SAPSUCKER HYBRIDIZATION IN BRITISH COLUMBIA: CHANGES IN 25 YEARS

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Howell (1952) reported interbreeding between two races of the Yellow-bellied Sapsucker, *Sphyrapicus varius ruber* and *S. v. nuchalis*, in the Cariboo area of south-central British Columbia, Canada. The American Ornithologists' Union Check-list (1957, 1973) treated these populations as conspecific, but Mayr and Short (1970) considered them as distinct species, *S. ruber* and *S. nuchalis*. In particular, Howell (1952) noted that the former replaced the latter within a distance of less than 8 km, centered approximately on the village of Kersley (see maps in Howell 1952: 260, 266). While working in British Columbia in 1973, Ankney collected eight sapsuckers in the area studied by Howell. He collected three at McLeese Lake, about 50 km by air S of Kersley. He found none at Kersley but collected five at Bouchie Lake, about 25 km by air NNW of Kersley. Two of these were *nuchalis*-like. In 1950, "all those found north of Kersley were typical *ruber*" (Howell 1952:265). Thus, the sample from Bouchie Lake suggested that the zone of contact had extended northward since 1950. Because information on spatial changes in overlap and hybrid zones is not abundant (Selander 1971), we attempted in 1974 to confirm the inferred change in the contact zone between *ruber* and *nuchalis*.

METHODS

COLLECTING SITES

Between 14 and 28 June, Jarosch collected 32 adult sapsuckers, all with broodpatches, at selected localities between Alexandria (21 km by air S Kersley) and Stoner (90 km by air N Kersley). We chose these localities to reexamine the interaction between the taxa in the vicinity of Kersley and to determine the northern edge of the zone of contact. Collecting sites in 1973 and 1974 are listed below in approximate order from south to north. Co-ordinates given are those of the collecting sites, not of the associated communities.

1. McLeese Lake (52°23′ N, 122°17′ W, Canadian National Topographic Sheet—Soda Creek 93 B/8 W, 1:50,000). Three birds collected 5 June 1973.
2. Alexandria (52°38′ N, 122°27′ W, C.N.T.S. Alexandria 93 B/9, 1:50,000). One bird collected 1.5 km E Alexandria, 26 June 1974.
3. Kersley (C.N.T.S. Quesnel River 93 B/16 W, 1:50,000; sites 4 to 6 also shown on this map). Seven birds collected 28 June 1974 at 52°47′40″ N, 122°23′40″ W, mostly in a 10 hectare area 2.1 km E of the southern limit of Kersley indicated by a sign on Highway 97.
4. Narcosli Creek. Six birds collected 21 June 1974, 6.7 km due W Site 3, east of Narcosli Creek at 52°47′45″ N, 122°29′45″ W, in a 40 hectare area.
5. NE of Dragon. Two birds collected 26 June 1974, 11.3 km N Site 3 at 52°53′45″ N, 122°24′55″ W, 2.4 km NE of the village of Dragon.
6. N of Dragon. Four birds collected 22 and 26 June 1974, 14.5 km NNW Site 3, adjacent to Highway 97 and 4.5 km N of Dragon.
7. Bouchie Lake (53°02′ N, 122°40′ W, C.N.T.S. Cottonwood Canyon 93 G/2, 1:50,000). Five birds collected 7 June 1973.
8. Stoner (C.N.T.S. Red Rock 93 G/10, 1:50,000). Ten birds collected 14 and 18 June 1974 in the area around 53°37′ N, 122°39′ W, south of Stone Creek which flows through Stoner to the Fraser River. Single specimens obtained about 3 km N and S of the main collecting area. Stoner is 35 km by road S of Prince George on Highway 97.

Howell's (1952) principal study site was 16 mi (26 km) by road S of Quesnel, which would place it within 1.5 km of our Site 3, which was slightly east of a point on Highway 97, 27 km by road from the center of Quesnel.

ANALYSIS

To analyze our collection we established a phenotypic score for each specimen (Sibley and Short 1964). Lacking extensive series of known *S. v. ruber* and *S. v. nuchalis*, we relied heavily on published descriptions of these races (Ridgway 1914, Howell 1952). We selected nine characters that appeared to distinguish *ruber* from *nuchalis*. The characters and the scores assigned to each phenotype were: (1) Middle pair of rectrices: mostly black, 0; intermediate, 1; mostly white, 2, (2) Back: little white, 0; intermediate, 1; much white, 2, (3) Subauricular stripe: all red, 0; some red, 1; no red, 2, (4) Auricular region: all red, 0; black or tinged with red, 2, (5) Postocular stripe: red, 0; incomplete, 1; complete, 2, (6) Black malar stripe: completely obscured by red, 0; at least partly visible, 2, (7) Red nape: completely confluent with red on crown, 0; incompletely separated from red on crown, 1; completely separated from crown by black border, 2, (8) Pectoral patch: all red, 0; some red, 1; all black, 2, and (9) Rudimentary primary: no white spots, 0; one white spot, 1; two or more white spots, 2. For each character, 0 and 2 indicate *ruber* and *nuchalis* phenotypes, respectively.

