SPECIATION IN SAPSUCKERS (*SPHYRAPICUS*): II. SYMPATRY, HYBRIDIZATION, AND MATE PREFERENCE IN *S. RUBER DAGGETTI* AND *S. NUCHALIS*

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ABSTRACT.—The Red-breasted Sapsucker (*Sphyrapicus ruber daggetti*) and Red-naped Sapsucker (*S. nuchalis*) are sympatric and hybridize in south-central Oregon, northeastern California, along the California-Nevada border, and in southern Nevada. We examined the overlapping distribution, nature of hybridization, and mate preference in these two taxa. Using a "hybrid index" system, we identified 13 phenotypic classes that represent the range of variation seen in typical parental types and their hybrids. Variation of parental forms in regions of allopatry was used to distinguish parental phenotypes from hybrids in the zone of overlap and hybridization. The percentage representation of various categories of mating (conspecific, 75.8%; backcross, 16.6%; hybrid, 1.4%; and interspecific, 6.2%) shown by 145 nesting pairs in the zone of overlap was used to infer the relative fitness of F_1 and F_2 generation hybrids. Although interspecific matings produce fully viable F_1 offspring in numbers proportional to expectation, hybrid and backcross matings apparently are selected against. We suspect that F_1 individuals and various recombinants have partial sterility barriers. In interspecific matings and in backcrosses, the male nearly always is *S. r. daggetti* or the redder mate. The data agree most closely with the dynamic-equilibrium model (stable-zone hypothesis), which has been proposed to explain zones of sympatry and hybridization in which gene flow from the extensive regions of allopatry of parental forms is balanced by selection against hybrids. In view of the preponderance of conspecific matings where *S. r. daggetti* and *S. nuchalis* occur together, they are regarded as biologic species. This decision is most appropriate for these taxa despite their low degree of hybridization and their near genetic identity as shown by electrophoresis. *Received 9 March 1984, accepted 5 September 1984.*

INFORMATION from zones of natural hybridization in animals has been a cornerstone of models of speciation and evolutionary theory (Mayr 1963, Woodruff 1973, Dobzhansky et al. 1977, Endler 1977, Moore 1977, Barton and Hewitt 1981). Analyses of such zones in birds continue to play a significant role in the development and interpretation of these models (Selander 1971, Meise 1975, Barrowclough 1980). Avian material provides several important advantages for the study of hybridization and speciation (Miller 1955). First, most bird species can be watched easily as free-living organisms; their habitat preferences, pairing behavior, mate choice, and reproductive success are clearly revealed in the field. Furthermore, avian reproductive isolating mechanisms emphasize features of color, pattern, and/or voice that are obvious and relatively easy to analyze. Finally, it is possible to see their responses to the environment, "particularly to the barriers and discontinuities ... important in the processes of geographic differentiation" (Miller 1955: 15).

Avian examples in which very different phenotypic forms occur in sympatry and interbreed to varying degrees are especially intriguing. Two forms of specialized woodpeckers, the

Red-breasted Sapsucker (*Sphyrapicus ruber dag-getti*) and the Red-naped Sapsucker (*S. nuchalis*), clearly illustrate this situation where they locally overlap and hybridize in the western United States (Howell 1952, Short 1982, Johnson and Zink 1983). Although the general position of their zone of interaction has been known for many years (Grinnell and Miller 1944: 235–236), Howell (1952) was the first to investigate it in the field during the breeding period. His work was followed by new information on distribution in Oregon (Browning 1977, Johnson 1978), a review of the status of the "*Sphyrapicus varius* group" in California (Devillers 1970), and by data that indicated change in the geographic position of *S. r. dag-getti* in the overlap-hybrid zone (Johnson 1970). Recently, Johnson and Zink (1983) presented data on genic differentiation for all species of *Sphyrapicus*. *Sphyrapicus r. daggetti* and *S. nu-chalis*, despite their profound dissimilarity in appearance, are virtually identical at 39 presumptive genetic loci revealed by gel electrophoresis.

