

A SECOND HYBRID WILLIAMSON'S × RED-NAPED SAPSUCKER AND AN EVOLUTIONARY HISTORY OF SAPSUCKERS

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The discovery of a second hybrid between the Williamson's Sapsucker (*Sphyrapicus thyroideus*) and the Red-naped Sapsucker (*S. nuchalis*) is noteworthy because the first reported hybrid of these woodpeckers (Oberholser 1930) was only casually mentioned and incompletely described. Hybridization between these sapsuckers also is interesting in view of the hybridization among the three species (*S. varius*, *S. ruber*, *S. nuchalis*) comprising the superspecies *Sphyrapicus varius* (Howell 1952; Short 1969). The hybrid reported by Oberholser, a female (Carnegie Museum collection, bearing Cleveland Museum no. 10042), was obtained 25 October 1929 at an elevation of 6000 ft in the Huachuca Mountains of Arizona by W. W. Brown. We found in the collection of the American Museum of Natural History a male hybrid (no. 56494) taken by F. Robinette on 1 January 1891 at Rancheria de los Apaches, northern Chihuahua, México. Both hybrids are adults, and both resemble the Williamson's Sapsucker more closely than they do the Red-naped Sapsucker. In contrast to the almost completely allopatric distribution of the three sapsuckers comprising the *S. varius* complex, the Williamson's Sapsucker is widely sympatric with the Red-naped Sapsucker and, to a lesser extent, with the Red-breasted Sapsucker (*S. ruber*); it is not sympatric with the Yellow-bellied Sapsucker (*S. varius*). Both hybrids reported herein were collected south of the breeding ranges of all of the sapsuckers. Both Williamson's Sapsucker and the Red-naped Sapsucker regularly winter in southern Arizona and Chihuahua, where the hybrids were found. The Red-breasted Sapsucker is unknown in Mexico, except for Baja California, and it occurs rarely to casually in Arizona (A.O.U. 1957).

DESCRIPTION OF THE HYBRIDS

The male hybrid is similar in appearance to an adult male Williamson's Sapsucker. It differs most conspicuously in its smaller size, the

presence of a red crown patch, and its more extensive red throat. Its crown patch is less extensive posteriorly than is that of the Red-naped Sapsucker, and it is mixed with (about one-third) black. The throat patch is unusual in that the red extends farther posteriorly than in *nuchalis*, nearly bisecting the black breast band and closely approaching the yellow of the lower breast and abdomen. This red area is narrow; if broader and accompanied by red on the face, it would suggest the influence of *S. ruber*. The red of the crown and throat is orangish (even yellowish), like the throat of variant Williamson's Sapsuckers and not the darker red of *nuchalis*. Although approaching *thyroideus* in most of its color patterns, the hybrid exceeds variation in males of that species, and tends toward *nuchalis* in the following features. A white superciliary line is present and the subocular stripe is broader. The central rectrices are asymmetrically barred, with three moderately broad white bars on the inner vane of the left feather, but only one broad bar on the right feather. The bases of these feathers are broadly white. Males of *thyroideus* usually have no barring, and, if barred, have up to three very narrow white bars. The black of the breast of the hybrid is less extensive, especially laterally, where it is broken by pale tips of the black feathers. Feathers at the sides of its breast have white bars, as in *nuchalis*, whereas the black feathers of this area in *thyroideus* have gray bars. The hybrid differs especially from *nuchalis* and strongly tends toward *thyroideus* in its lack of a red nuchal patch, its black back (feathers with white bases, as in many *thyroideus*), its broader white wing bar, and its much brighter yellow abdomen.

In various mensural features (table 1) the male hybrid resembles *nuchalis* in wing length and tail length, while its tarsal length and the length of its hallux fall within the range of *thyroideus*. In other features (including some not listed in table 1) the two species overlap broadly, and the hybrid falls within the range of overlap. The search for mensural characters

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TABLE 1. Comparison of measurements (in mm) of *Sphyrapicus nuchalis*, *S. thyroideus*, and their hybrids.*