As controls for the series taken in the area of contact, we used three specimens collected near Vancouver in 1964 and 1965 and one taken at Nanaimo, Vancouver Island in 1973 as representative of "pure"

TABLE 1. Phenotypic scores of 51 sapsuckers from various localities in Alberta and British Columbia.

Locality	Phenotypic Score																
	Ruber-like								*Nuchalis*-like								
	0–2		3–5	6–8	9–11	12–14	15–17	18	19–21	22–24	25–27	28–30	31–33		34–36		
Rocky Mountains																	
SW Alberta													♂			♂ ♂	♂
SE B.C.															♂ ♂	♂ ♀	♀
South-central B.C.[a]																	
1. McLeese Lake											♂		♂				♀
2. Alexandria																	♂
3. Kersley							♂					♂ ♂	♂			♂ ♀	♀
4. Narcosli Creek		♂	♂				♂						♂ ♀				♀
5. 2.4 km NE Dragon													♂				♀
6. 4.5 km N Dragon			♂	♂	♂												♂
7. Bouchie Lake		♂				♂	♂				♀		♂				
8. Stoner	♂ ♂ ♂ ♂		♂ ♀	♂ ♀	♂	♀											
Coastal British Columbia																	
Vancouver	♂ ♂			♀													
Vancouver Island	♀																

[a] Localities described in the text.

ruber. Nine birds collected in 1973, four from Bob's Creek about 64 km SW Nanton, Alberta and five from the Kootenay Valley in southeastern British Columbia, served as a standard for *nuchalis* (Johnstone 1949, Munro 1950, Godfrey 1966). In these areas, several hundred kilometers from our study site, little introgression was expected.

We examined 53 specimens, including 40 recently collected in the Cariboo area. The series was randomized by grouping the birds according to the last digit of the catalog number of a specimen. Each was examined and scored independently by Ankney and Scott, and the scores were summed. Thus, the possible extremes were 0 (for most *ruber*-like) and 36 (for most *nuchalis*-like). Scores from 9 to 27 probably indicate hybrids. Scores from 6–8 and 28–30 may indicate hybrids. However, the characters used are not absolute in distinguishing between the taxa. This, added to some uncertainty in scoring resulting from abraded plumage and shot damage, prevents us from saying categorically that certain specimens are hybrids or extremes in the range of variation of *ruber* or *nuchalis*. For our present purposes, this is unimportant, particularly as Howell's conclusions were based not only on collected specimens but also upon sight observations. In these, slight introgression of some characters (such as spotting of the rudimentary primary) would be undetected. Accordingly, to facilitate comparison between our data and Howell's, we group our specimens (table 1) only as *ruber*-like (scores 0–17) or *nuchalis*-like (scores 19 to 36).

RESULTS AND DISCUSSION

In figure 1, we compare our data from south-central British Columbia with data extracted from Howell's (1952:265–268) records of adult birds. His observations for Kersley include all birds seen 14.7–16 mi S Quesnel. North of Kersley he saw only typical *ruber*. These comprised three seen 10 mi and 12.7 mi S Quesnel and three seen when Howell (in litt.) travelled 67 mi north of Prince George hoping to find *S. v. varius*. Howell's observations of an "intermediate" at Kersley (1952:267) and "numerous" *nuchalis* in the vicinity of Alexandria have been omitted from figure 1. Howell (in litt.) described the intermediate as "looks like *nuchalis* > *ruber*; lots of red on the face." We have added to figure 1 our sight observations of a *ruber*-like bird at Stoner and two *nuchalis*-like birds, one at Australian and one 0.6 km E Alexandria.