In this paper, we report on the sympatric distribution, hybridization, and mate choice in the same two taxa. We describe (1) the geography and dimensions of the zone of sympatry and hybridization, (2) the nature of phenotypic variation in allopatry vs. that in sympatry, (3) the degree of intermating of the various phenotypes found in the region of overlap and interbreeding, based on a very large sample, and (4) we estimate the relative fitness of hybrids as a basis for inferring the evolutionary status of the taxa in the zone of overlap and hybridization. Such data conclusively resolve the decades-long debate (Grinnell 1901; A.O.U. 1910, 1957, 1983; Howell 1952; Short 1969, 1982; Mayr and Short 1970; Johnson and Zink 1983) over the taxonomic status of the two forms. In the following discussion, *S. r. daggetti* and *S. nu-chalis* will be referred to as "*daggetti*" and "*nu-chalis*."

MATERIALS AND METHODS

Field work was begun in the nesting season of 1963 in the mountains of southern Nevada (Johnson 1965) and continued over 12 of 16 summers through 1978. Initially, the main effort was to define in detail the breeding distributions of *daggetti* and *nuchalis* and to collect geographically representative specimens as a basis for interpreting character variation. Later, we concentrated on finding nests in the zone of sympatry and hybridization in order to determine the phenotypes of mated adults. All important localities of sympatry and hybridization were visited at least twice, but not in succeeding years. This allowed for local population recovery after collecting. Except in a few instances, when we attempted to obtain mated pairs and their young for studies of character inheritance, only one parent was taken at a nest. Collecting was unnecessary for many nests because the parental phenotypes could easily be determined. If one parent was more difficult than the other to characterize according to a hybrid index system (see next section), because of plumage wear or damage from tree pitch or because of apparent intermediacy, this individual was the one taken. The surviving parent typically remained to attend to the eggs or young.

The major collection studied was that obtained by the first author in Oregon, California, and Nevada (223 specimens). We also had available for comparison the 14 adult specimens taken in Modoc County, California in 1948 and 1949 by Howell (1952) and the other breeding specimens he mentioned from the Warner Mountains, Modoc County and from the Sweetwater Mountains and Glass Mountain, Mono County. These specimens are all stored in the Museum of Vertebrate Zoology, where many breeding specimens of both forms from regions of allopatry also are available. A total of 499 breeding specimens of both forms and their hybrids was examined.

