors influenc-



ing carotenoid pigments are different from those influencing the melanins, for a number of examples are known in which melanin is lacking and carotenoids are unaffected. A mounted specimen of *Dendrocopos nuttallii* in the Los Angeles County Museum (LACM no. 4821) is pure white except for a normal red crown patch. Deane (1880), in his list of abnormally colored birds, mentions a Golden-winged Woodpecker (= *Colaptes auratus*) which is white except for normally colored areas of yellow and red. Two specimens of the Red-shafted Flicker (*Colaptes cafer*) in the Donald R. Dickey Collection have the usual pattern of melanin coloration, but in one it is extremely pale (UCLA no. D-517) and in the other it is exceptionally dark (UCLA no. A-101). Neither shows any paling or darkening of the red of the remiges and rectrices. A specimen of *Balanosphyra (Melanerpes) formicivora* in the Museum of Vertebrate Zoology at Berkeley is pale brown in the areas of melanin pigmentation which are normally black in this species; yellow and red are unaffected. A specimen of *S. v. nuchalis* in the Dickey Collection (UCLA no. 50091) has a red-tipped white feather in its crown, an area in which the subterminal parts of the feathers are normally black.

This phenomenon is not restricted to the Picidae. Deane (1876) also refers to an Eastern Kingbird (*Tyrannus tyrannus*) which is yellowish white except for its orange-red crown patch, to a Redpoll (*Acanthis linaria*) which is white except for its red "poll," and to a White-throated Sparrow (*Zonotrichia albicollis*) with its head white except for its yellow superciliary mark. Robinson (1888) records a Cedar Waxwing (*Bombycilla cedrorum*) which is "an almost perfect albino; feet and bill pale yellow; irides pink; a few dark feathers in the wings, rest of plumage pure white except that the yellow tips of the tail feathers and the yellow of the belly and the scarlet wax drops of the wings remained unchanged."

Such evidence indicates that melanin pigmentation may be intensified, diluted, or lacking completely while carotenoid pigmentation remains normal. This strongly suggests, as does the chemical difference between the two kinds of pigments, that the melanins and carotenoids are controlled by different genetic factors. The fact that both pigments are sometimes lacking or diluted together need not affect this conclusion.

*Summary of racial characters of pigmentation.*—*S. v. varius* is generally the least heavily pigmented, both in carotenoid and melanin, shows the most sexual dimorphism, and is highly migratory.

*S. v. nuchalis* is more heavily pigmented, shows less sexual dimorphism, and is less migratory.

*S. v. daggetti* is still more heavily pigmented, especially in carotenoid; sexual dimorphism is slight or absent; migration is much less extensive.

*S. v. ruber* is larger and most heavily pigmented; there is no sexual dimorphism in color, and migration is slight or absent.

There is good evidence that color differences between the sexes and the races are not under endocrine control.

#### LIFE HISTORY

A general picture of the life history of the species is provided here in order that similarities and differences among the races may be pointed out, particularly in relation to courtship and reproduction. I have not observed *S. v. varius* except on its wintering grounds, but numerous authors have written incompletely on its breeding activities, and Bent (1939) quotes a number of these sources. The published data on this subspecies do not seem to differ materially from the following account, which is drawn from my field notes on *S. v. nuchalis*, *S. v. daggetti*, and *S. v. ruber* as observed at localities in California and British Columbia.

Sapsuckers of both sexes are present on their nesting grounds early in the spring; in many areas this is before heavy snowfall has ceased. The males of the migratory races seem to arrive a few days before the females. The presence of the birds is made known by frequent drumming or tattooing of a characteristic rhythm, distinct from that of other woodpeckers. This tattooing is difficult to describe adequately, although a single hearing is enough to enable one to recognize it at once thereafter. The tattoo is of about three to five seconds' duration and starts with a steady roll for one or two seconds which is followed by a series of loud taps at irregular intervals for two to four seconds. The Williamson Sapsucker (*S. thyroideus*) uses the same rhythm but a slightly slower tempo. Any resonant surface on which the sapsucker can perch may be used for tattooing. The trunks and limbs of dead trees, especially at great height, are most often used, and dry stubs of branches broken off close to the trunk are much favored. Tattooing may be heard at any time of the day during the entire breeding season, even after the young have left the nest, but it occurs most frequently from dawn through about the first half of the morning during the pre-nesting period. It continues well into the period of nest-construction and slackens off thereafter. Imitations of the tattoos, even if crude, may get a good response before, during, and immediately after nesting. An imitation tattoo near a recently emptied nest usually brings one or both parents to the nest tree and even to the entrance.

The stimuli for tattooing seem to be varied and frequently not determinable with certainty. The birds appear to indulge in it as a general announcement of territory, as part of courtship, and at times of emotional stress.

Adults have five distinct calls in addition to their tattooing noise. The most common is a nasal scream, somewhat reminiscent of the cry of the Blue Jay (*Cyanocitta cristata*). The scream is given at times of alarm or excitement and on many other occasions when no cause is obvious; it may be repeated up to seventy times without pause. A series of retching squawks is given almost invariably during the breeding season when two birds meet, and only then. Rarely, a sound like a combination of a scream and a squawk is produced. A loud series of cries which I call yelps, remotely similar to the yip-yip-yip call of the flicker or the Pileated Woodpecker (*Coeophloeus pileatus*) but slower, is given far less often and I have not been able to correlate it with any particular stimulus. A fifth sound is a faint rattling cry given only when a bird leaves the nest during construction. This peculiar call is uttered as the bird half flutters, half glides from the site; Saunders (1929) has compared this activity with the attitude of other birds in flight song.

Young birds not over a day old are capable of faint cheeping, and from this time on their cries increase in volume and deepen in pitch. Noise is almost continuous for the entire day, and a nest of young over two weeks old can be heard at least a hundred yards away. During the last week of their stay in the nest, the juveniles frequently make a clapping sound which is presumably produced by opening and closing the beak rapidly and repeatedly. In the last two or three days before leaving, the young give occasional screams similar to those of the adults.

I was unable to be on the breeding grounds of the sapsuckers before the start of nest construction except in the case of *S. v. nuchalis*, but since behavior identical to that exhibited by this race in the pre-nesting phase was observed at slightly later stages in both *S. v. nuchalis* and other subspecies, it seems reasonable to assume that the latter behaved similarly at an earlier stage. The following description is typical, then, of at least one race in the pre-nesting period and of this race and two others when observed after nest construction had just begun.

One bird takes a position on a favorable tree and gives several tattoos. Answering

tattoos from one or two birds may come immediately, or several minutes may elapse with no answer. In the latter case, the birds may be silent for a short period, usually about fifteen or twenty minutes, and then start up again. In the event of a nearby tattoo from a different bird, tattooing by the first one continues. The sapsuckers do not seem to wait for an "answer" to be completed, and their noise-making frequently overlaps or almost coincides. Usually three birds are involved, but often two or four and rarely more. Soon one flies over to another, followed by a third, and all begin squawking. At the same time, they hitch about toward and away from one another, bobbing their foreparts up and down and sideways and erecting the feathers of the crown. One bird then flies, followed by the others, and they weave about through the trees within a radius of approximately 100 yards. They alight, and there is more bobbing and squawking and raising of crown feathers. This may take place several more times. Then they separate, and in a few minutes a bird begins tattooing and the whole pattern starts again.

It is noteworthy that in *S. v. nuchalis*, the sexes of which are usually distinguishable in the field, the female sometimes initiates the tattooing and participates in it at least part of the time. Merriam (1879) mentions tattooing by both sexes of *S. v. varius*, and Bolles (1892) records it in captive juveniles of both sexes of this race. Individuals of *S. v. daggetti* which were seen tattooing and later collected proved to be females. Whether or not the female *S. v. ruber* tattoos is unknown.

Bendire (1888) noted such activities among Red-breasted Sapsuckers around Fort Klamath, Oregon, in the range of *S. v. daggetti*, on April 4, which was probably before nesting had begun. He mentions a flock of "at least twenty" birds.

On one occasion I observed tattooing by examples of *S. v. nuchalis* in which one bird tattooed while a second on a nearby branch drummed a brief "roll" at about the midpoint of each tattoo by the first. The duet continued for several minutes until broken up by the arrival of another sapsucker. Because of distance and weather conditions, the sexes of these birds were not determinable with certainty, but the first appeared to be a male and the second a female.

It is difficult to determine whether this sort of behavior is all territorial or whether courtship is involved and, if so, to just what degree. I have not observed any attempts at copulation until well after nest construction has started, and only once have I seen any blows exchanged between sapsuckers regardless of how aggressively they acted. It is possible that courtship and territorial behavior are so closely interwoven that they are not clearly distinguishable—one may be a modified form of the other. From the literature previously mentioned and from my own observations, it is evident that behavior such as that described above begins before nest construction, continues intermittently all through the breeding cycle, and may even occur among the adults of family groups of post-nesting birds.

Territories are variable in size, ranging from an area around the nest site with a radius of roughly 50 yards to over 150. In general, the size of the territory seems to depend on how heavily the area is wooded. On open slopes, territories average larger; in dense groves, smaller.

Copulations or attempts at copulation were observed in *S. v. ruber*, in a male *S. v. ruber* and a female *S. v. nuchalis*, in *S. v. daggetti*, in intermediates between *S. v. daggetti* and *S. v. nuchalis*, and in *S. v. nuchalis*. Successful or not, all attempts agree in that a certain pattern is almost always followed. The female perches crosswise on a branch, and the male approaches her from one side. He moves lengthwise along the branch, fluttering his slightly drooping wings, squawking, and raising his crown feathers. If the female is receptive, she tilts her head far back, sometimes appearing to rest it

on her interscapular region. The male then mounts for about five seconds or less, hops off to the branch, and flies away or begins some other activity. If the female is not receptive, she may actively resist or simply show no head-tilting or cooperation of any kind. All the attempts observed, a total of ten, were made at a time when nest construction was well under way or, in one case, when there were already eggs in the nest.

Nests are excavated in dead trees or in live ones with decayed interiors. The western subspecies are especially partial to large aspens, doubtless because of the soft core of these trees which makes for easy digging. Selection of a site seems to depend purely on local conditions, however, for often a dead or partially dead conifer may be selected even though aspens or other trees of apparently equal suitability are close by. The height at which the nest is constructed varies considerably, although it is usually 20 feet or higher if in a dead conifer. I have seen several nests in aspens which were only 5 feet or a little less above the ground, and in any large tree the nest may be placed at a height of 70 feet or more.

Several excavations may be begun on one or more trees before a final one is selected. Often a tree which has been used in previous years will be chosen. The task of digging is shared equally by both sexes, and a frequent work interval is about half an hour, although this is by no means the rule. Construction is begun at dawn and continues until dusk; it lasts from six days to two weeks, depending on the hardness of the wood. The work is frequently interrupted by long periods of preening or of complete inactivity. The opening to the nest is exceptionally small, and the birds invariably have to struggle to enter and leave. The cavity, like other woodpecker nests, is hollowed out below the entrance and is sufficiently large to allow the adult to turn around inside. The sapsucker nest is about 10 or 11 inches deep and about 3 to 5 inches wide at the maximum, and the opening is usually slightly less than 1.5 inches in diameter.

Eggs are laid and incubation begun as soon as nest construction is complete. The duties of incubation are shared equally by the sexes, and they relieve each other at irregular intervals varying from less than five minutes to an hour and a half. Squawks are almost always exchanged when one bird replaces another, and the nest is rarely left unoccupied for more than a moment. Both sexes have well developed brood patches.

Incubating birds are amazingly reluctant to leave the nest when disturbed, and I have often been unable to count the eggs in a nest because the parent would not come out even though a mirror was poked in or the tree thumped vigorously and repeatedly.

Three to seven pure white eggs are laid, and they hatch in approximately fourteen days. The young are naked when hatched, bright pink in color, and capable of uttering feeble cries. At about seven days unopened pin-feathers have appeared on the major tracts, but the eyes are not yet open. At ten days they are partly fledged, with eyes half open. At fourteen days they appear fully fledged and their eyes are open, but the birds are still small and growth continues for about another ten days. The young then leave the nest singly, and over a period of at least two days.

From the time the young hatch until they reach the age of about six days, the parent always enters the nest to feed them and usually remains until the other adult arrives with food. Occasionally one bird enters while the other is still inside, but they rarely remain in together for more than a moment or two. During the next ten days, the parent enters the nest to feed the young but usually comes out without waiting for its mate. When the young have reached the age of about sixteen days, the parents no longer enter the nest except to clean it and to roost at night. Both sexes clean the nest at irregular intervals, but the male usually does it much more often. The débris is usually carried to the same place each time to be dropped, most often to a tree within 20 yards of the nest.

In the few instances in which I have been able to determine which bird roosts in the nest, it has always been the male. He does this until all the young have left.

Visits to the nest with food are made about every seven minutes for the first five or six days and more rapidly, about every two minutes, thereafter. Feeding continues at this pace from dawn to dusk. This is no apparent coordination of visits by the parents. They may arrive at the nest alternately, together, or one may make several trips between arrivals of the other.

Food for the young consists principally of insects, especially large ants such as those of the genus *Camponotus*, which can be gathered rapidly for the voracious nestlings. In addition, the birds rely heavily on trees close to the nest which are drilled extensively. One or two trees within 5 to 100 yards of the nest site are worked constantly for a supply of vegetable and insect food for both parents and young.

Juveniles are large by the time they leave the nest and may be within a gram or two of the weight of the parents, although the wing and tail measurements are considerably less. For two or three days before emergence the young indulge in periods of hanging half to two-thirds out of the nest entrance. Then, without any apparent stimulus, the young bird pops out and flies unsteadily away. Sometimes the juvenile gets no farther than the ground a few feet from its point of departure, but usually it goes to a tree close by or up to 75 yards away, depending on the height of the nest site. Parents may show great concern over a juvenile which is just out, especially the first one, or they may give it no apparent attention, at least at first. When attention is shown, the parent seems to try to lead the young one to higher elevations and/or to one of the well worked trees in the vicinity. Feeding of the young still in the nest continues at the same rapid pace during some intervals, but with interruptions of a few minutes to almost an hour. The adults also feed the emerged juveniles, but not regularly, and the latter begin to attend to their own wants almost immediately. Their dull mottled plumage is quite effective as concealing coloration. A family group appears to be maintained for at least three or four days after all the young are out; how much longer the association continues is not known.