A more important addition to figure 1 is that of two birds collected about 2 km apart near Stoner where the other 10 collected were very *ruber*-like. One, a female, is clearly *S. v. varius* while the other, a male, is intermediate between *nuchalis* and *varius*. Because the latter is recognizably different from the *nuchalis* collected farther south, we emphasize this difference in figure 1 by designating the specimen as *varius*-like. The female (UWO) lacks any red, except on the crown, and is indistinguishable from six female *S. v. varius* from Ontario. Furthermore, the more pronounced postocular and subauricular stripes, apart from their lack of red, distinguish her from our female *nuchalis* from British Columbia. The male (UWO 6584) differs from typical male *nuchalis* in several respects: only six widely separated feathers slightly tinged with red comprise the nuchal patch; the malar stripe is predominantly black and interrupted posteriorly but not laterally by red; the black occipital crescent is much more extensive than in *nuchalis* and appears identical with that in eastern *S. v. varius*; the white postocular and subauricular stripes are also broader as in *varius*. The red on the throat is more extensive

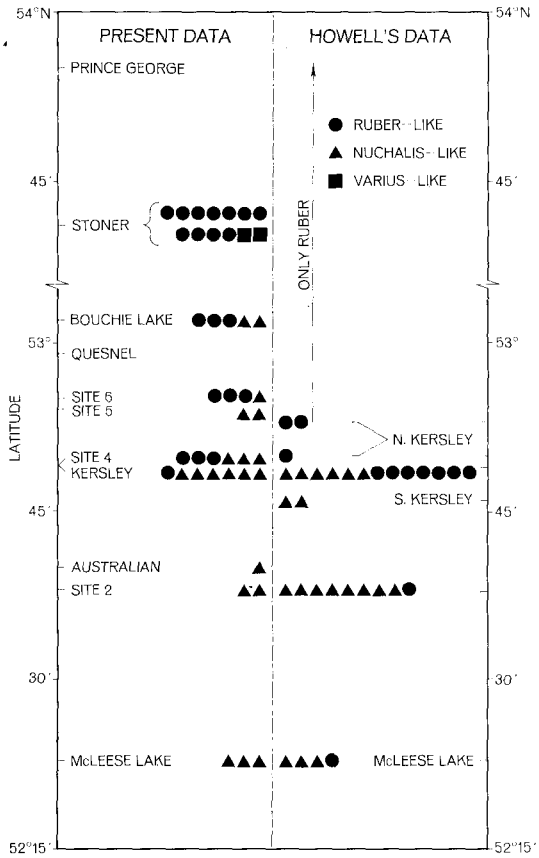

FIGURE 1. Diagrammatic comparison of the distributions of S. *v. ruber*, *nuchalis*, and *varius* in 1973–74 with those observed by Howell in 1950 in the Cariboo region, British Columbia. The east-west distance between Stoner and McLeese Lake is 25 km.

than in S. *v. varius* and is similar to this character in *nuchalis*. This and the traces of red in the nuchal region and on the malar stripe are the only characters that distinguish this bird from S. *v. varius*.

Ruber-like birds perhaps are now less common at the southern edge of the area of contact. At Kersley, Howell found the ratio of *ruber*-like to *nuchalis*-like birds to be 7 to 6 or 7 to 7 if the intermediate referred to earlier is treated as *nuchalis*-like. In 1974 it was 1 to 6; the one *ruber*-like bird (fig. 1) had a phenotypic score of 16. However, its head and breast are so *nuchalis*-like that this bird would appear *nuchalis*-like in the field. The Narcosli Creek sample did not have more *nuchalis*-like than *ruber*-like birds, but it is not properly comparable with any of Howell's samples as it is not known how far west of Kersley the area of contact extended in 1950. Furthermore, the samples south of Kersley and just north of Kersley are consistent with the suggestion of a decreased frequency of *ruber*-like birds in the south. Howell observed two *ruber*-like birds far south of Kersley whereas we found none in our admittedly small samples. Within 8 km to the north of Kersley Howell saw no *nuchalis* and three *ruber*, whereas our sample of six from near Dragon had equal numbers of *ruber*-like and *nuchalis*-like birds.

Nuchalis-like birds now occur appreciably farther north, at least as far as Bouchie Lake, 25 km NNW Kersley. Howell did not observe *nuchalis* north of Kersley, whereas in our samples from that area (near Dragon and Bouchie Lake) the ratio of *nuchalis*-like to *ruber*-like birds was 5:6. Our contention that *nuchalis*-like birds at Bouchie Lake are of recent occurrence is supported by Munro (1947) who spent three weeks there in June, 1944. After an extensive survey, he observed at least three *ruber*, but found neither *nuchalis* nor hybrids at Bouchie Lake or in a large area extending northwest from Quesnel and Prince George to Hazelton, about 400 km distant.