RESULTS

HYBRID INDEX SERIES

All breeding-season specimens of *daggetti* and *nuchalis*, whether they are from regions of allopatry or from the more limited areas of sympatry, can be categorized according to a "hybrid index series" (Anderson 1949) based on their head patterns. Other differences between these taxa, in degree of spotting and barring, are too slight and too influenced by wear to be of value in distinguishing breeding specimens. Thirteen categories were identified (Fig. 1). These form a visually graded series from the reddest *daggetti* (score of 0), i.e. specimens with very limited and subdued black-and-white head striping and a very faint shadow of a breast band, to the most extreme examples of *nuchalis* (score of 12), in which the red is confined to the throat, crown, and nuchal patch, the black breast band is wide, and the black-and-white head striping is well defined. The 13 specimens representing each of the hybrid index scores formed a reference series with which all other
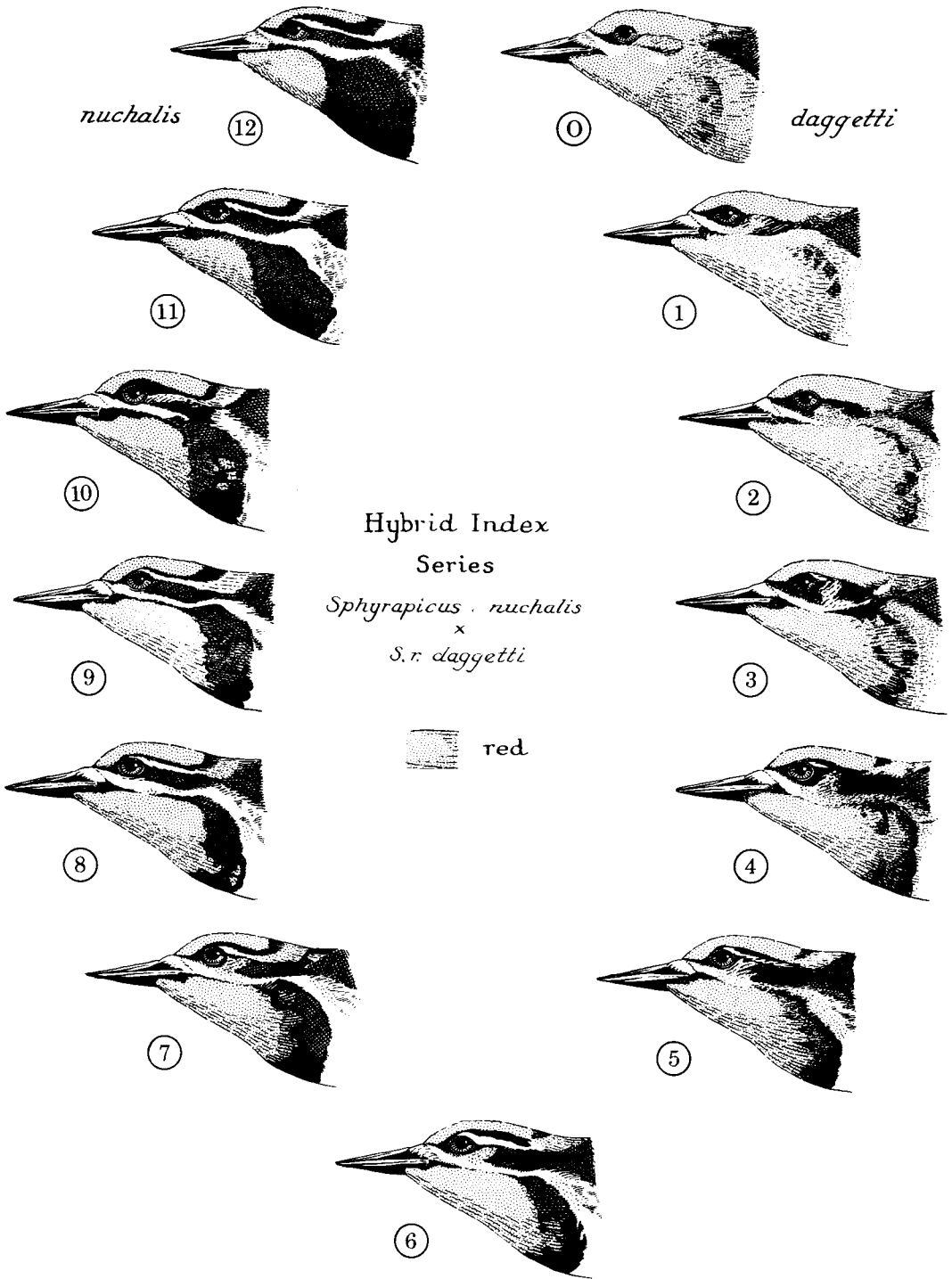
Fig. 1. Illustrations of specimens representing the 13 categories (scores 0–12) of the hybrid index series between the Red-breasted and Red-naped sapsuckers. Typical *daggetti* fall into scores 0–2; typical *nuchalis* fall into scores 11 and 12. Parental Red-breasted Sapsuckers, especially females, rarely have scores of 3 and parental Red-naped Sapsuckers, especially males, rarely are scored as 10.

specimens were compared for determination of their scores.