Nesting sapsuckers show aggressive behavior principally toward others of their own species (even if the intruder is of a different race) and other woodpeckers of similar size, such as Hairy Woodpeckers (*Dendrocopos villosus*). As a rule non-picids are not attacked even though they may attack the sapsucker. At sap workings behavior is sometimes different, and other birds may be chased or given battle.

#### INTERBREEDING OF DAGGETTI AND RUBER

The breeding ranges of these two subspecies meet in southwestern Oregon in an area between the Klamath Lake region and the coast. Birds from the interior part of the contact are usually very close to one race or the other (Gabrielson and Jewett, 1940), but along the coast the characters of the two forms blend gradually. Grinnell (1937) assigned all Californian specimens to *daggetti*, but some birds from the northwest coast of California are indistinguishable from examples of *ruber* which have slightly more than the usual amount of white spotting. It is true, however, that no Red-breasted Sapsuckers from California are as dark as the darkest examples of *ruber*, but any line drawn to separate the two races along the coast is an arbitrary one. Interbreeding of coastal populations of these races appears to be extensive, as would be expected in the absence of abrupt habitat differences and in view of the fact that these two races are the most similar to each other of the four.

#### INTERBREEDING OF DAGGETTI AND NUCHALIS

Intermediates between these two races are fairly common in collections, but the zone of interbreeding is limited and narrow. *S. v. nuchalis*, primarily a bird of the Rocky

Mountain region, extends its range westward to the east slope of the northern Sierra Nevada and that of the entire Cascade range. Thus, in east-central and extreme north-east California and in the Cascade region of southern Oregon, the range of *nuchalis* touches the more limited one of *S. v. daggetti*, which is restricted principally to the Sierra Nevada. Intermediates have been collected during the breeding season in Mono County, California, and especially in parts of Modoc County, California, by parties from the Museum of Vertebrate Zoology.

Adult birds showing characteristics of both these races are classified here into seven phenotypic categories ranging from *daggetti* to *nuchalis*. These may be characterized and numbered as follows:

1. Typical *nuchalis*.
2. Close to *nuchalis*, but with traces of *daggetti* characteristics.
3. Some definite *daggetti* characteristics, but decidedly closer to *nuchalis* than to *daggetti*.
4. Approximately intermediate between *nuchalis* and *daggetti*.
5. Some definite *nuchalis* characteristics, but decidedly closer to *daggetti* than to *nuchalis*.
6. Close to *daggetti*, but with traces of *nuchalis* characteristics.
7. Typical *daggetti*.

As the characters involved do not lend themselves to precise quantitative treatment, the categories are necessarily somewhat arbitrary and subjective. A more specific classification would, however, be spurious. Wear frequently causes pre- and post-nesting birds to appear very different, although they might be almost identical in fresh plumage. I have therefore placed the birds in the categories listed only after examining the specimen, if present, and the description in my field notes. There is, unfortunately, no way of being absolutely certain that some of the birds classed as type 2 or type 6 are not extreme variants of one or the other race, but as they were observed in a zone of intergradation between two forms the number of such errors is probably small.

No satisfactory way of classifying juvenal intermediates into more than three categories has been found. Darker and sootier color of the head region and the lack of a white postocular stripe are characters of *daggetti*, and lighter, less sooty head coloration and the presence of more than a small spot of white in the postocular region are *nuchalis* characters. Sometimes these characters are clearly visible in the field, as when a juvenile thrusts its head out of the nest entrance and cries for food. It was thus possible in some instances to record that the young of a certain pair were of "*daggetti*-type" or "*nuchalis*-type" or both, even though they were not collected. The distinctness of such characters depends to some extent, however, on the age of the young bird, and as my specimens are in many cases of different ages it seems unwise to try to fit intermediate juveniles into a system such as that used for classifying the adults. Therefore, juveniles with plumage characters close to those typical of one race are referred to as *daggetti*-type or *nuchalis*-type, and those not especially close to one or the other race are referred to as intermediate in plumage characters. When young from the same nest show intermediate characters but are not identical, they are referred to as variously intermediate.

Of eleven breeding sapsuckers from 9 miles west of Benton, elevation 8300 feet, Mono County, California, ten are typical *daggetti* and one is type 3 *daggetti* (MVZ no. 84843). A bird taken at a point 7 miles west and 2 miles south of Benton, elevation 9000 feet, is typical *daggetti* (MVZ no. 84852). Seven birds taken on Mount Patterson at elevations of 7900 to 8200 feet in the Sweetwater Mountains in Mono County are typical *daggetti*; a single typical *nuchalis* was taken at this same locality at an elevation

of 9000 feet. These areas in Mono County are largely within the main range of *daggetti*, and interbreeding with *nuchalis* is apparently extremely slight.

In Modoc County, *S. v. nuchalis* is the predominant form in the Warner Mountains in the extreme eastern part of the county. Of fifty-four breeding birds and well developed juveniles from the Warner Mountains, fifty-one are typical *nuchalis*. One adult from Pine Creek, elevation 8500 feet, is typical *daggetti*; one adult from Sugar Hill is *daggetti* or possibly type 6; one adult from the east face of Warren Peak is type 4.

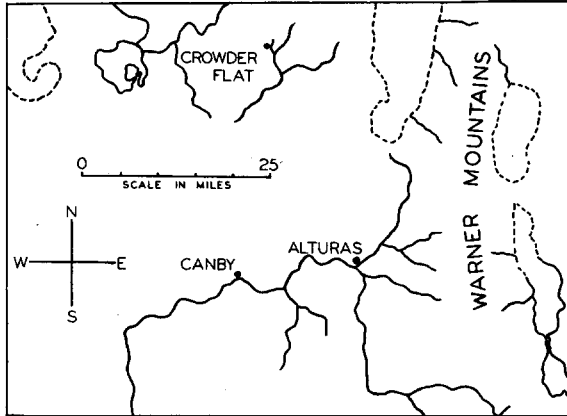


Fig. 3. Map of Modoc County, California, showing localities mentioned in text. Broken lines indicate borders of intermittent lakes.

From the area about 40 miles west of the Warner Mountains at a point 8 miles west of Canby, Modoc County, three specimens are typical *daggetti* and one is type 4. The latter, a female (MVZ no. 115754) was presumably mated to one of the *daggetti* males (MVZ no. 115775), for the two were collected at the same nest excavation, but one day apart. Several other typical *daggetti* were seen in this region, but no *nuchalis*.

At Crowder Flat about 20 miles west of the Warner Mountains and 38 miles north-west of Alturas, Modoc County, *daggetti* is also the predominant form. The elevation at Crowder Flat is about 5200 feet, and the yellow or ponderosa pine is the most conspicuous tree. Associated with it are mountain mahogany (*Cercocarpus*), manzanita (*Arctostaphylos*), *Ceanothus prostratus*, and, bordering the numerous creek meadows, aspen. To the east, the elevation decreases and a broad stretch of about twenty miles of juniper (*Juniperus occidentalis*) and sagebrush (*Artemisia*) separates the area from the Warner Mountains. The expanse of juniper and sagebrush forms something of a barrier for sapsuckers, as they do not breed in this association, but it is hardly insurmountable as the birds might readily cross it.

In 1948 sixteen specimens of *S. varius* were secured at Crowder Flat. In the spring of 1949 I returned there and stayed for forty-five days. Twelve successful sapsuckers nests were found and studied, and twenty-four specimens were collected. The characteristics of adult sapsuckers collected or closely observed during these two years are summarized in the following table.

Table 1

Phenotypes of Adult Sapsuckers Collected or Closely Observed at Crowder Flat in 1948 and 1949							
Type	1	2	3	4	5	6	7
No. of individuals	8	1?	1	1	7	10	14

Thus, of forty-two individuals, twenty-two are typical of one race or the other (types 1 and 7) and twenty show intermediate characteristics. The fact that only about half of the birds can be safely assumed to be of mixed racial stock indicates that interbreeding is moderate but not free.

In the following section a brief history of each of the nestings studied at Crowder Flat is given, illustrating the varied phenotypes of the breeding stock, the participation of the parents in nest activity and the reproductive success. The nests are listed in the sequence in which they were discovered. (See fig. 4 for location of nests.) Observations were usually made for a two-hour period at as many different times of day as possible.

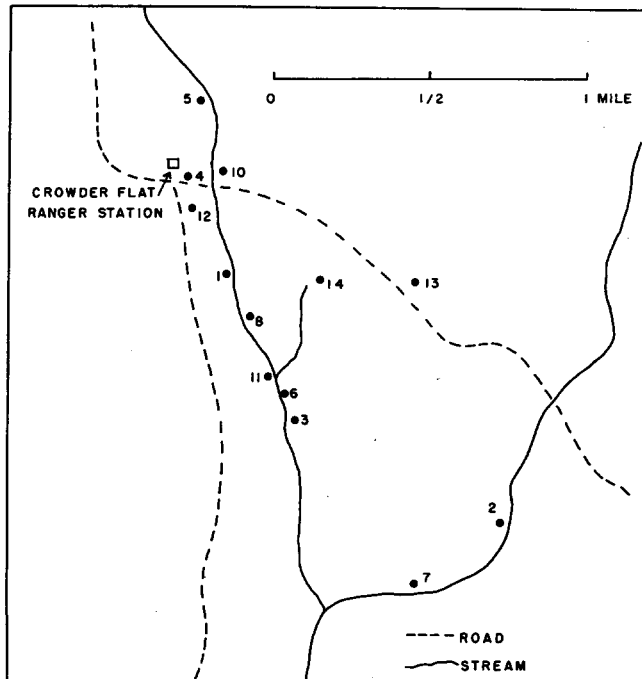


Fig. 4. Vicinity of Crowder Flat, Modoc County, California, showing locations of Yellow-bellied Sapsucker nests in 1949.

Counts of eggs and observations of young were made by inserting a dentist's mirror into the nest and reflecting a flashlight beam down to the bottom. Except for these intrusions, special care was taken to disturb the birds as little as possible; such precautions necessarily involved inexactness in counting the young, especially at the more active ages.

In those cases in which nests were within 150 yards of each other, it was possible to estimate territorial size; when the distance between nests was greater, the birds had so few occasions for territorial defense that no accurate estimation of the size of the territory was possible. In general, it appeared that the sapsuckers would defend an area around their nests within a radius of about 50 or 75 yards. The cruising range of the birds was much greater, extending at least 200 or 300 yards from the nest provided that the territory of another was not penetrated.

#### Nest 1

This nest was observed for approximately forty-two hours over a period of thirty-nine days, from May 21 to June 29. It was situated about five feet above ground in a dead aspen which contained many other woodpecker holes.



*Parents.*—Male, type 6; female, type 3 (MVZ no. 117131). Sometime after June 21, the male disappeared; he was not seen again after that date.

*Territory.*—The size of the territory was not determined, but the nest closest to this one was no. 8, 350 yards away.

*Eggs and young.*—At least three eggs were seen on May 24, and five were counted on May 26. They were hatched by June 5. At least four young were raised and a fifth one may have been present; an exact count was not possible without destroying the nest before their emergence. The first two to emerge were of *daggetti*-type plumage; two others which were collected (MVZ nos. 117132-117133) show intermediate characters. The young were in the nest for a minimum of twenty-three days, and they left on June 28 and 29.

*Incubation and feeding.*—Both parents participated. A mountain mahogany about forty or fifty yards from the nest was commonly used as a food source. Visits as usual were not coordinated. On one occasion the birds collided in mid-air in front of the nest as they approached from opposite directions.

*Roosting.*—On May 30 the male roosted in the nest. On June 21 and June 26 the nest was watched until dark, and the female did not roost in it. The male was no longer present.

*Nest sanitation.*—The male was seen to clean the nest twenty-nine times; the female was never observed in this activity.

*Remarks.*—On two occasions a *nuchalis*, a different one each time, alighted on the nest tree, but the parent birds were not present and the visitor flew off undisturbed. The only bird which elicited an aggressive response was a Hairy Woodpecker which came to within 10 yards of the nest. The female chased it as she came out of the nest from feeding the young, and the male did exactly the same thing about a minute later. The chases, however, were somewhat lethargic, for no sounds were uttered, no physical contact made, and the Hairy Woodpecker showed no resistance.

The nesting was successful despite the fact that the male parent disappeared at the time that most intensive feeding was in progress. The female and two of the young were collected.

#### Nest 2

This nest was observed for a total of approximately two hours over a period of twenty days, from May 21 to June 2, and from June 25 to July 2. The nest was in a live aspen at a height of about four feet. In the same aspen were several other woodpecker holes.

*Parents.*—Male, type 6 (MVZ no. 117148); female, type 4 (MVZ no. 117147).

*Territory.*—The size of the territory was not determined, but the nest closest to this one was no. 7, over 500 yards away.

*Eggs and young.*—Five eggs were seen on May 26; when next examined, on June 2, the nest was empty. A second laying was probably begun about June 7. The second nesting was in the same hole as the first. Cries of young were heard on June 25, and there were four in the nest on July 2, when they were collected. Their age was approximately ten days (T.R.H. field nos. 398-401). Plumage is intermediate in character.

*Incubation and feeding.*—Both parents participated.

*Remarks.*—On May 21 two attempts at copulation were made by this pair in the manner described in the section on life history. This was on the day that I found the nest, and I did not look in it then. However, as the male went into the nest and apparently incubated immediately after the mating attempts and as three eggs were seen in the nest the next day, May 22, it is evident that the copulations were attempted after eggs had already been laid.

#### Nest 3

This nest was observed for approximately thirty-two hours over a period of forty-two days, from May 22 to July 3. It was situated about 8 feet up in a live aspen which contained other woodpecker holes.

*Parents.*—Male, *daggetti* (MVZ no. 117145); female, *daggetti* (MVZ no. 117146).

*Territory.*—The nest closest to this one was no. 6, 100 yards away. A territory around the nest with a radius of about 50 yards was maintained.

*Eggs and young.*—The eggs were not seen until the time of hatching, on June 3. An attempt to see them was made earlier but the parent would not leave the nest. On June 3, the parent remained

in the nest but shifted enough so that a newly-hatched young bird and half an eggshell could be seen. At least three young were raised, all *daggetti*. All left the nest on June 28 and 29; thus, the maximum period in the nest was twenty-six days, from June 3 to 29.