Character	<i>S. nuchalis</i>			Hybrid	<i>S. thyroideus</i>		
	n	Range	Mean		n	Range	Mean
Males							
Wing length	25	121-131	126.3	126	133.5	129-140	18
Tail length	24	69.7-78.9	74.5	78.6	83.5	80.4-88.5	17
Gonys length	14	16.0-20.6	17.7	16.7	17.2	16.4-19.1	10
Tarsal length	14	18.8-20.2	19.4	21.7	21.0	19.0-21.0	10
Bill width	13	5.9-6.9	6.5	6.0	5.7	5.4-6.3	8
Hallux length	9	6.8-7.5	7.2	6.5	6.4	6.1-6.7	9
Females							
Wing length	11	123-132	126.9	130	133.4	130-138	12
Tail length	11	74.0-82.5	76.7	78.0	83.5	74.4-87.1	9
Gonys length	12	15.2-18.3	17.6	18.5	17.5	15.9-19.5	11
Tarsal length	12	18.0-19.9	19.1	18.8	20.5	19.2-21.5	11
Bill width	9	5.8-6.7	6.1	5.6	5.5	5.2-5.9	9
Bill tip depth	9	0.95-1.10	1.01	0.90	0.87	0.80-0.95	8
Hallux length	12	6.1-8.3	6.9	5.2	6.1	5.6-6.8	12

* Adult males taken December-February, adult females, September-November. All specimens of *S. thyroideus* represent the race *nataliae*. Wing length is the chord, bill width was taken at the center of the nostrils, bill tip depth is the depth at the tip of the mandible, and hallux length is without the claw.

in which the two species did not overlap clearly indicated to us the great structural similarity of these distinctively patterned woodpeckers.

The female hybrid resembles rather closely the adult female Williamson's Sapsucker, from which it differs most notably in having a pale red crown patch (paler red than in *nuchalis*, but as extensive, and with some yellowish posteriorly). Otherwise it appears superficially to be a small female of *thyroideus*. However, details of its color pattern show many tendencies toward *nuchalis*. These are summarized below.

Head. As noted by Oberholser (1930), the head pattern of the hybrid tends toward *nuchalis* in its well-developed red crown patch, and in the faint indication of a superciliary stripe and a dark postocular line. The subocular region is paler brown than in *thyroideus*, tending toward the white stripe of *nuchalis*. The hybrid also has its hind-crown posterior to the red patch partially colored black. A few females of *thyroideus* have a black area here, and many are barred in this region (see discussion below). As in the male hybrid, a red nuchal patch is lacking.

Upperparts. The hybrid is barred above, like *thyroideus*, but the bars tend to be irregular in shape. The pale interspaces are whiter, tending toward *nuchalis* (Oberholser, op. cit.). Also the dark bars tend to be narrower in the center of the back and broader to the sides, tending toward the unbarred condition of feathers in the central back region of *nuchalis*.

Wing. A moderately broad wing bar is present, half the size of that found in *nuchalis*; *thyroideus* females lack a wing bar. However,

the wing bar is much more pronounced on one wing than on the other. The hybrid's wings are blacker and less heavily barred than in *thyroideus* (Oberholser, op. cit.). The inner secondaries and tertial feathers are barred, but the barring is not the same on inner and outer vanes as in *thyroideus*. Rather, the inner vanes have broader white bars tending toward the bar-patches of *nuchalis*.

Underparts. The hybrid's throat is tan as in *thyroideus*, its breast has a black patch (present in *nuchalis*, present or absent in females of *thyroideus*), its sides are barred, and its abdomen is pale yellow (as *nuchalis*; paler than that of any female *thyroideus* we have seen). Subtle tendencies toward *nuchalis* are evident, other than the color of the abdomen. Lateral to the black breast patch the barring (a trait of *thyroideus*; *nuchalis* lacks barring there) is irregular, and the light interspaces are paler. Likewise, the flanks and sides are barred, but the bars tend toward a chevron shape that is characteristic of *nuchalis*.

Oberholser (1930) did not compare measurements of the hybrid female with the parental species. The female hybrid mensurally (table 1) tends to be intermediate or more like *thyroideus* (gonys, bill width, depth of bill at tip, hallux length) in most measurements. The greater overlap in measurements of females, compared with males, appears due to female Red-naped Sapsuckers exceeding males in tail length and possibly wing length (see Short, in press, concerning such sex reversal).