The plumages of the two forms are well described in the literature (Howell 1952: 240–245, Devillers 1970, Dunn 1978), and only a brief summary is given here. The differing head patterns of *daggetti* and *nuchalis* are based simply on an interplay between varying proportions of carotenoid and melanin pigments. When carotenoid pigments dominate the barbs of the head feathers, especially their tips, the relative amount of melanin present is reduced and the *daggetti* phenotype is seen. Conversely, when black melanin pigment is packed into the feathers of the breast and those of the sites of the black head stripes, the *nuchalis* phenotype emerges. Although only the feathers of the sites of the white head stripes and those of the throat and crown never have black pigment, all sites can have red pigment, especially in the barb tips, except for small lateral stripes at the base of the upper mandible that always remain whitish. However, even in the reddest individuals of *daggetti*, a reduced quantity of melanin pigment still is present as a narrow dark band in the middle and basal portions of the feathers of the head and breast, forming an underlying "shadow" that is reminiscent of the melanistic breast band, cheek patch, and head stripes seen so vividly in *nuchalis*. This is easily demonstrated by clipping the tips off the barbs of feathers in the relevant areas of the head and breast. This point is of special significance because progressive wear of the head and breast feathers during the nesting season, caused primarily in adults when they squeeze through the nest opening, exposes increasing amounts of blackish or dusky color and causes normal *daggetti* to be identified incorrectly as hybrids. The presumption of all earlier authors that hybridization between *daggetti* and *nuchalis* is very common has been based on the routine underestimate of the amount of black normally hidden below the red barb tips of the head and breast feathers in *daggetti*. This problem is perpetuated in even the most recent field guides (National Geographic Society 1983: 269).

Because of the simple relationship of carotenoids and melanins in the expression of coloration and pattern of the head and breast plumage in *daggetti* and *nuchalis*, it was unnecessary to use a scheme in which scores for "separate" characters (e.g. amount of black in breast band or redness of head plumage) were summed to yield a total hybrid index score for individual specimens. Such an approach is more suitable for studies in which a complex array of characters vary independently. Short (1963) provides an example of such a study in warblers.

Genetic control of head and breast coloration.—It is well established that carotenoid and melanin pigments in feathers differ in their origin (Fox 1976), the former being manufactured by plants and subsequently ingested either directly or indirectly by birds and the latter being synthesized by the bird itself. Despite their independent origin and their probable separate genetic control in all birds, including *Sphyrapicus* (Howell 1952: 244), these major categories of pigments appear to interact in a simple manner in the sapsucker taxa under consideration. When carotenoid pigment is present in the outer barbs of a given feather of the head or breast, melanin is confined to a medial position and forms a narrow band. Conversely, when the outer barbs are filled with melanin, carotenoid pigment apparently is absent. At least to the eye, therefore, the outer barbs are filled with either carotenoids or melanins, but not both. However, the feathers of the head and breast have not yet been examined microscopically to determine if the two pigments occur together at the same sites in individual feathers, with one pigment partially or completely masking the other. This condition has been reported in other birds (Brush 1970, Lucas and Stettenheim 1972: 401–402).

The extent of both carotenoid and melanin pigmentation in the feather barbs of the head and breast shows a pattern of continuous variation from *nuchalis*, through the hybrids, to *daggetti*. Reddish carotenoid pigments gradually subdue the black-and-white head striping and black breast band of typical *nuchalis* until the head and breast are completely red, as in *daggetti*. Continuously varying traits can be controlled by a system of additive polygenes. Because carotenoids and melanins probably are under independent genetic control, two distinct series of genes may play a role, one for the deposition of each category of pigment. We suggest further that these two independent series of additive genes may in turn be controlled by a regulatory gene or switch gene that dictates the relative amount and position of each