*Incubation and feeding.*—Both parents participated in incubating and feeding. Two clumps of mountain mahogany, each about 60 yards from the nest, and an aspen about 5 yards from the nest tree were used as food sources.

*Roosting.*—By June 26 it was possible to distinguish between the parents through a difference in plumage abrasion. Roosting had been noted on June 20 and 25, but it was not possible to tell which bird was involved. On June 28, the day before the last of the young emerged, the now-distinguishable male roosted in the nest.

*Nest sanitation.*—The nest was cleaned frequently, but it was not possible to tell whether one or both parents did the cleaning.

*Remarks.*—One of the sapsuckers chased a *daggetti* that had come close to the nest from some other territory, and on another occasion an intermediate-plumaged sapsucker was chased by a bird from nest no. 3. Chipmunks were chased twice. Flickers, Hairy Woodpeckers, and various passerine birds were ignored. On May 22, while I was marking the nest tree, one of the adults flew to a dead branch of a tree about 5 yards away and tattooed loudly. On June 27 the female was heard tattooing; no stimulus was apparent. On July 1, after all her young were out, she tattooed in the course of chasing another sapsucker from near her empty nest.

#### Nest 4

This number was given to a site by which much sapsucker activity was noted on May 23, but which was not used for nesting. In all probability the birds observed were those which later nested at no. 10 and no. 12. Forty minutes of courtship and/or territorial behavior among three birds, all type 6, was witnessed at "nest" no. 4 on May 23, and a typical copulation attempt was observed in the course of this activity. At one point two birds scuffled bill to bill in the air about 4 feet above the ground and then fell into the grass below. For the most part, their behavior involved tattooing, chasing each other, and squawking when they alighted.

#### Nest 5

This nest was observed for approximately eleven hours over a period of eight days, from May 23 to May 30, and again on June 26. The birds abandoned the excavation at some time between May 26 and 30, and a visit on June 26 showed that the site had not been put to any further use. The excavation was about 7 feet from the ground in a live aspen which contained several other woodpecker holes.

*Parents.*—The sexes could not be distinguished. One bird was typical *daggetti* and the other type 6.

*Territory.*—The size of the territory was not determined, but the nest closest to this one was no. 10, about 400 yards away.

*Construction.*—Both birds participated in the construction work.

*Remarks.*—This pair was first seen at a slight excavation 2½ feet above ground in a live aspen about 10 yards from the site on which the most work was done. The latter had already been started before the other was attempted. The reasons for abandoning either or both were not apparent; possibly the proximity of a Douglas squirrel nest was a factor. A Hairy Woodpecker was chased by a sapsucker from close to the nest site to 20 yards away, after which the birds were lost to sight. Pursuit was silent and not very aggressive.

#### Nest 6

This nest was observed for approximately eighteen hours over a period of forty days, from May 24 to July 3. The nest was between 4 and 5 feet above ground in a live aspen which contained several other woodpecker holes.

*Parents.*—Male, type 6 (MVZ no. 117150); female, type 5 (MVZ no. 117149).

*Territory.*—This site was between nests no. 3 and no. 11 and 100 yards from each; a territory around the nest with a radius of about 50 yards was maintained.

*Eggs and young.*—Five eggs were seen on May 25, and all were hatched by June 5. There were at least four young later, and their head patterns showed that two were of *daggetti*-type and two were intermediate. It was impossible to make an exact count without destroying the nest and it is

entirely possible that a fifth young bird was present. They left the nest over a period of three days, July 1 to 3, which indicates a minimum time in the nest of twenty-six days and a maximum of twenty-eight.

*Incubation and feeding.*—A minimum incubation period of eleven days is indicated. Both parents participated in incubation. An aspen 10 yards from the nest tree was used extensively as a food source.

*Roosting.*—Although the parents could be told apart, the nest site was too dark at dusk to tell which bird roosted in the nest. One of the parents did so on the evening of July 1, after at least one of the young had left.

*Nest sanitation.*—Only the male was seen to clean the nest; this was observed six times.

*Remarks.*—A pair of House Wrens had a nest in an old sapsucker hole about 1 foot below nest no. 6. The sapsuckers were frequently flown at or struck by one of the wrens as the former came to feed their young; once the male sapsucker was driven to the ground by his smaller assailant. Usually the sapsuckers attempted to dodge the wren, and they never struck back at it.

On June 30, a juvenal sapsucker (probably from no. 3) flew over to the aspen used for feeding by the adults from no. 6 while they were there and begged from them. Both the adults, especially the female, attacked the juvenile viciously although it continued to approach them and beg. On that date the young of no. 6 were not out of the nest yet, and this fact may have enabled the parents to know that the young one was not their own. The juvenile obviously reacted to these adults as it would to its own parents, even after it was attacked.

#### Nest 7

This unusual nest, involving one male and two females, was observed for approximately forty-two hours over a period of thirty-eight days, from May 26 to July 2. The nest was between 10 and 11 feet above ground in a live aspen with many other woodpecker holes in it.

*Parents.*—Male, *daggetti* (MVZ no. 117144); female, *nuchalis* (MVZ no. 117143); female, type 5 (MVZ no. 117142).

*Territory.*—The size of the territory was not determined, but the nest was about 500 yards from no. 2 and about 880 yards from no. 3.

*Eggs and young.*—On June 8, six eggs and two newly hatched young were seen. Exchange of places in the nest was noted on May 24, and eggs were probably present at that time. Five young were raised to an approximate age of twenty-four days, at which time they were collected (MVZ nos. 117137-117141). All proved to be males, and the plumage types include one *daggetti*-type, one *nuchalis*-type, and three intermediates. The fate of the other three eggs is not known.

*Incubation and feeding.*—All three birds participated in incubation. The two females were in together frequently but usually only momentarily; occasionally they were in joint occupation for over nine minutes. The male often went in when either one of the females was inside, but the female generally emerged as soon as the male entered. No favorite feeding tree was discovered in this case, but the small willows (*Salix*) along a creek about 40 yards away were often visited.

*Roosting.*—On two occasions it was determined with certainty that the male roosted in the nest. At one of these times it is possible that the intermediate female also roosted in the nest, but this is uncertain.

*Nest sanitation.*—All three birds cleaned the nest frequently, but the male did this most often.

*Remarks.*—On May 26, the male appeared to fly at a White-headed Woodpecker (*Dendrocopos albolarvatus*) which came to within 10 yards of the sapsucker nest. On June 8, a Hairy Woodpecker tapping on the nest tree was ignored. On the latter date the intermediate female chased a House Wren from near the nest. On June 10, a possible type 2 came to the nest tree, hitched about, and squawked a little. The intermediate female was in the nest at the time. She looked out, saw the stranger, and then came out of the nest and chased the bird away with great vigor.

Occasionally two of the three birds, male and female or the two females, chased one another and squawked at each other with their crown feathers raised, but there seemed to be no real conflicts.

This nest was at least partly successful in that five young were raised under very unusual circumstances. The adults and young behaved exactly as those involved in a normal nesting. Considering this fact, it seems likely that the offspring were derived from both females, although it is impossible to determine which young had which mother.

## Nest 8

This nest was observed for approximately three hours over a period of thirty-five days, from May 26 to June 29. It was situated about 7 feet above the ground in a live aspen which contained a few other woodpecker holes.

*Parents.*—Male, *daggetti* (MVZ no. 117136); female, type 6 (MVZ no. 117135).

*Territory.*—The size of the territory was not determined, but the nest was about 350 yards from no. 1 and about 400 yards from no. 11.

*Eggs and young.*—There were at least three eggs, for on June 5 one newly hatched young and two hatching eggs were seen. My presence at this moment put the parents in such an agitated state that I did not take time to make sure that there were no more eggs or young. The three young all seemed to be of the *daggetti*-type plumage. They left the nest by June 29, twenty-four days after hatching.

*Incubation and feeding.*—Only one bird, the male, was seen to incubate, but only two hours and twenty minutes were spent observing before the young hatched. This did not provide sufficient evidence to suggest that one bird did all the incubating. Both parents participated in feeding the young.

## Nest 9

This nest was found at Howard's Gulch, 2½ miles west of Canby, Modoc County, California. It was observed only on June 4, for less than one hour. It was situated about 7 feet from the ground in a live aspen.

*Parents.*—A *daggetti* was seen at this nest several times; it was not possible to tell whether this was the same bird each time.

*Young.*—There were at least three naked, recently-hatched young.

## Nest 10

This nest was observed for about five hours over a period of nine days, from June 20 to 28. It was situated about 50 feet from the ground in a dying ponderosa pine which contained numerous other woodpecker holes.

*Parents.*—The sexes could not be distinguished; both were type 6.

*Territory.*—This nest was about 150 yards from no. 12; the territory of no. 10 extended about 75 or 100 yards in that direction.

*Eggs and young.*—The nest was not discovered until after the eggs were hatched. The inaccessibility of the nest prevented an accurate count of young.

*Feeding.*—Both parents participated.

*Nest sanitation.*—Both parents were observed to clean the nest.

*Remarks.*—On June 21 a *daggetti* alighted at the top of the nest tree and began to tap, not tattoo, on a branch. The brooding adult came out of the nest, and another, presumably its mate, flew up to the nest tree. A confused chase followed, and one sapsucker, probably the intruder, was driven off. A moment later one adult came to the nest with a large-winged insect and went in; a minute later, the other member of the pair came to the nest and places were exchanged. Thirteen minutes later two Mountain Chickadees (*Parus gambeli*) came close to the nest entrance; the brooding adult looked at them but did not come out. Earlier a White-breasted Nuthatch (*Sitta carolinensis*) had scrambled around noisily about 18 inches from the nest and the brooding adult had come to the entrance and looked at it. It appeared that the sapsuckers investigated any tapping or scratching noise on the nest tree and became aggressive if the noise-maker was another sapsucker.

This nest was on a later schedule than the others at Crowder Flat. The young had emerged from all the other sapsucker nests under observation except no. 2 by July 3; by this date the young in nest no. 10, to judge by their cries and the behavior of the parents, were about sixteen days old. The adults described under "nest" no. 4 were probably from this nest and nest no. 12.

## Nest 11

This nest was observed for approximately one and three-quarter hours over a period of twelve days, from June 22 to July 3. The nest was about 11 feet from the ground in a live aspen which contained several other woodpecker holes.

*Parents.*—The sexes could not be distinguished; one bird was *daggetti*, and one was type 6.

*Territory.*—This nest was 100 yards from no. 6 and 400 yards from no. 8. A territory extending about 50 yards in the direction of no. 6 was maintained.

*Eggs and young.*—The nest was not discovered until after the eggs were hatched and an accurate count of young was not possible. Only the *daggetti*-type plumage was noted among them. They had left the nest by July 2.

*Feeding.*—Both parents participated in feeding the young.

#### Nest 12

This nest was observed for approximately three hours over a period of ten days, from June 22 to July 1. It was situated about 45 feet up in a dead ponderosa pine which was broken off at the top 2 feet above the nest. There were several other woodpecker holes in the same tree.

*Parents.*—The sexes could not be distinguished; one bird was type 6, the other type 5.

*Territory.*—This nest was about 150 yards from no. 10; the territory of no. 12 extended about 75 yards in that direction.

*Eggs and young.*—The nest was not discovered until after the eggs were hatched. At least three young were out of the nest on July 1, and they appeared to be of the *daggetti*-type or possibly intermediate.

*Feeding.*—Both adults participated.

*Nest sanitation.*—Only the type 6 bird was seen to clean the nest; this was observed five times.

*Remarks.*—The adults described under "nest" no. 4 were probably from this nest and nest no. 10.

#### Nest 13

This nest was not discovered until June 23; it was observed for approximately one hour over a period of three days, from June 23 to June 25. The nest was about 50 feet above the ground in a dead ponderosa pine which contained numerous other woodpecker holes.

*Parents.*—The sexes could not be distinguished; both adults were type 5.

*Territory.*—The size of the territory was not determined, but the nest closest to this one was no. 14, 600 or 700 yards away.

*Young.*—An accurate count was not possible.

*Feeding.*—Both parents participated in feeding the young.

*Remarks.*—The nest was empty and the adults were absent from June 25 on. Presumably the young left the nest between June 23 and 25, as they appeared to be over twenty days old when discovered on June 23.

#### Nest 14

This nest was not found until June 29; it was observed for approximately one hour over a period of four days, from June 29 to July 2. The hole was about 50 feet above ground in the dead top of an otherwise live ponderosa pine.

*Parents.*—The sexes could not be distinguished; one adult was a *daggetti*, and the other type 5.

*Territory.*—The size of the territory was not determined, but the nest closest to this one was no. 13, 600 or 700 yards away.

*Young.*—An accurate count was not possible. Those that were seen looking out of the nest entrance were of the *daggetti*-type.

*Feeding.*—Both parents participated in feeding the young. A mountain mahogany about 100 yards from the nest was extensively used as a food source.

*Nest sanitation.*—Only the *daggetti* parent was seen to clean the nest; this was observed four times.

*Remarks.*—All the young had left the nest by the afternoon of July 2; one was seen in the nest on the morning of that day.

#### SUMMARY OF DATA ON NESTINGS IN MODOC COUNTY

*Locations.*—Ten nests were in aspens and three in ponderosa pines.

*Parents.*—The adults included typical *daggetti*, typical *nuchalis*, and all stages of intermediate plumage.

*Territories.*—The minimum distance between nests was 100 yards, and the minimum territory seemed to be an area around the nest with a radius of about 50 yards. Maximum territories were not determined.

*Nest building.*—This was observed in only one pair (no. 5); both adults participated equally.

*Eggs.*—A minimum of three and a maximum of five eggs were noted among the pairs. Nest 7, with three adults, had eight eggs but only five young were raised.

*Incubation.*—Both sexes participated equally in incubation.

*Young.*—The plumage of the young ranged from typical *daggetti* through all stages of intermediacy to typical *nuchalis*. Twenty-three to twenty-eight days elapsed between hatching and leaving the nest.

*Feeding.*—Both sexes participated equally in feeding. Mountain mahogany and aspen were used extensively as food-gathering places, and large ants and insects caught on the wing formed a large part of the diet of the young.