Thus, in color pattern both hybrids tend more toward *thyroideus*, while in measurements they are intermediate or show a mixture

of resemblances to *nuchalis* and to *thyroideus*. The male hybrid is clearly in adult plumage. The female was thought to be an immature bird by Oberholser (op. cit.), but it too is an adult. Immature females of Williamson's Sapsuckers attain full adult plumage well before late October, when the hybrid was taken. On the contrary, immature Red-naped Sapsuckers do not completely attain their adult plumage until late fall or winter. Molting immature Red-naped Sapsuckers can be distinguished from adults by a mixture of barred juvenal breast feathers around incoming (adult) black feathers in the breast patch area. Adult females retain a black breast patch through the molt, although incoming feathers are buffy tipped, giving a scalloped effect and tending to obscure the breast patch; they lack *barred* (juvenal) feathers on the breast, however. It should be noted that females of the Red-naped Sapsucker are colored like males, although many show some white at the anterior end of the red throat region, which is entirely red in males. Female Williamson's Sapsuckers are completely different from males, having a barred pattern like that of the juvenal female and very like the juvenal plumage of sapsuckers of the *S. varius* superspecies.

The two hybrids are considered to represent a cross between Williamson's Sapsucker and the Red-naped, rather than the Yellow-bellied Sapsucker because the latter is not sympatric with *thyroideus*, and, in view of that fact, the occurrence of two separate instances of hybridization between Yellow-bellied and Williamson's sapsuckers is improbable. The Yellow-bellied Sapsucker infrequently reaches Arizona (Phillips et al. 1964:72), and has not been reported from Chihuahua (Miller et al. 1957:37). The Red-breasted Sapsucker was eliminated from consideration as a possible parent by virtue of the hybrids' lack of red on the face, and their tendency toward the chevron-barred sides of *nuchalis* rather than the streaked sides of *ruber*.

VARIANT FEMALE WILLIAMSON'S SAPSUCKERS

In addition to the hybrid specimens discussed above, we found several peculiarly plumaged female Williamson's Sapsuckers. These females are peculiar in their tendency toward male plumage in several features. The adult female plumage of the Williamson's Sapsucker is especially variable. It is largely like the juvenal female plumage, and thus resembles the juvenal plumage of other sapsuckers as well. Some females, as noted above, have a

black breast patch which may be quite extensive. This may represent a vanishing element of an earlier, blacker, male-like plumage. It is certain of these black-breasted females that exhibit some red in their throats, and show other male-like attributes. The characteristics of four of these specimens are summarized below. (Two others were seen by Short in the Carnegie Museum and Field Museum of Natural History collections.)

1. Female A.M.N.H. no. 755216, taken 15 April 1921 at Colonia Pacheco, Chihuahua, México. This specimen has a nearly complete, male-like red throat patch, the red being orangish with some yellow traces. Its belly is bright yellow as in males and unlike the pale yellow typical of most females. The breast patch is fully developed and black; the sides of the throat and malar areas are black with paler edges, and the hind-crown is almost entirely black, thus tending toward the adult male plumage.

2. Female A.M.N.H. no. 363044, taken 5 July 1918 at Taos Peak, Colfax County, New Mexico. Three or four red feathers mark the anterior throat of this specimen. This worn-plumaged specimen has a fully black hind-crown which connects with black lines extending over the eye suggesting the male's black crown patch. Its malar region is almost all black and connects with the black sides of the throat. The larger black breast patch extends anteriorly to the white posterior edge of the throat patch, around it to the malar area, and onto the sides, very much as in the adult male. However, its yellow belly is not unusually bright for a female.

3. Female A.M.N.H. no. 363050, collected at Taos Peak, New Mexico, on 13 July 1918. This female has red, orange-red, and yellow feathers scattered throughout its throat region. It is intermediate between the above two females in the extent of black on its breast, sides of the throat, malar region, and hind-crown. Its belly is yellow as in typical females.

4. Female A.M.N.H. no. 755200, taken in the Chiricahua Mountains, Arizona, on 7 October 1918. This female has some red traces in its throat, and is the least melanic of all such specimens that we have seen. Its breast has only a small black mark, and its crown has some black bars (like many other females). It is otherwise colored like normal females of this species.

DISCUSSION

The occurrence of these two hybrids, and the variation in female Williamson's Sapsuckers described above, are significant with regard