pigment type, so that when the carotenoid se-
ries is switched on, the melanin series is
switched off, and vice versa. Such a regulatory
system could facilitate the special interactive
mode of color expression already described. We
speculate also that the number of gene pairs in
each hypothesized series is approximately six.
This figure is based on our ability to identify
13 intergrading phenotypic classes of pigmen-
tation among the specimens examined. Thir-
teen is the number of phenotypic classes of off-
spring expected when both parents are
heterozygous for the trait in question and when
six additive gene pairs are operative (Winches-
ter 1977: 196). Admittedly, this genetic model
is tentative and exploratory; as such it is offered
primarily for its possible heuristic value. But in
the absence of the refined breeding data nec-
essary to determine the genetics of color traits
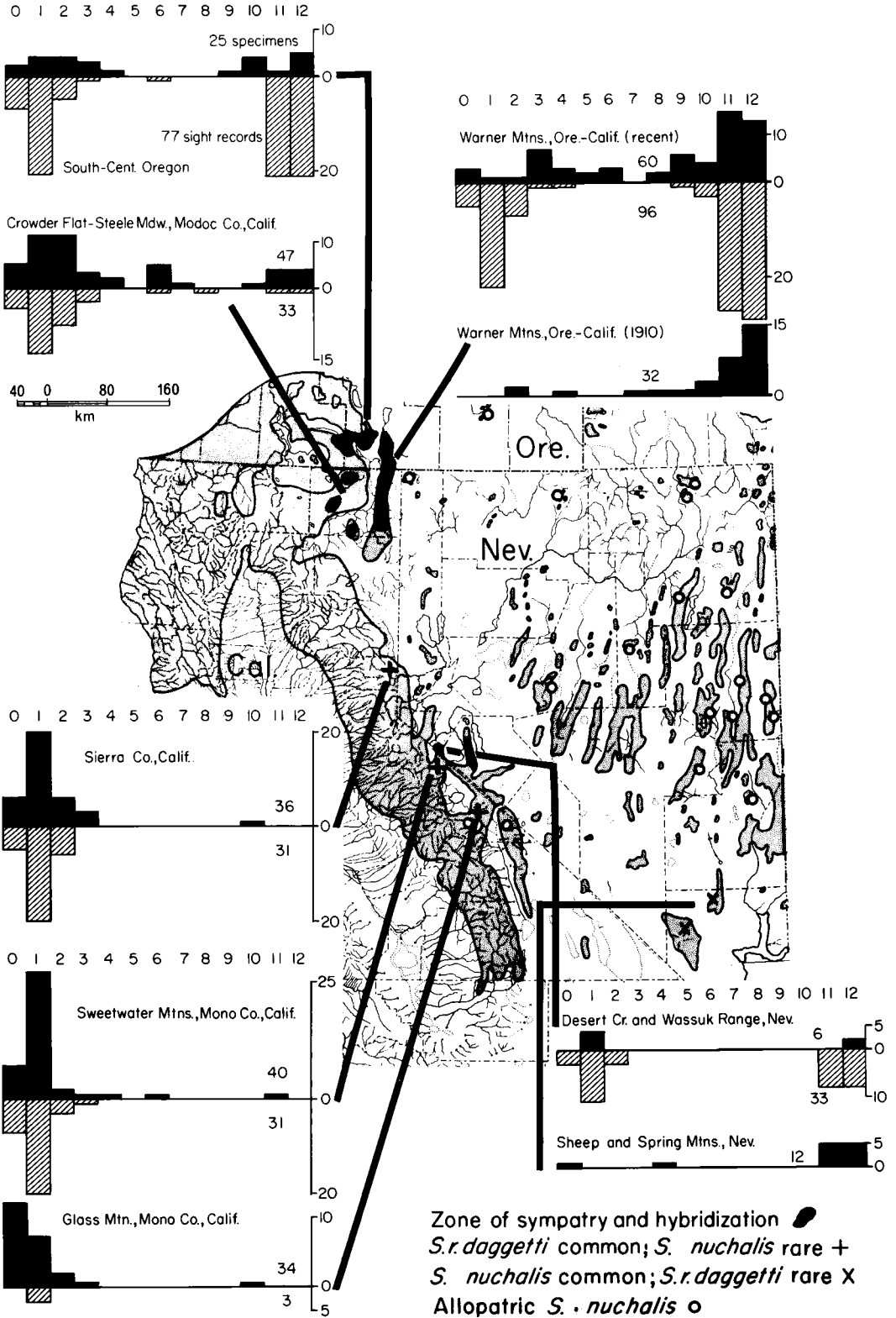in sapsuckers, further speculation seems un-
warranted.