*Roosting.*—Only males were seen to roost in the nest, although it is possible that females did also. In at least one instance an adult roosted in the nest after one or more of the young had left.

*Nest sanitation.*—Both sexes were seen to clean the nest, but males did this much more often than females.

*Behavior toward other animals.*—Occasionally chipmunks and Hairy Woodpeckers were chased. Once a White-headed Woodpecker was chased and once a House Wren. A sapsucker which ventured near the nest of another was always chased if seen. No other birds or small mammals elicited an aggressive response even if they attacked the sapsuckers, as one House Wren did.

*Reproductive success.*—There was no evidence of any lack of viability or fertility among the birds showing intermediate racial characters. An unusual nest involving three birds, two of different races and one an intermediate, was at least partly successful. Other nests involving intermediates, such as no. 1 and no. 2, were successful despite adverse conditions. Birds of mixed and unmixed racial stock seemed to be equal as regards reproductive success. However, since only twenty-one out of forty-six adult birds collected or observed at Crowder Flat during two breeding seasons showed intermediate characteristics, interbreeding between the races is apparently moderate but not free.

#### INTERBREEDING OF VARIUS AND NUCHALIS

The breeding ranges of *S. v. varius* and *S. v. nuchalis* presumably meet along the eastern edge of the Rocky Mountains in western Alberta, an area which has not been extensively collected, and the amount of interbreeding which takes place is thus difficult to determine. The status of the two races in this region is still obscure (Rand, 1948), and I have not been able to locate a specimen of a breeding intermediate. Mr. W. Earl Godfrey informs me (*in litt.*) that in the National Museum of Canada there is only one example of *nuchalis* from Alberta, and that there are "specimens of *varius* from localities east of the Rockies which show more or less red coloration on the nape. Such males are from Edmonton and Wood Buffalo Park, Alberta; Flotten Lake, Saskatchewan; Lake Winnipegosis, Manitoba; Kapuskasing, Ontario; and Megantic County, Quebec. The last, incidentally, has the nape more extensively red than any of the other specimens of *varius* listed above. These birds, as would be expected, show not the slightest tendency toward *nuchalis* in any other character."

Variation in one race never produces an individual indistinguishable from examples of the other race, but such variation may overlap the characteristics of birds intermediate between the two. This fact makes it impossible to identify positively some birds which may be either intermediates or extreme variants of one or the other subspecies. Some specimens must remain indeterminate because the collector lost many of the nape

feathers in skinning out the head through a slit in the back of the neck—a common practice in preparing woodpecker skins. Females can be classified in this regard with some assurance if they are blacker than typical *varius* and have either a white nape and red spotting on the throat or a red nape with a white or almost completely white throat. There is a greater possibility of error in identifying males as intermediates because the entire throat is red in this sex in both races, but the color of the nape and the amount of black generally gives some indication of mixed or unmixed heritage.

Mr. H. G. Deignan kindly examined the series of hundreds of sapsuckers in the United States National Museum and selected only five as possible intermediates. These are a male (USNM no. 27140) from Fort Rae, Mackenzie, no date, with considerable red on the nape; a female (USNM no. 140600) from Flathead Lake, Montana, July 12, 1895, which is like *nuchalis* but with no red on the nape; a similar, unsexed bird which is clearly a female (USNM no. 10779) from Fort Bridger, Wyoming, May 18, 1858; a female (USNM no. 10184) from Wind River, Nebraska, May 27 (!), 1860, which resembles *nuchalis* except for a white nape; and a female (USNM no. 112922) from San Antonio, Texas, February 22, 1887, which is like *varius* but with the throat heavily spotted with red. Of these five, I regard the Montana bird as the most questionable as some of the nape feathers are missing, the Texas and Nebraska birds as intermediates, and the other two as possibly so.

I have also examined a series of fifty-one sapsuckers from México in the Robert T. Moore Collection and found one which seems definitely an intermediate. This bird (RTM no. 27012) is a female resembling *varius* but with red spotting on both nape and throat; it was collected one mile north of Tapalpa, Jalisco, México, on April 2, 1940.

It is readily apparent that the amount of interbreeding between these two races is indeterminate at present, but in view of the scarcity of even likely intermediates it is probably not extensive. It also seems probable that the contacts between the two races during the breeding season are somewhat limited.

#### INTERBREEDING OF VARIUS AND RUBER

Contacts between the ranges of *S. v. varius* and *ruber* are known only in northern British Columbia, and there are only two published records of the meeting of *varius* and *ruber* on the nesting grounds. Swarth (1922) reported three sapsuckers observed about 5 miles from Telegraph Creek, British Columbia, two of which were collected. One (MVZ no. 39780) is a typical male *S. v. varius*; the mate of this bird was seen and described as having "a great deal of red about the head, almost obliterating the black pectoral patch." These two had a nest "twenty-five feet from the ground, in a dead birch in rather open woods." On June 19, the next day, another male sapsucker was taken about half a mile away; this bird (MVZ no. 39781) has red tips to the feathers of the black auricular patch, the black malar stripe, the white subauricular stripe, the nape, and the black pectoral patch, the posterior border of which is still sharply defined. As Swarth noted, this specimen bears a curious resemblance to a *nuchalis* with tendencies toward *ruber* or *daggetti*. There can be no doubt, however, that it is an intermediate between *S. v. varius* and *S. v. ruber* as Telegraph Creek is hundreds of miles outside the ranges of *nuchalis* and *daggetti* and typical *ruber* was found at Doch-da-on Creek, 50 miles to the southwest.

Cowan (1939) found a pair of typical *ruber* excavating a nest in an aspen on May 23 at Tupper Creek, British Columbia, in the Peace River parklands. This author also noted that 8 feet away (unusually close) a pair of *S. v. varius* was nesting, and that another pair of *varius* had a nest within a radius of 50 yards of the other two. There

were no other *ruber* discovered in this region, which is within the normal range of the race *varius*.

There are no other accounts of the meeting of these two races on their breeding grounds, and the two intermediates recorded by Swarth are the only ones known. Probably the relationship between *ruber* and *varius* is very similar to that between *ruber* and *nuchalis*, as in the latter case there is also an extreme scarcity of intermediates as well as side by side nesting of pairs of each subspecies. Further data are needed from presently inaccessible regions in northern British Columbia.

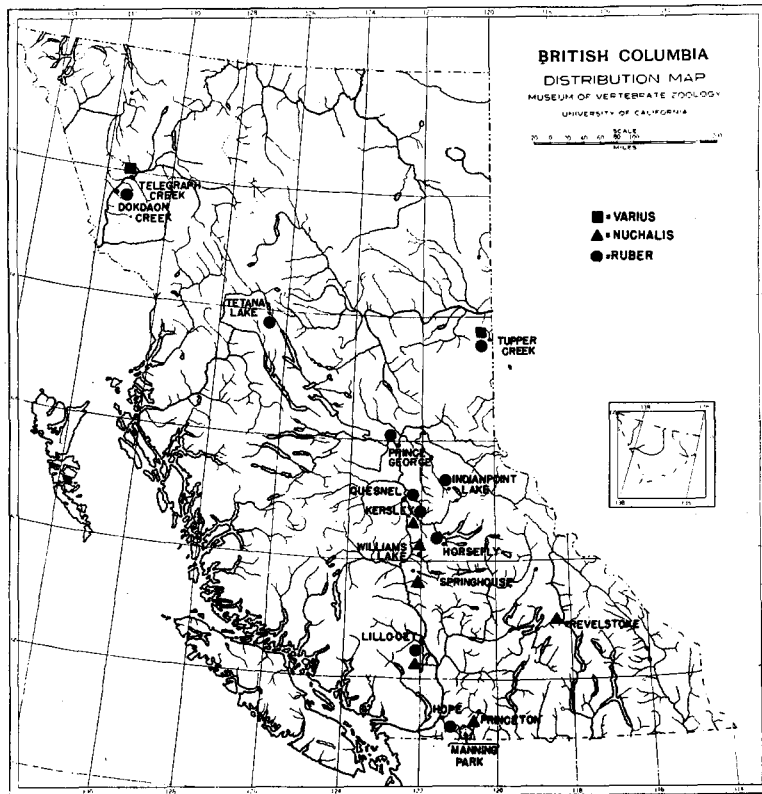


Fig. 5. Breeding localities at or near the peripheries of the ranges of the three subspecies of Yellow-bellied Sapsucker in British Columbia. There are summer records but not definite breeding records of the forms shown at Lillooet.

#### INTERBREEDING OF NUCHALIS AND RUBER

*Washington and Oregon.*—The breeding ranges of these races come in contact along the Cascade Mountains from southern Oregon north across the international boundary and from there north through the Cariboo region in central interior British Columbia. In general, *nuchalis* occurs east of the contact and *ruber* to the west, but at the northern limit the range of *ruber* extends east to the western slope of the Rocky Mountains; along this boundary *ruber* is found to the north and *nuchalis* to the south.

The Cascade Range seems to provide an effective barrier between the races, for only two intermediates have been recorded from Oregon, only two from Washington, and



none from southern British Columbia. The birds from Washington showing intermediate characters were collected at Cabin Creek, 33 miles west of Yakima, Yakima County, by Mr. John B. Hurley. He collected six birds at this locality from May 16 to May 23, 1948. Four of these (MVZ nos. 116134-116137) are typical *ruber*, but two show definite intermediate characteristics. Using the same system of categories as that employed for specimens of *daggetti* and *nuchalis* but substituting *ruber* for *daggetti*, MVZ no. 117606, taken May 16, 1948, is type 2; MVZ no. 117607, taken May 23, 1948, is type 6. The locality at which they were taken is on the east slope of the Cascade Range.

In June of 1948 a party from the Museum of Vertebrate Zoology collected sapsuckers on both slopes of the Cascade Range in central Oregon. Descriptions of the flora in the area are drawn from the field notes of Dr. Alden H. Miller. On the west slope of the mountains at North Santiam River, elevation 3400 feet, Linn County, the forest growth is "fir, hemlock, alders, willows;" here five typical *ruber* were collected. On the east slope, at a point 4 miles north and 9 miles west of Sisters, elevation 4000 feet, Deschutes County, there are "clumps of aspen, park-like yellow pines, groups of firs and occasional lodgepole pines;" here two typical *ruber* were collected, and one type 5 (MVZ no. 83412). Four miles away, at a point 7 miles northwest of Sisters, elevation 3300 feet, the vegetation is similar—"aspen and mixed forest;" here six typical *nuchalis* were collected and one type 2 (MVZ no. 83393). It appears that in this region there are definite ecologic differences between the races, for although *ruber* seems to have pushed out of its usual habitat successfully for a short distance it is replaced within a few miles by *nuchalis* in the aspen-conifer mixed forest. Interbreeding is apparently very limited as only two intermediates were found.

*Manning Park area.*—In 1950 I spent the period from May 9 to June 6 in E. C. Manning Provincial Park, between Hope and Princeton, British Columbia. This area, in the northern Cascade Mountains, has recently been made accessible by an excellent highway connecting the two towns, but snow conditions prevented any field work except that within a mile of the road in the critical localities.

Approximately 50 miles by speedometer southwest of Princeton, the road crosses Allison Pass at an elevation of 4400 feet. The humid coast climate and the coast forest appear to reach their easternmost limit in the park at this pass; to the east, the elevation declines and the climate becomes progressively drier. In the terminology of Munro and Cowan (1947), the region west of Allison Pass is in the coast forest biotic area, and that to the east is in the subalpine forest biotic area. A useful indicator of these areas in Manning Park is the western red cedar (*Thuja plicata*), which occurs in the coast forest west of the pass but which is absent to the east of it. Trees found on both sides of the pass but not necessarily throughout both biotic areas include western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga taxifolia*), alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea Engelmanni*), lodgepole pine (*Pinus contorta*), black cottonwood (*Populus trichocarpa*), and aspen.

Unfortunately, a forest fire in July of 1945 destroyed almost all the timber over hundreds of acres in an area on either side of the road from about 2 miles west to 5 miles west of the pass. The burn is ellipsoidal and its greatest dimensions are approximately 2.7 miles by 1.2 miles. The Hope-Princeton highway runs through the burn parallel to its long axis and almost bisects it. This gap of 2.7 miles seemed to constitute a barrier for sapsuckers, as typical *S. v. nuchalis* was found nesting up to its eastern edge and typical *S. v. ruber* was found nesting up to the western edge. As the fire occurred in July it is probable that any nests of mixed pairs or intermediates which may possibly have existed were destroyed, for sapsuckers nesting on either side of the burn still had young

in the nest on July 13, 1950. In any event, the status of the races in this area at the present time is as follows.

*Ruber* occurs commonly at Hope and for 30 miles farther east to a point 53 miles southwest of Princeton. A pair of *ruber* had a territory at a point 61 miles southwest of Princeton; these birds were seen copulating on May 13, but their nest was not found. At 56.6 miles southwest of Princeton, a typical *ruber* was seen on May 16. At 53 miles southwest of Princeton, the western border of the burn in Manning Park, a typical *ruber* was seen and heard tattooing on May 23, and the same or another bird was seen later in the day about 200 yards away. On July 12, at almost the exact spot where the bird was seen tattooing on May 23, a typical *ruber*, possibly the same one or its mate, was

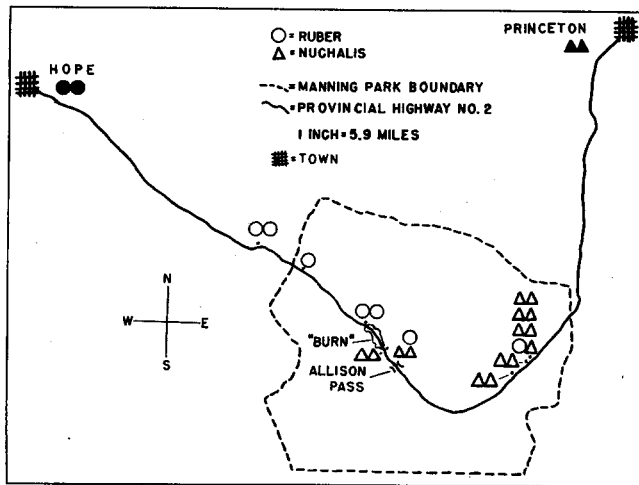


Fig. 6. Distribution of *S. v. ruber* and *S. v. nuchalis* in Manning Park area, British Columbia. Solid symbols indicate common occurrence as breeding birds of one form only. Pairs of open symbols indicate records of mated pairs, the left symbol representing the male. Single open symbols mark records of adults not definitely known to be mated.

observed gathering insects from a tree trunk in the manner of a parent obtaining food for its young. Although a nest could not be found, there can be little doubt that there was one at this locality. With two exceptions which will be discussed later, no *ruber* were seen east of the burn.