to the evolution and relationships of the sapsuckers. The genus *Sphyrapicus* clearly belongs to the melanerpine assemblage of woodpeckers (Bock and Short, MS) by virtue of its internal and external morphology and habits, and is a specialized ("sapsucking" habits) derivative of *Melanerpes*. Its closest relatives probably include the Acorn Woodpecker (*Melanerpes formicivorus*) and Red-headed Woodpecker (*M. erythrocephalus*) group of the genus *Melanerpes*. The ancestor of *Sphyrapicus* probably was characterized by: (1) an adult plumage of unknown pattern, but resembling somewhat that of the Acorn Woodpecker; (2) no (or little) sexual dimorphism in plumage; and (3) a distinct juvenal plumage like that of *M. erythrocephalus* (and modern species of the *S. varius* superspecies). Following this view, the divergence of *Sphyrapicus* from *Melanerpes* involved, in addition to the evolution of distinctly different habits (and related structural modifications), the evolution of a distinctive head pattern (incidentally, convergent upon the head pattern of various species of *Dendrocopos*). Species of the *S. varius* complex particularly show the black (or red) and white head markings, while adult males of *S. thyroideus* exhibit them to a somewhat lesser extent. Another development in *Sphyrapicus* was the evolution of sexually very distinctive plumages in the ancestor of *S. thyroideus*.

We suggest that, among the plumages of modern species of the genus, the adult male plumage of *S. thyroideus*, although distinctive, is closest to that of the melanerpine ancestor of *Sphyrapicus*. The location of black in the adult male plumage of *thyroideus* resembles that of *M. formicivorus*, *M. cruentatus*, and other species of *Melanerpes*. The restricted throat patch of males of *thyroideus* resembles that found in *Xiphidiopicus percussus* and *Melanerpes (Trichopicus) cactorum*, two melanerpine species. (Such a narrow, brightly colored throat patch is rare in woodpeckers.) The white rump and wing patches, yellow belly, and tendency toward barred central rectrices in males of *thyroideus* are other melanerpine features shared to a greater or lesser extent with species of the *S. varius* complex. Juvenal males are colored strikingly like the adult male, as emphasized by Swarth (1917: 64). They differ from adults in having a white instead of a red throat patch. This is not by any means the only difference between juvenal and adult males of *thyroideus*, for, compared with adult males, juveniles exhibit browner coloration; paler yellow belly color;

more fully barred sides, abdomen, and under tail coverts; and more strongly barred central rectrices. Many juveniles have spots on the crown and traces of breast barring, and they average more barring in the wings and streaking on the back than do adults. All of these tendencies away from the condition found in adult males are toward the condition of these features in the juvenal female plumage. The juvenal female plumage of *thyroideus* differs little from the juvenal plumage of species of the *varius* complex; these juvenal plumages also resemble the juvenal plumage of the Red-headed Woodpecker.

The distinctive plumages of *S. thyroideus* and the occurrence of two hybrids between *thyroideus* and *nuchalis* suggest that *thyroideus* is very closely related to the species of the *varius* complex and that interactions between them have affected the evolution of their distinctive plumages. The Red-naped, Red-breasted and Yellow-bellied Sapsuckers diverged recently, and are barely specifically distinct (Short 1969). Their direct ancestor probably evolved in eastern North America as an isolate of a once continuous ancestral sapsucker population; the western isolate evolved into *S. thyroideus*. Both isolates were probably sexually monomorphic in plumage, but a tendency toward sexual dimorphism occurred in both. This tendency may have been emphasized in *thyroideus* and suppressed in the western populations of the *varius* complex, *ruber* and *nuchalis*, as a result of interaction between *ruber* and *thyroideus* and between *nuchalis* and *thyroideus* following their secondary contact.

Simple reversion to a juvenal pattern in female *thyroideus* sufficed to bring about a distinctive sexual difference in that species. Thus, in *thyroideus*, visual cues, whatever their nature, are sufficient for sexual recognition. The western species of the *varius* complex, *S. ruber* and *S. nuchalis*, are sexually monomorphic (the slight sexual difference in amount of red on the throat in *nuchalis* does not appear to involve all individuals), and sexual recognition must be based on other (behavioral) differences. The eastern (and northern) *S. varius*, allopatric with *thyroideus*, shows moderate sexual dimorphism (in throat color only). We view the variant *thyroideus* females described above as indicative of a former male-like plumage in females of the ancestor of modern *S. thyroideus*. The slight sexual dimorphism or monomorphism in adult plumages of other sapsuckers and of related species of *Melanerpes* also indicates that the

strong dimorphism in *thyroideus* is a derived condition. Swarth's (1917:64) view that the female plumage of *thyroideus* is "primitive" is, in a sense, correct; that is, ancestral sapsuckers had a similar plumage, but it was a *juvencal* plumage. Reversion to this type of plumage in the adult female is a derived condition, unique in melanerpine woodpeckers and perhaps in the Picidae.