ZONE OF SYMPATRY AND HYBRIDIZATION

The breeding distribution of *daggetti* is fairly
continuous through the Sierra Nevada, coast
ranges, and mountains of south-central Oregon
(Fig. 2). In contrast, in the western portion of
its nesting range, *nuchalis* forms scattered pop-
ulations in the mountains of the Great Basin.
In this general region, areas of contact between
the two species are interrupted and of limited
extent, the principal one being in Modoc
County, California and in adjacent Lake and
Klamath counties, Oregon (Crowder Flat–Steele
Meadow, South-Central Oregon, and Warner
Mountains in Fig. 2). A fairly local area of sym-
patry, where definite hybrids are not yet
known, occurs in the vicinity of Desert Creek
(Lyon County, Nevada and Mono County, Cal-
ifornia) and in the Wassuk Range, Mineral
County, Nevada. Five other sites are known
where one species is common and the other is
rare (Fig. 2). These sites occur along the eastern
side of the Sierra Nevada in Sierra County, Cal-
ifornia; in the Sweetwater Mountains and on
Glass Mountain, both in Mono County, Cali-
fornia; and in the Sheep and Spring moun-
tains, Clark County, Nevada. Therefore, *dag-
getti* and *nuchalis* are essentially allopatric in
this region.

Specimens and sight records from the afore-
mentioned areas were plotted in relation to
their hybrid index scores (Fig. 2) and tested
(Kolmogorov-Smirnov test) for possible differ-
ences in the estimation of intrapopulation phe-
notypes using specimens vs. sight records. For
4 populations, the distributions were signifi-
cantly different: South-Central Oregon ($d_{max.}$ =
0.305, $P < 0.01$), Crowder Flat-Steele Meadow
($d_{max.} = 0.240$, $P < 0.01$), recent Warner Moun-
tains ($d_{max.} = 0.270$, $P < 0.01$), and Desert Creek-
Wassuk Range ($d_{max.} = 0.243$, $0.01 < P < 0.02$).
In 2 samples, the distribution of specimens was
not significantly different from that for sight
records: Sierra County ($d_{max.} = 1.10$, $P > 0.2$) and
Sweetwater Mountains ($d_{max.} = 0.075$, $P > 0.2$).
Presumably, the statistically significant differ-
ences arose in the 4 samples because of oppos-
ing sources of bias in the two kinds of records.
Because we attempted to collect odd-appearing
birds to document the range of variation pres-
ent in natural populations, the specimen rec-
ords probably are slightly biased toward hy-
brids. In contrast, because the subtle hybrid
features of some presumptive backcrosses and
recombinant types are not always easy to detect
in the field, it is likely that the sight records
are slightly biased toward pure parental forms.

Three main points are evident from the his-
tograms of Fig. 2. First, the overwhelming pro-
portion of both specimens and sight records
are of normal parental phenotypes of either
daggetti or *nuchalis*; definite hybrids are rela-
tively scarce. Second, the populations of the
Warner Mountains have changed remarkably
since the specimens were taken there in 1910
(Kolmogorov-Smirnov test, recent vs. 1910 rec-
ords, $d_{max.} = 0.290$; $P < 0.01$). In the early sam-
ple from that region, *nuchalis* was by far the
most common form. Only 2 of the 32 specimens
taken in 1910 were *daggetti*. A few hybrids also
were taken. Since 1964, when the first samples
for the present study were collected, specimens
of *daggetti* have turned up regularly in the War-
ner Mountains. Furthermore, almost 100 sight
records obtained in the last 20 yr establish that
the Red-breasted Sapsucker is now a common
species in the Warner Mountains, where it oc-
curs in local sympatry with the Red-naped Sap-
sucker. It is of interest that the shape of the
histogram for the Warner Mountains in 1910
resembles that for the mountains of southern
Nevada. Indeed, they are not different statisti-
cally (Kolmogorov-Smirnov test, $d_{max.} = 0.11$;
$P > 0.2$). Third, the histograms and distribu-

0 1 2 3 4 5 6 7 8 9 10 11 12

25 specimens

77 sight records

South-Cent. Oregon

Crowder Flat-Steele Mdw., Modoc Co., Calif.

47

33

40 0 80 160

km

0 1 2 3 4 5 6 7 8 9 10 11 12

Warner Mtns., Ore.-Calif. (recent)

60

96

Warner Mtns., Ore.-Calif. (1910)

32

Ore.