*Nuchalis* occurs commonly at Princeton and for 50 miles to the southwest. Three nests of *nuchalis* were found 29 miles southwest, one 30 miles southwest, one 34 miles southwest, and two 50 miles southwest at the eastern edge of the burn in Manning Park. Other Red-naped Sapsuckers were frequently seen in the intervening areas, but none was found west of the burn. However, there is one record of *nuchalis* at Hope, where a single bird was taken on May 19, 1932 (Munro and Cowan, 1947).

Two examples of *ruber* were seen east of the burn. On May 30, a typical *ruber* was seen 50 miles southwest of Princeton, where it was harassed by a pair of *nuchalis*; the following account of this incident is quoted from my field notes:

"A creek runs from the southwest into Cedar Creek at this point; on one side, the timber is almost all green, and on the other the burn starts. The small valley in which

this creek runs extends to the southwest and provides green timber for several miles, quite possibly to the other side of the burn.

"At 10:25 I saw a *nuchalis* in a dead tree on the green side of the creek. Then a typical *ruber* flew to a small balsam (= alpine fir) near me, on the burn side. The *ruber* moved on up the slope a short distance and began to feed near and even on the ground, apparently on ants, which are large and abundant. The *nuchalis*, which I am virtually certain was a male by its color, followed and alighted in a spruce at a higher level than the *ruber*. Then it flew to a small dead tree and tattooed several times; the *ruber* paid no heed. The *nuchalis* did some fly-catching, then flew down to the *ruber*, "crest" up and squawking; the *ruber* flew off a little way and began feeding again. In the next 30 minutes, this was repeated several times, the *nuchalis* aggressively tattooing, the *ruber* flying off a short distance when approached and never tattooing. The action took place over a strip of hillside about 10 yards long. The *nuchalis* flew across the road to the east slope, a distance of several hundred yards, and in a few minutes was back. Another *nuchalis* appeared, probably the mate of the first. One *nuchalis*, presumably the male and the same one each time, continued to harass the *ruber*, tattooing loudly and then flying over to it in an aggressive way, squawking and with its "crest" up. The second *nuchalis* seemed to follow along, giving an occasional tattoo. The *ruber* always flew off when the *nuchalis* came up, but seemed determined to stay in the general area; the chase went back and forth, often involving the same trees. The *ruber* stayed consistently low or on the ground, but did a bit of fly-catching. The *nuchalis* tended to stay about 20 feet up, did quite a lot of fly-catching, but went to the ground occasionally. Finally, about 11:50, the *ruber* flew far up the creek, to the southwest, and the *nuchalis* followed. They went over the shoulder of the ridge, then came up again, and worked back toward me. Again they went off to the southwest, finally across the creek to far over on the green side, where I saw the two in the very top of a dead spruce over 200 yards away. I could barely make them out. Then the *ruber* went farther southwest, and I lost sight of it; the *nuchalis* remained in the tree a few moments, then went a little to the east, and I lost sight of it too. An area with a diameter of at least one-quarter mile was involved in this activity, which lasted until 12:05."

Cedar Creek, referred to in the first paragraph, is a small stream that parallels the road in the western part of Manning Park. On July 13, a *nuchalis* nest was discovered within 100 yards of where the beginning of this incident was observed. The pair of *nuchalis* behaved neither more nor less aggressively toward the *ruber* than they did toward other *nuchalis* that invaded their territory. As the *ruber* showed only passive resistance, it is unlikely that the bird was near its own territory. A search made the next day in the direction in which it was last seen to fly revealed not *ruber* but more *nuchalis*.

On May 9 I found a male *ruber* at a locality known as The Falls, 29 miles southwest of Princeton and over 20 miles east of Allison Pass. At this point the Similkameen River and the highway are roughly parallel. The banks of the river are lined with willow, black cottonwood, and aspen, and steep slopes rise on either side. The slopes are covered principally by conifers, but there are many broad gulleys about a quarter of a mile wide that are largely devoid of live trees but which have numerous charred and dead ones, indicative of a forest fire long ago. The total impression is one of wooded ridges separated by grassy stretches with stands of dead trees. The latter areas seem to be favored by the nesting sapsuckers, although there are frequent patches of aspen among the predominant lodgepole pine, Engelmann spruce, and alpine fir. Ponderosa pine is present but very scarce; it becomes abundant at lower elevations farther east.

This example of *ruber* was not typical in that he had more white in the back and

slightly more distinct traces of striping showing through the red of the head than is usual in that race. The bird was mated to a typical female *nuchalis*, and they chose as a nest site a thirty-foot tall dead conifer stub about 400 yards up one of the open gulleys just described. Three excavations, 90° apart, were started before one was settled on. All three were about 25 feet above the ground. The final one faced north, and it is possible that it was chosen to avoid the glare of the direct sun which appeared to bother the birds at the east- and west-facing excavations. Work had begun at all three places by May 9, when I first located this pair, but after May 17 the birds worked only on the north-facing nest. Construction continued until about May 28, and the birds appeared to begin incubation about June 2. The male did much more of the construction work than the female. During the construction period, both the male *ruber* and the female *nuchalis* frequently left the nest with the curious fluttering glide and soft rattling cry that was mentioned in the discussion of life history. I also noted this among pairs of *nuchalis*, as did Saunders (1929).

As the male of this pair was the only *ruber* in the vicinity, his activities were relatively easy to follow. The female *nuchalis*, unfortunately, could not be told from the numerous others nearby. The male *ruber* had a cruising range of 400 or 500 yards down the slope and to the west side of his nest. On the east side a pair of *nuchalis* defended a territory to within about 100 yards of the nest of the *ruber-nuchalis* pair, and the slope above the nest was not often visited by sapsuckers as this portion was covered by an almost unmixed stand of lodgepole pine and the birds much preferred to work on alpine fir and western hemlock. Near the limits of his cruising range the *ruber* often encroached on the territories of pairs of *nuchalis*, and he was always driven away from these although sometimes only after several minutes of tattooing, chasing, and squawking. He in turn was quick to challenge any sapsucker other than his mate that ventured within about 150 yards of his nest site, but the territory he defended successfully was about 50 yards less extensive. Twice he behaved aggressively toward a male Red-shafted Flicker which alighted on or near his nest tree and once showed agitation when a Sparrow Hawk (*Falco sparverius*) perched 20 yards away from the site, but such reactions toward these neighboring species were not the rule. On at least one occasion the *ruber* was assisted in territorial defense by the female *nuchalis*. This was on May 11, when, after a series of tattoos, a male *nuchalis* came to within 60 yards of the *ruber-nuchalis* nest. The *ruber*, followed closely by his mate, chased the intruder away in short flights of 5 to 10 feet. The male *ruber* tattooed loudly several times, and the female *nuchalis* tattooed softly; the pursued bird did not give an answering tattoo until his own territory was reached.

Three attempts at copulation by this mixed pair were observed, but only one of these appeared to be successful. On May 20 I happened to be standing in the open about 20 yards from the female when the male approached her in the usual sapsucker fashion; she was completely receptive, but just as the male mounted her he seemed to notice me and take alarm, for he hopped off her back immediately and flew away. The female remained in the copulatory position for a moment and then began to preen. On May 27 an apparently successful copulation between these two birds was observed. On May 28, the female *nuchalis* was seen working about in some conifers near the nest. She screamed loudly several times; the *ruber* flew over to her, and they approached each other, squawking. The female then seemed to invite copulation by perching crosswise on a branch and arching her head far back. The male approached, moving lengthwise, fluttering his slightly drooping wings, squawking, and raising his crown feathers. He did not mount her, however, although there was no apparent disturbance, and this time I was well hidden.

Between May 28 and June 2, the birds apparently stopped excavating the nest, for they no longer tossed out beakfuls of chips while inside it, but they continued to take turns staying in the nest. I assumed that egg laying and incubation had started, and on June 4 I left to investigate areas farther north. I returned on July 11 hoping to find young still in the nest or close by, but no trace of the parents or their possible offspring was found although I searched for three days. Hence, it is not known whether this nesting was successful or not.

The limits of the ranges of the two subspecies are sharply defined in the Hope-Princeton region, but the habits and behavior of both forms appears identical. Each race occupies a different biotic area and each is replaced by the other at the junction of those areas. However, several species of trees which are utilized by sapsuckers for food and nest sites are common to both areas, and it is difficult to believe that one race finds the biotic area occupied by the other wholly unsuitable ecologically. Nevertheless, replacement of one race by the other is abrupt and with little or no interbreeding. It may be that ecologic preferences or adaptations which are more clearly discernible in the climax portions of the two biotic areas are reinforced sufficiently by a slight geographic barrier at the junction of the two areas to block intermingling of the races at that point.

*Cariboo area.*—From June 8 to July 9, 1950, I carried on field studies in the central interior of British Columbia in the region along the Fraser River which is known as "The Cariboo." It is flat or gently rolling country without sharp changes in elevation, and most of it lies within the sub-alpine forest biotic area of Munro and Cowan (1947). Part of the central interior, with northern and southern limits roughly at Soda Creek and Clinton, respectively, has been designated by these authors as the Cariboo parklands biotic area.

The most conspicuous trees in this area are lodgepole pine, Douglas fir, black spruce (*Picea mariana*), birch, and aspen; the latter two are found together in dense stands. The sapsuckers are especially partial to birches for feeding and to aspens for nesting; all the thirteen nests I observed in the Cariboo were in aspens.

Between June 23 and 27 I followed Provincial Highway No. 2 to what was then its end point about 67 miles north of Prince George. I had hoped to find *S. v. varius* at that latitude, but I was unsuccessful.

Most of my time was spent at Alexandria, 28 miles south of Quesnel, and at Kersley, about 15 miles south of Quesnel. Another locality at which many observations were made was McLeese Lake, south of Alexandria and about 20 miles north of Williams Lake.

Weeks of field work may be summarized by stating that, with two exceptions, all the sapsuckers found south of Kersley were typical *nuchalis* and all those found north of Kersley were typical *ruber*, and at the juncture of the ranges of the two races a very small amount of interbreeding took place. Within 1.5 miles, one form was completely replaced by the other. At least four adults of *ruber* were found at Kersley, and three north of there; at least five *nuchalis* were found at Kersley, and at least fifteen south of there.

More examples of *nuchalis* were seen than *ruber*, but this is probably due to the fact that I was staying at Alexandria and working north from there to the range of *ruber*. Since *ruber* had been reported as abundant in the immediate vicinity of Quesnel (Cowan, personal communication) and since almost as many *ruber* were observed at Kersley as were *nuchalis*, it is probable that the former race was as abundant north of that locality as *nuchalis* was south of it.

The two exceptions mentioned were a male *ruber* at Alexandria which was mated to a female *nuchalis*, and a male type 6 (MVZ no. 120932) at McLeese Lake which was

also mated to a female *nuchalis* (MVZ no. 120935). The coloration of the latter male is predominantly like *ruber*, but there is a trace of black and white facial pattern, and the red of the breast extends only far enough to cover the underlying black pectoral patch, so that the red is sharply demarcated from the yellow of the abdomen. Both these nests were completely successful. The male (MVZ no. 120933) and two of what seemed to be four young of the mixed pair at Alexandria were collected; the female was shot but not recovered. One of the young birds, a male (MVZ no. 120930), is indistinguishable from a juvenile of typical *ruber*, but the other, a female (MVZ no. 120931), shows

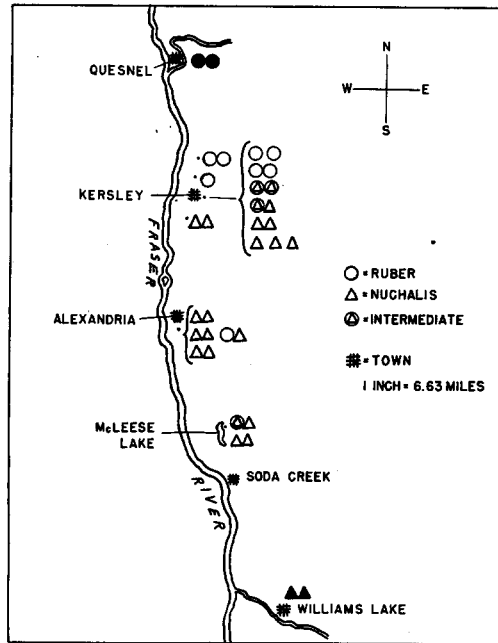


Fig. 7. Distribution of *S. v. ruber* and *S. v. nuchalis* in the Cariboo Region, British Columbia. Symbols as in figure 6.

intermediate characteristics. Both the parents and all four young (MVZ nos. 120936–120939) of the pair at McLeese Lake were also collected, and these young are variously intermediate but are closest to *nuchalis* in pattern. Except for these two adult males and their offspring, all the sapsuckers seen south of Kersley were typical *nuchalis*.

At Alexandria three nests of *nuchalis* were found in addition to the nest of the mixed pair, and numerous other *nuchalis* were seen in the vicinity. At a point 17.5 miles south of Quesnel, a nesting pair of *nuchalis* was collected. The male (MVZ no. 120921) is atypical in that the white postocular stripe is replaced by black, but this could scarcely be considered an indication of intermediacy toward *ruber*. *Nuchalis* was found farthest north at a point 14.7 miles south of Quesnel, in the vicinity of Kersley, where a nesting pair was collected.

One of a nesting pair of typical *ruber* was collected 10 miles south of Quesnel. At a point 12.7 miles south of Quesnel, a *ruber* was seen on June 13 but it could not be traced to a nest.

The following observations were made in the immediate vicinity of Kersley, but as the borders of this small town are rather indefinite the localities are given as miles south of Quesnel, measured by speedometer.