The occurrence of strong color (and presumably behavioral) differences between *S. thyroideus* and species of the *S. varius* complex, and the occurrence of the two hybrids discussed above are not the only evidence suggesting that they are still affected by selection against their hybridization and interaction. Although broad sympatry exists between *S. thyroideus* and *S. nuchalis* (Rocky Mountain region), and between *S. thyroideus* and *S. ruber* (California to British Columbia), *thyroideus* is largely ecologically separated from the other two species. In Nevada, Ridgway (in Bent 1939:142) found *nuchalis* "as strictly confined to the aspens as *S. thyroideus* was to the pines." Likewise, Bent (1939:156) stated that "all observers seem to agree" that *thyroideus* "is confined to the higher elevations among the pines, in sharp contrast to the haunts of the red-breasted sapsucker at lower levels among the deciduous trees." Such ecological separation may act as a reproductive isolating mechanism, as well as reducing competition between these species, since encounters between individuals of these species are reduced when they occur in different habitats. Detailed studies of the ecological and behavioral isolating mechanisms operating largely, if not completely, to prevent the interbreeding of *thyroideus* with *nuchalis* and *ruber* would be welcome, and they might provide data useful for analyses of isolating mechanisms operating among the species of the *varius* complex as well.

The presence of a closely related but distinct species of sapsucker (*thyroideus*) in sympatry with *S. ruber* and *S. nuchalis* may be affecting the evolution of reproductive isolating mechanisms and factors promoting reduced competition among the more recently evolved and interacting species of the *S. varius* complex. For example, *S. varius* and *S. ruber* ultimately may be able to evolve effective isolating mechanisms and come to coexist broadly north of, but not within, the range of *S. thyroideus*. Or, *S. nuchalis* and *S. varius* ultimately may be able to coexist outside (north and east) the range of *thyroideus*. Likewise it may be impossible for *ruber* and

nuchalis ever to overlap broadly because each is broadly sympatric with *thyroideus*, with which interactions, even including hybridization, are still occurring. It is questionable whether as many as three species of sapsuckers can coexist, but at any rate this is unlikely to occur as long as hybridization, however rare, remains possible.

It is tempting to suggest that the genes responsible for the distinctive male and female plumages of the Williamson's Sapsucker are largely dominant to those of the Red-naped Sapsucker. Hybrids, even of the F₁ type, may vary tremendously. Also, there is the remote possibility that the two known hybrids represent backcross, rather than F₁ hybrids. Rather than speculate on the possible dominance of *thyroideus* genes over those of *nuchalis*, we prefer simply to note that *thyroideus* features do predominate in the two known hybrids representing this cross.

SUMMARY

An adult male hybrid Williamson's × Red-naped Sapsucker from Chihuahua is described, and an adult hybrid female, reported earlier by Oberholser (1930) as an apparent juvenile, is more fully described. Also described are several variant female Williamson's Sapsuckers which tend toward males in their plumage. The two hybrids and the variant females form the basis for an hypothesized evolution of the genus *Sphyrapicus*. The major features of the proposed evolutionary history are: (1) the evolution of distinctive "sapsucking" habits in a line of melanerpine woodpeckers, the ancestor of *Sphyrapicus*; (2) the evolution of eastern (ancestor of *varius* group) and western (pre-*thyroideus*) sapsuckers, both with a patterned face, melanerpine juvenal plumage, and both sexes colored alike or nearly alike; (3) secondary contact of *thyroideus* and western populations of the *varius* complex resulting in reinforcement of isolating mechanisms, initial hybridization lessening with time, and competitive interactions; (4) enhancement of sexual dimorphism in *thyroideus* (through reversion to a juvenal plumage by females), its suppression in *ruber* and *nuchalis*, and increased ecological separation of the two groups; and (5) the evolution of partial isolating mechanisms and secondary contacts among *varius*, *ruber* and *nuchalis*. The continued interaction of *thyroideus* with *ruber* and *nuchalis* may be affecting the course of evolution in relation to feature (5). The hybrid sapsuckers discussed in this report tend toward the Williamson's Sapsucker in appearance.

ACKNOWLEDGMENTS

This report was the result of research conducted with support of the National Science Foundation (grant GB-5891 to Short), to the authorities of which we are grateful. We thank K. C. Parkes for calling to our attention the presence of one of the hybrids in the Carnegie Museum, and Dr. Parkes and E. R. Blake for facilitating studies by the senior author in the collections under their charge. W. Bock kindly commented on the manuscript, offering helpful suggestions.

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Accepted for publication 31 December 1969.