Lacking samples between Bouchie Lake and Stoner, we cannot locate accurately the northern limit of the contact zone between *ruber* and *nuchalis*. Evaluating the northward extent of introgression by *nuchalis* is complicated also by the presence of S. *v. varius* at Stoner. If the latter were absent, the hybrid nature of some birds at Stoner would be readily attributable to introgression from *nuchalis*. As it is, we do not know the influence of S. *v. varius* upon *ruber* in this area. The male *varius*-like bird from Stoner appears at first to be a *nuchalis* × *varius* hybrid but possibly it is a *ruber* × *varius* hybrid. Although knowledge of *ruber* × *varius* hybrids is limited, it may be significant that a male sapsucker collected by Swarth (1922, cited in Howell 1952) in the zone of overlap of *ruber* and *varius* in northern British Columbia had "a curious resemblance to *nuchalis*." Although the distribution of *ruber*-like and *nuchalis*-like birds has clearly changed since Howell's time, we cannot estimate the extent of the change. Unfortunately, the shape of the area of contact remains poorly defined. Between 1929 and 1941, judging from the analysis made by Dickinson (1953), *nuchalis* and *ruber* overlapped at Anahim Lake and Cottonwood, respectively 200 km WSW and 25 km E Quesnel. Information on areas between these two points is largely lacking except for Munro's observations and ours at Bouchie Lake. We do not know the direction of the spread of *nuchalis*. It may be northwards up the Fraser Valley from the Cariboo Parklands or on a wide front from east of the Fraser Valley.

The presence of a breeding female *S. v. varius* at Stoner indicates that this race has now penetrated farther south in central British Columbia than formerly indicated by the breeding record at Tupper Creek and an August specimen from Vanderhoof (Munro and Cowan 1947). Godfrey (in litt.) collected a male of the "*varius* phenotype" in 1969 about 40 km N Prince George. If the range extensions we observed continue, then three largely allopatric populations of sapsuckers shortly should come into contact south of Prince George.

Our data support the view that *ruber* and *nuchalis* are species (Mayr 1963:374, Short 1969). Intermediates are relatively scarce where the two populations are in contact. Thus, in the zone of overlap, barriers to free interbreeding seem to exist. However, the rather common occurrence of male intermediates (scores 6–30) in the area between Kersley and Bouchie Lake suggests that isolating mechanisms still are not highly effective. Indeed they may be less effective than indicated by Mayr (1963: 374, 1970:223). He said that Howell's observations on pair composition at Kersley showed deviations from random mating and implied that isolating mechanisms must be operating between *ruber* and *nuchalis*. However, Mayr incorrectly reported Howell's data on pair composition at Kersley. Mayr (1970:223) stated, "If incipient isolating mechanisms had developed prior to fusion, one should expect definite deviations from random mating. This is what Howell (1952) found in the sapsucker genus *Sphyrapicus*. Where the ranges of *nuchalis* and *ruber* meet at Kersley, British Columbia, one form is replaced by the other within the short stretch of 1.5 miles. Among pairs observed in the area, five appeared to be *nuchalis*, three *ruber*, and three pairs either mixed *ruber* × *nuchalis* or *nuchalis* × hybrid, or both hybrids. In such cases of partial breakdown of reproductive isolation a decision on the taxonomic treatment (species or subspecies) is often difficult, but these *Sphyrapicus* forms are best considered species since the majority of pairs are conspecific." Actually, "within the short stretch of 1.5 miles" referred to by Mayr, Howell (1952:266–267, fig. 7) recorded only four certain pairs of sapsuckers of which seven birds were collected and one, an intermediate, was only seen. Additionally, Howell saw "possibly two family groups" whose adults were a *ruber* and three *nuchalis*. So, at Kersley, Howell saw at most six pairs, not eleven as indicated by Mayr. Mayr apparently included *all* the pairs shown in Howell's figure 7, not just those at Kersley. Of the four pairs certainly identified by Howell, one was *ruber* × *ruber*, one was *nuchalis* × *nuchalis*, one was intermediate × *ruber*, and both birds of the remaining pair were *ruber*-like hybrids. If the four other adults referred to above were members of two pairs, the matings must have been *nuchalis* × *nuchalis* and *ruber* × *nuchalis*. Clearly, Mayr's conclusion that most pairs were conspecific does not follow from Howell's observations at Kersley. If only the four pairs involving mates of typical *ruber* or *nuchalis* are considered, the observed ratio of pairs (1 *ruber* : 1 mixed : 2 *nuchalis*) is not significantly different ($P > 0.9$) from the ratio (1 *ruber* : 2 mixed : 1 *nuchalis*) expected with random mating. Unfortunately, we did not observe pair composition. Thus, conclusive evidence on mating preferences is still lacking, and intensive field work and behavioral studies in the area of contact between *ruber* and *nuchalis* are needed.

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