A typical *ruber* was seen at close range 14.8 miles south of Quesnel on June 19. On June 20, 16 miles south of Quesnel, I found a nesting pair of sapsuckers which showed mixed characteristics of *ruber* and *nuchalis*. At this time they were busy feeding their vociferous young. On June 28 this pair was again observed feeding their noisy brood. The parents were collected on July 7 and 8, after the young had already emerged. In both cases the adults were attracted to the nest from at least 50 yards away by imitation tattoos given within 10 yards of the nest tree. Both sexes responded with loud tattoos after the first few imitations. The male is the redder of the two, and represents type 6 (MVZ no. 120941); the female represents type 5 (MVZ no. 120940).

On June 28 another nest was found not over 400 yards from the one described above. The adults were seen at close range, and one was an intermediate between *nuchalis* and *ruber* and the other appeared to be typical *nuchalis*. I was able to locate this nest by the loud cries of the young, of which there must have been several. On July 6 the nest was empty and an unsuccessful attempt was made to collect the intermediate parent; this bird was not seen again. The next day I found three juveniles at a birch "feeding tree" about 50 yards from the nest. An adult *nuchalis* came and fed them several times. On July 8 an adult female *nuchalis* flew to this spot and tattooed on a dead branch in reply to my imitations and was collected. Although not certain, it is likely that this female was the mate of the intermediate, which would therefore be a male, and that the juveniles were their offspring.

About 100 yards south of this nest, on July 7, I found a *ruber* tattooing loudly on a dead stub. I shot and wounded this bird, but unfortunately I was unable to recover it.

At a point about half way between the two nests involving intermediate birds, the following incident occurred on July 8, and it is quoted verbatim from my field notes: "a loud tattoo came from the top of a tall dead tree right overhead. The sky was overcast with haze, and I could not see very well as far as colors go. There were more tattoos, and I noticed a group of at least 3 juveniles lower down, all of which looked like *nuchalis*. An adult *nuchalis* came up and chased a juvenile, and a large juvenile seemed to do some chasing itself. Then, suddenly it seemed, there was a wave of sapsuckers involving at least 5 juveniles and 4 adults—possibly two family groups. The adults worked very high, going from dead-tree-top to dead-tree-top, tattooing and screaming, and squawking when two or more got together. Once 4 adults were at the top of the same dead tree. I was sure I saw one *ruber*, possibly more, and am positive of 3 *nuchalis*. The juveniles all had at least some head-stripping. Suddenly, the birds stopped tattooing and dispersed, and all was quiet."

A few minutes later I was attracted to another nest about 300 yards away from both others by the loud cries of a nestful of young at least three weeks old. The parents were collected at the nest—both typical *ruber*.

Thus, within an area about 400 yards in diameter the following were found nesting: a pair of typical *ruber*, a pair with mixed characteristics of *ruber* and *nuchalis*, and a pair that seemed to consist of a male intermediate and a female *nuchalis*. In addition, at least three other *nuchalis* were seen here and at least one other *ruber*, as well as five or more juveniles of indeterminate parentage. 1.3 miles farther north a pair of typical *nuchalis* was collected, but all other sapsuckers seen north of 16 miles south of Quesnel were typical *ruber*. All the nests were in exactly the same type of woodland and all were about 25 to 40 feet above the ground in large aspens.

Munro (1945) places the northern limit of the Cariboo parklands at about 9 miles north of Williams Lake. Munro and Cowan (1947) state that "to the north it [Cariboo parklands biotic area] merges into the sub-alpine forest." An exact boundary would

probably be arbitrary, but as McLeese Lake, Alexandria, and Kersley are from 12 to 27 miles north of the one given by Munro (1945), it is virtually certain that the mixed pairs and intermediates did not occur where the gradient between the Cariboo parklands and sub-alpine forest biotic areas is steepest. There seemed to me to be no perceptible change in ecology or geography at Kersley which might influence the sapsuckers, and there is certainly no abrupt transition from one biotic area to another. None of the trees utilized by the sapsuckers for food and nest sites reaches the limits of their ranges there, and nothing in the physical appearance of the terrain suggests a limiting factor. As in the Hope-Princeton region, there was no noticeable difference between the races in any aspect of behavior. In contrast to the Hope-Princeton region, however, there are no sharp changes in environment or topography at this point in the Cariboo region where *nuchalis* and *ruber* meet.

It is possible that the general ranges of the races in this area—*nuchalis* in the Cariboo parklands and *ruber* in the sub-alpine forest to the north—are in some measure the result of habitat preference or ecologic suitability, but it is very difficult to account for the abrupt replacement of one form by another in an area of apparently uniform environmental conditions on such a basis. The possibility that an extremely narrow zone of equilibrium between the two races has been established through differential survival in a habitat in which conditions are not optimal for either subspecies cannot be ruled out, but at present there is no evidence that the habitat in which one race is replaced by another is one in which the reproductive potential or viability of either of the races is lowered. On the contrary, the presence of numerous breeding sapsuckers of both races in this habitat, especially at the point where the ranges of the two meet, is evidence that the environment is quite suitable to both.

#### DISCUSSION OF RELATIONSHIP AND ISOLATING MECHANISMS

In the foregoing discussions, the sapsuckers studied have been treated as members of a single polytypic species. The reasons for regarding them as such should now be examined. No one criterion is necessarily sufficient for classifying forms as races or as species, but criteria which, considered jointly, are commonly regarded as a good test of the kind of relationship involved are as follows: 1) allopatry or sympatry, 2) similarity or difference in behavior and life history, and 3) interbreeding in nature with the production of fully viable and fertile offspring, or failure to do so. Information on these three points is available for the sapsuckers and has been presented in the preceding sections of this paper, but a brief summary is in order.

Examination of ranges of the sapsuckers as given previously shows that the four forms studied are allopatric, as they occupy breeding ranges that are geographically complimentary. Zones of interbreeding, if present, are usually narrow, but in other respects the geographic picture is similar to that found in many avian polytypic species.

The life history of the forms, including food habits, vocalization, and the critical factor of breeding behavior, is almost identical except for differences in migration. The latter topic will be treated subsequently; at this point it suffices to mention that variation in migratory tendency is found among many unquestioned subspecies such as the races of the Song Sparrow (*Melospiza melodia*) and the Allen Hummingbird (*Selasphorus sasin*).

Evidence has been presented to show that between *S. v. daggetti* and *S. v. ruber* there is extensive interbreeding; between *S. v. nuchalis* and *S. v. daggetti*, and probably between *S. v. varius* and *S. v. nuchalis* there is definite but not unlimited interbreeding; between *S. v. ruber* and *S. v. nuchalis* and between *S. v. ruber* and *S. v. varius* interbreeding appears to be extremely scarce and does not seem to occur invariably where



their breeding ranges meet. All intermediates between *S. v. daggetti* and *S. v. nuchalis* and between *S. v. ruber* and *S. v. nuchalis* which were studied seemed fully viable and fertile, and an intermediate between *S. v. ruber* and *S. v. varius* has been observed in the early stages of nesting. There is, therefore, no evidence that intermediates between the different forms are less viable or fertile than typical examples of any of them.

Considering the information presented above, the relationships of these sapsuckers seem to be best expressed taxonomically by classifying them as subspecies of a single species, as has been done by the majority of recent authors. On the other hand, it is apparent that relationship is not equally close between all the races and that interbreeding between the contiguous ones is not as extensive as in most subspecies. What, then, are the factors restricting interbreeding between the races?

Physical and geographic barriers such as the Great Plains, the Great Basin, and some of the western mountain ranges clearly prevent contact between the races over large areas, but it is highly doubtful that similar barriers in the form of habitat unsuitable for sapsuckers are alone responsible for the differences in the amount of interbreeding that occurs where the subspecies do meet one another. There is some evidence that unfavorable terrain inhibits interbreeding between *S. v. nuchalis* and *S. v. daggetti* in California and between *S. v. nuchalis* and *S. v. ruber* in Oregon, Washington, and southern British Columbia, but in another place where *S. v. nuchalis* and *S. v. ruber* meet and in instances of contact between *S. v. varius* and *S. v. ruber*, in which interbreeding is extremely limited, physical barriers may be non-existent.

There is no evidence of physical incompatibility between any of the subspecies. *S. v. ruber* averages larger than the other three, but there is considerable overlap between its dimensions and those of the other races.

There must be some differences in habitat preference or adaptation to environment between subspecies of *S. varius* or one would have to assume that such distinct geographic differentiates were purely the result of random fixation of non-adaptive characters developed in sufficiently small and rigidly isolated populations. This may have occurred in the formation of some insular forms, but it is highly unlikely that the wide-ranging continental subspecies of *S. varius* developed in such a way. Ecologic differences between the races are therefore of probable importance in limiting interbreeding between them through effecting differential survival and reproductive potential in areas where the breeding ranges of the races meet.

If only ecologic factors are operative, and if intermediate birds are fully viable and fertile, one might expect that as the ranges of two subspecies approach one another the characters of the races would blend in a gradient proportional to the steepness of the gradient of change between their respective habitats. If one type of environment merges almost imperceptibly into another, a wide zone of intergradation between the races is to be expected; if the environment changes more abruptly, an equally abrupt replacement of one form by another may be looked for. In the event that the ranges of two races meet in an area between their optimum habitats, in an environment to which neither is significantly better adapted than the other, a broad zone of intergradation would be expected if both forms are moderately successful in such a region or a narrow zone through scarcity of breeding individuals might develop. In any of the above situations, a physical or geographic barrier in the area of environmental change would further restrict interbreeding, and a combination of the foregoing factors could bring zones of intergradation to very narrow limits.

As there is much evidence that intermediates between the races of *S. varius* are fully viable and fertile and no evidence except their scarcity that they are not, it may be asked

whether factors other than degree of ecologic difference and geographic barriers need be invoked to account for the variation in interbreeding between these subspecies. The following discussion of the forms, race by race, attempts to provide an answer.

It appears that, at least in the western part of its breeding range, *S. v. varius* prefers or is better adapted to somewhat open stands of deciduous trees, particularly aspen and birch, than to mixed deciduous and coniferous forest. Cowan (1939) found *S. v. varius* more abundant in climax type aspen forest than in dense stands of second growth aspen (in which the trees are probably too small to provide suitable nest sites) or mixed aspen and spruce in the Peace River district of British Columbia. He did not find this race in pure coniferous forest. Munro and Cowan (1947) report *S. v. varius* as common in the aspen associates of the boreal forest biotic area in British Columbia. Swarth (1922) found only two typical examples of *S. v. varius* at Telegraph Creek, and those that he found were nesting "... in a dead birch in rather open woods." This locality is very close to if not actually at the western limit of the range of *S. v. varius*. Soper (1949), in a portion of northwestern Alberta, found this race most numerous in the area adjacent to the Peace River parklands of British Columbia; it is not clear from his paper whether the birds were found in mixed coniferous and deciduous woods or in primarily deciduous stands. Soper did not find *S. v. varius* or any other sapsucker in the higher country along the eastern edge of the Rocky Mountains; it may be that farther south where it seems to be rare (Rand, 1948), *S. v. varius* also finds higher elevations unsuitable in some way.

*S. v. nuchalis* appears to breed primarily in mixed coniferous and deciduous forest containing aspen, but the race may nest in almost pure stands of either forest type. In the mountainous country between Hope and Princeton, British Columbia, *nuchalis* was found far more commonly in open stands of conifers than in the aspens and cottonwoods along creeks and rivers, but at Dry Lake, 15 miles north of Princeton, this race was found nesting only in the aspens and cottonwoods around the lake and not in the conifers. In the Rocky Mountain region *nuchalis* seems to nest primarily in aspen groves (Bailey, 1928, and Bent, 1939); in the Cariboo region of British Columbia the race was found nesting only in aspens but in both mixed and unmixed stands of this tree. *Nuchalis* is never found breeding in the humid coast area or anywhere west of the Cascade Range, and it seems likely that ecologic differences and the barrier formed by the higher elevations of the Cascade Range are largely responsible for the extremely limited interbreeding between *nuchalis* and *ruber* in Oregon, Washington, and southern British Columbia. The relation between these two races in the Cariboo region will be considered in the discussion of the ecology of *ruber*.

Over a large part of their breeding ranges, *S. v. nuchalis* and *S. v. daggetti* are found in very similar habitats of mixed coniferous and deciduous forest, but *S. v. nuchalis* in addition breeds in areas of generally higher elevation and of higher latitude than does *S. v. daggetti*. There is also evidence that *nuchalis* winters in some parts of the Sierra Nevada that have been vacated by *daggetti* (Grinnell and Storer, 1924).

As higher latitudes and higher elevations have in common lower extremes of temperature than occur in more southern and lowland areas, there may be a difference between these races in their tolerance of the environmental conditions associated with such temperatures. *Nuchalis* appears to have a wider range of tolerance to these conditions, as it breeds both in habitats closely similar to those in which *daggetti* breeds and also at higher elevations and farther north; but *daggetti* may have some adaptive advantage over *nuchalis* in the Sierra Nevada region. In any event, the two forms are largely isolated by the Great Basin, and there are minor discontinuities in suitable habitat separating them at least partially in Modoc County, California, which is the principal zone of

contact between *daggetti* and *nuchalis*. In this region there is moderate interbreeding between the two, and it is quite possible that a combination of the ecologic and geographic factors have limited this interbreeding to its present extent.

*S. v. daggetti* breeds across northern California into the coast region from Mendocino County, California, to Josephine County in southern Oregon. Between Josephine and Coos counties, Oregon, *daggetti* is replaced by *ruber*. Little is known of the relative abundance of the birds in the zone of intergradation. Birds from the extreme northern coast of California are often darker than typical *daggetti*; Gabrielson and Jewett (1940) state that breeding sapsuckers of the Rogue River Valley are much closer to *daggetti* than to *ruber*, and that those from Coos County north are typical *ruber*. In view of the fact that *ruber* is primarily a humid coast race and *daggetti* primarily an interior forest type, it is likely that ecologic differences play a large part in the replacement east of the coast forest of one race by the other. *Daggetti* may reach the limit of its optimum habitat in the Klamath Mountains and give way to *ruber* north of that region. No data are available on how abruptly one form is replaced by the other. However, the general darkness of *daggetti* from the extreme northern California coast (birds from this area were once considered to represent *ruber*) indicates that the two races may exhibit little if any reproductive isolation where their ranges meet along the coast. This is what might be expected in the absence of abrupt change in habitat or major geographic barriers.

The ecology of *S. v. ruber* is puzzling in that this sedentary race, with a center of distribution in the humid coast forests of the Pacific Northwest, is an abundant and successful breeding bird in the summer-dry interior forests of north-central British Columbia east of the Cascade and Coast Ranges, and at least one pair has reached the climax aspen forest east of the Rocky Mountains. Although there can be little doubt that this race as a whole is better adapted to the humid coast than are the other races, its adaptations do not seem to put it at a disadvantage in the interior. It is difficult to see what adaptive advantage *ruber* has over *varius* in the north-central interior or over *nuchalis* in the Cariboo region. It is quite possible, of course, that populations of *ruber* that breed in the interior do not have the same adaptations or preferences as the coastal breeders. This could account for the success of *ruber* in areas outside the "typical" habitat of the race, but it still does not explain the great restriction of interbreeding of *varius* and *nuchalis*.

Many essentially eastern species and subspecies of passerines are found over the north-central interior of British Columbia, where they meet related western species or races from the south-central interior. One might expect that *varius* and *nuchalis* would meet and interbreed somewhere in the broad area which instead is occupied by *ruber*. The two known instances of the meeting of *ruber* and *varius* have been discussed previously, and it may be that ecologic factors are important in limiting interbreeding between these races. The relation of *ruber* to *nuchalis* in the Cascade region seems accountable on the basis of ecologic differences and geographic barriers in the form of terrain unsuitable for either race. The relation between these two races in the Cariboo region is much less easily explained, for as pointed out in an earlier section there are no geographic barriers and the influence, if any, of ecologic factors is too subtle to be readily apparent. Nevertheless, replacement of one race by the other is abrupt and with a minimum of interbreeding. In this instance the possible influence of factors other than those mentioned above should be explored.

One possible factor is the homing tendency of the intermediates. When non-migratory races interbreed freely, the zone of intergradation is usually broad and constant as the intermediate offspring spread their characteristics in both directions into the parent

populations until an equilibrium in gene flow is reached. On the other hand, when one or both interbreeding races are migratory, many intermediates may not return to breed within a few territories of the area in which they were raised. If these intermediates wander rather widely and breed within a pure population of one or the other race, their mixed characteristics will probably be largely swamped within a few generations. The narrower the zone of intergradation, the less chance there is of an intermediate returning to it in the spring unless the homing tendency is very strong. This tendency is well marked among some intermediates at least, or there would be no stable area where birds of mixed characteristics may be found year after year as they are in part of Modoc County, California. On the other hand, some birds of mixed heritage do breed outside the usual zone of intergradation between two races; examples are the *ruber* with traces of *nuchalis* ancestry at McLeese Lake, British Columbia, and the two intermediate birds from a large population of pure *nuchalis* in the Warner Mountains in California. As homing instinct in intermediate birds is certainly not infallible, the zone of intergradation is doubtless narrower between the races of sapsuckers which leave their common breeding grounds in the fall than it would be if both races were resident there. This would be true, of course, only when limited interbreeding is involved; otherwise dispersal resulting from migratory movement of numerous intermediates would tend to broaden rather than restrict the zone of intergradation. It is perhaps significant that among the essentially resident coastal populations of *daggetti* and *ruber* there is a broad zone of intergradation, although sedentariness is certainly not the only cause.

An important physiological factor is the difference in migratory tendency between the races. *S. v. varius*, it will be recalled, is highly migratory, *S. v. nuchalis* less so, *S. v. daggetti* still less so, and *S. v. ruber* almost not at all. For a bird that depends for food on fruits, berries, soft parts under the bark of trees, running sap, and active, exposed insects, a severe winter climate presents great difficulties. Whatever the basic cause, migration to a milder temperature zone in winter is of great selective advantage to such a species. In eastern North America, *S. v. varius* moves south, often far beyond the southern limits of its summer range. In western North America, *S. v. nuchalis* and *S. v. daggetti* can to some extent substitute altitudinal for latitudinal migration in the southern parts of their ranges. This is especially true of *daggetti*, for the equable climate of the California coast is close by. As the range of *ruber* is largely in a coastal region where winters are not too severe to prevent sapsucker feeding, most members of this race can remain in the same area the year around.

The movements of the populations of *ruber* inhabiting the interior are poorly known. All winter records of this race in British Columbia are from the coast, but this may reflect a lack of field work in the interior at that season rather than an absence of the birds. The fact that winter temperatures may be below  $-50^{\circ}\text{F}$ . in this region even at elevations between 1000 and 2000 feet makes it seem doubtful, however, that many sapsuckers remain there during the cold months. The paucity of field observers is likewise understandable.

When migrating *S. v. varius* and *S. v. nuchalis* return to northwesterly areas in the early spring, it is entirely possible that their advance is eventually checked by the presence of the essentially non-migratory *ruber*, already on its nesting territories but not necessarily ahead of the other races in breeding activities. If *ruber* leaves the interior for the coast in the winter, these birds may move northeast and occupy territories before the arrival of the other races from the south. The north-south relation of *ruber* to *nuchalis* in the Cariboo region of British Columbia is explicable on this basis, as is the fact that *ruber* may occasionally breed within the usual range of *varius* and *nuchalis*, whereas

the latter two races have never been found breeding within the usual range of *ruber*. If *ruber* does pre-empt territories in such a way, this would account for the sharp lines of demarcation between the subspecies as opposed to the mixture of races over a relatively wide area which would occur if two highly migratory forms arrived in the same region at the same time. It would also follow that opportunities for interbreeding would tend to occur along a line rather than in depth, and mixed matings would consequently be much restricted. Unfortunately, this hypothesis can be verified only by intensive observation in interior western Canada in late winter and early spring, a time at which field work is most difficult.

Finally, there is possibly a psychological factor acting to limit interbreeding between the races of sapsuckers. In the four mixed pairs that were studied, three involving typical or almost typical *ruber* and typical *nuchalis*, and one involving typical *daggetti*, an intermediate, and a typical *nuchalis*, the male bird was of the race with the most red, that is, *daggetti* or *ruber*. In a mating involving intermediates of *ruber* and *nuchalis* the male of the pair was the redder, and an intermediate between these two races which was mated to a typical *nuchalis* was almost surely a male. In four matings involving intermediates of *daggetti* and *nuchalis* in which the sexes were identified, the redder bird was the male in each instance. In the one known pair in which a *varius* was mated to an intermediate, the male was typical *varius* and the female was the intermediate (*varius* x *ruber*) and therefore redder than the male. Thus, in four matings involving birds of different races, the males were the redder, and in matings involving birds of different and mixed racial stock, including the type 5 female in the threesome, the males were the redder in seven out of eight instances. These data suggest that the amount of red in the plumage may be a factor in courtship and mate selection in *nuchalis* and intermediates between *nuchalis* and *daggetti* or *ruber*. If so, this is probably the case with *S. v. varius*, a race which shows sexual dimorphism also, although the only exception to the male being redder than the female in mixed matings involves a cross of *varius* and *ruber*.

A female *nuchalis*, for example, might be receptive to a male *daggetti* or *ruber* but a female of one of the latter two races might not be receptive to, or especially might not be courted by, a less-red male *nuchalis*. The same reasoning may apply to *S. v. varius* in relation to *S. v. nuchalis* and *S. v. ruber*, the females of which are much redder than those of *varius*. A male of *ruber* or *daggetti*, on the other hand, belonging to a race in which sex recognition cannot depend on color, might be expected to respond to reproductive behavior in females of the less-red races, since such behavior does not differ from that of the redder ones. This has been observed and described previously in this paper.

If the foregoing hypothesis is correct, the effect of such reactions would be to reduce mixed matings to one-half the number which would be expected to occur if an equal number of males and females of two different races mated at random. One can hardly expect mate selection between the races to apply so strictly, but it may be a means by which partial reproductive isolation is maintained or augmented.

It is not unreasonable to suppose that red coloration is of some importance in the mating behavior of *Sphyrapicus varius* and in other woodpeckers as well, for in practically all the Picidae sexual dimorphism in color is manifested principally by the presence or greater extent of carotenoid pigment, especially red, in the male. The most obvious significance, since such coloration in woodpeckers is neither protective nor disruptive, or no more so in the male than in the female, would lie in sex recognition for reproductive behavior (Noble and Vogt, 1935). The objection might be raised that if sexual dimorphism in color is of importance in the mating activities of sapsuckers, why should

it be lacking in *daggetti* and *ruber*? The best explanation is that other characters of greater selective advantage are in some way associated or linked with the heavier pigmentation that obscures sexual dimorphism in these races.

There is, then, some evidence that by influencing mate selection the color differences between the races of *S. varius* may serve to maintain or augment partial reproductive isolation. Thus, color differences such as those between the races of sapsuckers, regardless of any other importance the differences might have, may contribute to the origin of new forms by acting to reduce gene flow between populations. Color differences among these subspecies may therefore be of some evolutionary significance other than as a part of geographic variation.

Significant or not, the color variation can be accounted for most simply and reasonably on the basis of minor and cumulative genetic changes, for steps by which color differences may have developed are clearly discernible in these birds. The question then arises as to how the populations became sufficiently isolated for their respective differences to have become established, and this necessitates a consideration of the possible history of the group.

#### HISTORY OF SPHYRAPICUS VARIUS

The genus *Sphyrapicus* occurs only in North America, and there seems to be no reason to suppose that its range ever extended to other continents. The distribution of the group does not seem in any way to be restricted by competition with other species. Sapsuckers construct nests frequently in areas where other woodpeckers are abundant. The sap- and cambium-eating habits, which make up at the very least sixteen per cent of the diet (Beal, 1911), are virtually unique and are not confined to any major or minor group of trees or shrubs. The only insect group that seems to be preferred to others is the ants—a group of cosmopolitan distribution and great abundance.

If the genus ever occurred outside of North America or if it originated elsewhere, as appears to be true in the case of *Dendrocopos* (Voous, 1947), it is difficult to see why it should not be found elsewhere today. Indeed, it is difficult to see why *Sphyrapicus* is not more widespread in North America than it is, for *S. varius* is able to get along well in México and Central America during the winter months, and trees—at least dead trees—suitable for nesting sites are certainly available there. As *Sphyrapicus* is widely successful in its present range and since within that range it is not restricted to a highly specific habitat, there is little reason to regard its distribution as relictual.

The feeding habits of *Sphyrapicus* mark the genus as a specialized one, and this impression is confirmed by the anatomical studies of Burt (1929, 1930). Burt points out that *Picoides*, *Dendrocopos* and *Sphyrapicus* have similar adaptive modifications by which they have achieved greater specialization for arboreal life than any other genera of North American woodpeckers. He also demonstrates that *Sphyrapicus* is aberrant in pterylography and offers an interesting opinion on the reduction of the capital apterium in this genus. "If, as appears to be the case, this apterium was brought about, in the evolution of the race, by the presence of the hyoid bones beneath the skin, through pressure or some other agency, it seems that the condition of shorter hyoids in *Sphyrapicus* is a reduction of what were at one time better developed structures, and that the vestige of an apterium is a character rapidly disappearing in *Sphyrapicus*." (Burt, 1929:434).

*Sphyrapicus*, then, is probably not primitive and has as its closest relatives *Picoides* and *Dendrocopos* (including *Xenopicus*). *Picoides*, according to Burt (1930) is the North American genus most specialized for arboreal life; it is also unusual in having yellow and not red markings on the head, and in having only three toes on each foot. *Sphyrapicus* also has yellow in its plumage, but never on the head, and it has four toes

on each foot as do all other North American picid genera except *Picoides*. *Sphyrapicus varius* and the American species of *Dendrocopos* are roughly similar in plumage in that they all have red markings on the head, a black and white facial pattern (concealed in *S. v. daggetti* and *S. v. ruber*), and body, wings, and tail variegated with black and white. The male *S. thyroideus* is much blacker than *S. varius*, but not as black as *D. albolarvatus*; the barred back of the female *S. thyroideus* is matched by that of *D. scalaris*, *D. nuttallii*, and *D. borealis*. These color and pattern resemblances are hardly reliable tests of relationship, however; they are mentioned merely to show that *Sphyrapicus* is as similar in coloration to *Dendrocopos* as it is to *Picoides*.

The tongue of *Sphyrapicus*, as mentioned earlier, differs from that of all other picid genera in that the hyoid elements do not extend beyond the occiput, and in that it is armed only with fine hair-like spines which give it a brushy appearance. Lucas (1895) noted a similarity in the tongue bristles of adult *Sphyrapicus* and those of a fully-fledged nestling of the Downy Woodpecker (*Dendrocopos pubescens*), but the latter was apparently only one of a very few juveniles available to him. A comprehensive survey of the tongues of both adult and young picids has not been made to my knowledge, and consequently it is not known whether the adult sapsucker tongue resembles especially that of the juvenile of any particular genus. However, the sapsucker tongue may have developed in the following way. A mutation or mutations causing arrested development of the tongue at the juvenal stage in some other genus would result in a tongue resembling that of the adult *Sphyrapicus*. A woodpecker so endowed would not be ill-adapted for feeding on exposed and flying insects and sap and cambium; it would certainly be ill-adapted for a diet of wood-borers. Would such a bird be able to alter its feeding habits? Other woodpeckers are known to feed from sapsucker workings, and the Downy Woodpecker has been observed drilling rows of holes in bark and eating sap from them (Forbush, 1921). Townsend (1932) criticized the accuracy of most reported instances of such behavior by the Downy Woodpecker, but the foregoing reference, which offers eye-witness accounts and a photograph, was apparently unknown to him. The answer, then, should probably be in the affirmative.

In view of the fact that one member of the genus *Dendrocopos* occasionally feeds in a *Sphyrapicus*-like manner, and since *Sphyrapicus* resembles *Dendrocopos* more closely anatomically than it does any other North American genus, including *Picoides*, one may reasonably propose that the genus *Sphyrapicus* has developed from *Dendrocopos* or a *Dendrocopos*-like form, and that the tongue differences may have arisen through a process resembling paedomorphosis.

Today there are two polytypic species of *Sphyrapicus*, *S. varius* and *S. thyroideus*, which occupy the same range over much of the western United States but in different ecologic situations. How these two species differentiated and whether or not there were others in the past are matters of pure speculation which it does not seem profitable to pursue unless much more evidence than is now available comes to light.

Differentiation in the species *Sphyrapicus varius* is more hopeful of elucidation, for intraspecific variation is arranged into well marked, but not completely discontinuous, racial groups. At one variational extreme is *S. v. varius*, highly migratory and showing the least pigmentation and the most sexual dimorphism. At the other extreme is *S. v. ruber*, essentially sedentary, most heavily pigmented, and without sexual dimorphism in color.

One might postulate that *ruber* is the most recently developed race of *S. varius* (a reasonable proposition, as will be shown later), and that its characteristics represent the culmination of a trend toward decline in migratory tendency and toward heavier pigmentation and consequent reduction in sexual dimorphism. This suggests that *S. v.*

*varius*, at the opposite extreme of the trend, is the oldest of the races, and that the sequence of racial development has been from *S. v. varius* to *S. v. nuchalis* to *S. v. daggetti* to *S. v. ruber*, for the middle two, in the order listed, show progressive change toward the characteristics which reach their extremes in *S. v. ruber*. Such an hypothesis is by no means the only possible one, however; the sequence could have proceeded in the opposite direction. Still another possibility, which seems most reasonable and least presumptuous to the author, is that the characteristics in *S. varius* which are now segregated into distinct racial groups were formerly less strongly developed and distributed along a cline. In other words, there may have occurred at one time, across most of that part of the North American continent habitable for sapsuckers, almost continuous populations of *S. varius* with characteristics similar to those now found in the races arranged in a smooth gradient from east to west. Then, if such continuously interbreeding populations were broken by some agency or agencies into partly separate groups, the eventual result would be breaks or steepenings in the formerly smooth gradient of characteristics. If enough isolation developed between populations, the species would be differentiated into recognizable subspecies.

Do historical events justify the contention that the differentiation of *Sphyrapicus varius* may have occurred in this way? The following evidence is submitted. Paleobotanical information is from Axelrod (1948) unless otherwise noted.

In Miocene and Lower Pliocene time, the forests of most of western North America where sapsuckers now occur appear to have been of generalized composition, including trees now found in the Redwood, Sierra-Cascade and Rocky Mountain forests and species whose closest counterparts are at present found in eastern North America. As many modern genera of birds are known as far back as the Miocene (Howard, 1950), it is not unreasonable to suppose that *Sphyrapicus* was in existence at least by Lower Pliocene. In view of the fact that the topography, climate, and vegetation of western North America were not as highly differentiated at the beginning of the Pliocene as they are today, it is entirely possible that a forest-dwelling bird such as *Sphyrapicus varius* may have shown variation only along an east-west cline in the early part of that epoch instead of forming a chain of distinct races geographically isolated from each other over most of their ranges. In western North America in the Middle Pliocene, however, there was large-scale mountain building, a lessening of summer rain, and a great reduction in the eastern elements of the flora. It was during this period that the flora of the present Great Basin area acquired a semi-desert character which made it largely uninhabitable for sapsuckers. Progressive aridity in the west continued in the Upper Pliocene, and the forests of the Coast Ranges, the Sierra-Cascade Range, and the Rocky Mountains were segregated into associations similar to those found in these areas today. Thus, in the Upper Pliocene there might have been three groups of sapsucker populations—one group east of the Great Plains, one group in the Rocky Mountain region, and one in the Sierra-Cascade and Coast Ranges. These three groups would have been geographically isolated from one another in all but the northern parts of their breeding ranges by the Great Plains and the Great Basin. By the end of the Pliocene, then, the species *Sphyrapicus varius*, showing variation along an east-west cline, may have been divided into the progenitors of the races *varius*, *nuchalis* and *daggetti-ruber*. How far differentiation might have proceeded by this stage can only be guessed. However, as climatic and floral conditions in western North America began during this epoch to approach those found in that region today, it is likely that any differences between the populations in adaptation to their environments or in habitat preference were initiated or, if already incipient, further developed in Middle and Upper Pliocene.



During Pleistocene glaciation possible northern contacts between the populations would have been displaced and perhaps reduced or broken. If broken, they may have been re-established during interglacial periods and then been separated by another descent of the ice. The glacial period most likely to have isolated sapsucker populations completely was the Wisconsin, which immediately preceded the Recent and during which the ice sheet reached its maximum extent. At this time the southern edge of the glacier was in the northern part of Washington, Idaho, Montana and North Dakota, and the ice covered most of the area between the Missouri and Ohio rivers and the New England states (Flint *et al.*, 1945). Clearly, if the Great Plains, Great Basin, and Columbia Plateau regions were no more forested than they are today, the eastern, Rocky Mountain, and Sierra-Cascade sapsucker populations would have been completely isolated from one another.

Such a convenient biogeographical situation is far from certain, however. A narrow strip of forest may have extended along the edge of the glacier (Gleason, 1922), or an expanse of tundra with or without a forest beyond it may have been present (Sears, 1935; Deevey, 1951). Evidence bearing on the Great Plains, Columbia Plateau and northern Great Basin is scanty. Most studies on late Pleistocene floras have been concerned with other areas, and papers on analysis of pollen deposits in these regions such as that of Hansen (1947) deal largely with postglacial floras. Chaney (1948) states that there are no known Quaternary forest remains from Oregon except in the coastal region. In view of the lack of specific information on the critical areas, it seems wise not to emphasize the Wisconsin period or the Pleistocene generally as a time of strong isolation of sapsucker populations. However, it seems likely that these populations were no less isolated during the Wisconsin and perhaps the other glacial periods than they were in the Upper Pliocene or in Recent times.

During the Wisconsin period a population of the *daggetti-ruber* type or its immediate progenitors may have occupied the unglaciated coastal region of Oregon and Washington, an area which was largely separated from the interior by an ice cap covering most of the Cascade Range. Such a population would be a logical one to have developed into *ruber* by means which will be discussed subsequently, either during the Upper Pleistocene or even following it.

With the retreat of the ice sheet, great floristic and faunistic movements were gradually set in motion. The flora occurring in the eastern United States during the Pleistocene furnished most of the stock which eventually spread over southern and subarctic Canada east of the Rocky Mountains. With it came many essentially eastern birds, probably including *S. v. varius*. Western montane floras extended north along the Rocky Mountains and the Cascade and Coast ranges, and with them probably came, respectively, *S. v. nuchalis* and possibly *S. v. ruber*. Why *daggetti* or its progenitors, if present at this time, did not move north along the east slope of the Cascade Range, an area now occupied by *nuchalis*, is not clear. It may be that *nuchalis* or its ancestors retreated into this region from the southwest slope of the Rocky Mountains during the late Pleistocene and pushed back *daggetti* or its immediate ancestors. As the *daggetti*-like population was probably moving south itself, such a turn of events is not impossible; little more can be offered in support of this surmise.

It was mentioned that *ruber* may have been differentiated from *daggetti* or *daggetti*-like ancestors only since the Upper Pleistocene or even later. The reasons for this point of view are as follows. McCabe (1936) in a study of endemism in the American Northwest, pointed out that in the coastal region of British Columbia and southeast Alaska there are twenty-three endemic races and only one endemic species. McCabe hypothe-

sized that in view of the parallel variation in most of these forms—more saturated pigmentation and generally smaller size than their nearest relatives—the recent availability of their present range, and the fact only one form has attained specific status, that the British Columbia-southeast Alaska coastal endemics were relatively young forms that had developed *in situ* since the retreat of Wisconsin glaciation. He pointed out that there are a number of endemic species as well as races in what were unglaciated areas in Alaska and in the western United States. Were the endemic races of the northwest coast restricted to one group of birds, one might argue that a slow rate of differentiation in that group was responsible for the lack of endemic species in the area, but as parallel variation at the subspecies level occurs in the Pacific Northwest in several different avian orders such an objection does not hold. To the present writer McCabe's hypothesis appears to be sound.

*S. v. ruber* is not restricted to the British Columbia-southeast Alaska coastal region just discussed, but its range lies primarily within that area and a similar one immediately to the south. The saturated pigmentation of *ruber* also indicates a faunal affinity with the endemic races of the humid coast region. The fact that it is a large race of its species is in contrast to the generally small size of Pacific Northwest races, but it is not unmatched among them. For example, large, dark subspecies of the Song Sparrow are endemic to the northwest coast area. The possibility that *ruber* is an old form cannot be excluded, but if it is an old form, where was it before it occupied its present range, and why did it retreat from its former range? An obvious point is that *ruber* may have differentiated before the Pleistocene and that its present range has been repopulated by birds surviving in the unglaciated portions of Alaska. It is extremely doubtful, however, that *ruber* or any other race of *S. varius* ever occupied the Alaska refugium, for if any did there seems to be no reason why sapsuckers should be absent from that area today, when conditions are surely more favorable than during the Pleistocene. It is difficult to believe that an entire population has deserted one range for another, especially as environmental conditions must have improved in the former while the latter was becoming available. Also, as previously mentioned, *ruber*, although primarily a humid coast form, is at present a successful breeding bird in habitats other than the humid coast, and there is no apparent reason why it should not still occur farther south than it does today if it ever occurred there at all. There can be no question that its present range in British Columbia and southeast Alaska has been occupied since Wisconsin glaciation, and its extension of range into the summer-dry interior of British Columbia and even east of the Rocky Mountains denotes an expanding and not a retreating form. To the writer, the sum of the available evidence indicates strongly that *S. v. ruber* is a relatively young race that has developed in the Pacific Northwest at least since the start of Pleistocene time, either in the coastal area of Washington and Oregon or in southwestern British Columbia since the retreat of the Wisconsin ice sheet.

This development may have come about through the loss of migratory instinct in members of a partly isolated coastal population of *daggetti* or a closely similar form. A humid coast flora with forest elements similar to those found there today probably existed in the northwestern United States during Pleistocene time (Hansen, 1947:95), and the winters were probably mild enough to permit sapsuckers to occupy the region throughout the year. As outlined previously, a non-migratory race might attain partial reproductive isolation from a migratory one by establishing territories on the nesting grounds before the latter arrived on them. A failure to migrate probably would not be disadvantageous to sapsuckers in a relatively mild winter climate, and the non-migratory individuals, if first on their nesting territories in the spring, would tend to mate with one another and thus establish the sedentary characteristic in the population.

A sedentary population, partially isolated geographically and at the northern extremity of the range of an otherwise migratory form, would stand a good chance of being sufficiently isolated reproductively to develop into a distinct subspecies. In such a population there also would be a selective advantage for large size.

Since contacts between the breeding ranges of *S. v. varius* and *S. v. nuchalis*, *S. v. nuchalis* and *S. v. ruber*, and *S. v. varius* and *S. v. ruber* occur today largely in areas which were totally uninhabitable during the late Pleistocene, it is quite possible that these contacts have been secondarily established since the retreat of the Wisconsin ice sheet and thus within the past 10,000 years. Furthermore, it seems virtually certain that in British Columbia *S. v. ruber* has met *S. v. nuchalis* and *S. v. varius* since the last glacial period and has met them there for the first time.

The view adopted, then, includes the following stages: A monotypic but clinal population of *Sphyrapicus varius* occurring over much of North America by Lower Pliocene; the partial division of that population into eastern, Rocky Mountain, and Sierra-Cascade-Coast Range groups with the geographic, climatic, and resultant biological changes of Middle and Upper Pliocene; the possible further reduction of most of the contacts between these three partly isolated populations by Pleistocene glaciation, especially in the Wisconsin period; and, finally, the establishment of present-day contacts between the populations, by now differentiated into well-marked subspecies, after the retreat of the last great glacier. A fourth race (*ruber*) developed subsequently from an isolated population of one of the other three (*daggetti*).

It is not possible to say which of the present-day races is closest to the ancestral type, but it seems clear that any one of the modern subspecies could have been derived from any of the others through minor and cumulative genetic changes. The extreme forms have attained almost complete reproductive isolation although they may still interbreed in nature and produce fertile and viable offspring. However, it is not difficult to envision how the historical and biological factors such as those responsible for the differentiation of these races could proceed a step farther and complete the division of one species into two.

#### SUMMARY

The Yellow-bellied Sapsucker (*Sphyrapicus varius*) comprises four well marked subspecies, *varius*, *nuchalis*, *daggetti*, and *ruber*, which are considered by some to represent two species. *Varius* and *nuchalis* have a black, white, and red pattern on the head and breast and show sexual dimorphism in color. *Daggetti* and *ruber* have the head and breast all red, obliterating an underlying pattern similar to that of the other two races, and they show little or no sexual dimorphism in color. The red pigment is composed of carotenoids and the black is composed of melanins; probably these two pigment types are controlled by different genetic factors and are not modified by sex hormones even in *varius* and *nuchalis*.

In general, *varius* breeds in the eastern United States and Canada east of the Rocky Mountains; *nuchalis* breeds in the Rocky Mountains north of México and along the east slope of the Cascade Mountains; *daggetti* breeds in the Sierra Nevada; *ruber* breeds along the coast of the Pacific Northwest from Oregon to southeast Alaska and in central British Columbia.

Interbreeding between the races where their ranges meet is variable. It is apparently free between *ruber* and *daggetti*, moderate between *daggetti* and *nuchalis* and between *varius* and *nuchalis*, and rare or absent between *ruber* and *nuchalis* and between *ruber* and *varius*. The present investigation has attempted to find and evaluate some of the factors responsible for the complex relationships between these subspecies.

There seems to be no significant difference in the life histories of the four forms. Close study of nesting pairs involving birds of different and mixed racial stock reveals no evidence of lack of fertility or viability of intermediates. Isolating mechanisms consisting of geographic barriers and ecologic differences are thought to be of importance. Differences in homing and migratory tendencies and preferential mate selection on the basis of color may act to limit interbreeding.

Considered historically, the genus *Sphyrapicus* is probably derived from *Dendrocopos*, and the evolution of *S. varius* into races may have been initiated in response to orogenic and vegetational changes in North America in the Middle and Upper Pliocene, and may have been further influenced by Pleistocene glaciation. In all likelihood the action of factors of the same nature as those responsible for subspeciation could bring about further differentiation of *S. varius* into two full species.

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