Nev.

Cal.

0 1 2 3 4 5 6 7 8 9 10 11 12

Sierra Co., Calif.

36

31

0 1 2 3 4 5 6 7 8 9 10 11 12

Sweetwater Mtns., Mono Co., Calif.

40

31

Glass Mtn., Mono Co., Calif.

34

3

0 1 2 3 4 5 6 7 8 9 10 11 12

Desert Cr. and Wassuk Range, Nev.

6

33

Sheep and Spring Mtns., Nev.

12

Zone of sympatry and hybridization

S. r. daggetti common; *S. nuchalis* rare +

S. nuchalis common; *S. r. daggetti* rare X

Allopatric *S. • nuchalis* o

tions show that *nuchalis* maintains large populations at the extreme western periphery of its breeding range that are in contact with *daggetti*. This is true despite the major gap of habitat unsuitable for any sapsuckers that runs north to south in western Nevada. This gap isolates these sympatric populations from the main distribution of *nuchalis* in the mountains across the Great Basin to the east. A prominent gap, Owens Valley, also isolates the allopatric populations of *nuchalis* in the White Mountains from the range of *daggetti* in the Sierra Nevada. In the White Mountains, *nuchalis* does not seem to be influenced by the latter species; neither hybrids nor typical *daggetti* have ever been recorded there.

PHENOTYPIC VARIATION

Variation in regions of allopatry.—To assess variability in the regions of sympatry and hybridization, it is necessary to understand the breadth of normal variation shown by each species in regions of allopatry, away from the influence of the other species. This is demonstrated by the plotting of hybrid index scores of allopatric breeding specimens of 126 *daggetti* and 88 *nuchalis* in Fig. 3. Two main points emerge. First, parental populations of each species show a substantial range of variability. Scores for typical *daggetti* ranged from 0 to 3 ($\bar{x} = 0.97$) and those for typical *nuchalis* from 8 to 12 ($\bar{x} = 11.44$). Second, the sexes differ within pure *daggetti* ($\bar{x}$ of males = 0.58, $\bar{x}$ of females = 1.47) and within pure *nuchalis* ($\bar{x}$ of males = 11.23, $\bar{x}$ of females = 11.77). Thus, the reddest *daggetti* (specimens with very low scores) are predominantly males and the blackest *nuchalis* (specimens with very high scores) are mostly females. Stated another way, within pure *daggetti* most scores of 2 and all of 3 are of females, and within pure *nuchalis* most scores of 11 and both the single 10 and single 8 are
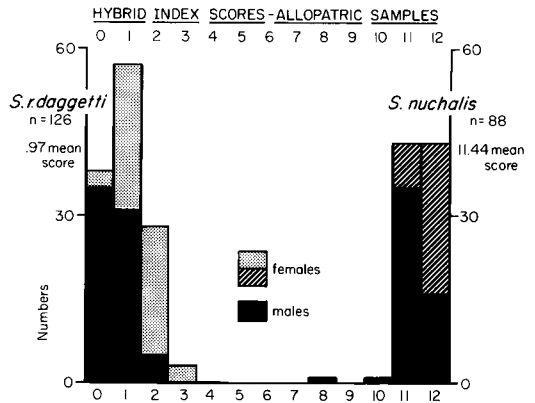

Fig. 3. Hybrid index scores of breeding specimens of *daggetti* from allopatric localities in Oregon, California, and western Nevada and of *nuchalis* from allopatric localities in Oregon, California, Nevada, Idaho, Montana, Utah, and Arizona.

of males. Within each species, the difference between the sexes in average score was highly significant (Kolmogorov-Smirnov test; for *daggetti*, $d_{max.} = 0.438$, $P < 0.01$; for *nuchalis*, $d_{max.} = 0.469$, $P < 0.01$). This suggests the presence of a consistent sexual dimorphism within each species that heretofore has not been appreciated.

Variation in the zone of sympatry and hybridization.—It is of special interest to determine the phenotypes of mated birds within the zone of sympatry and hybridization. The hybrid index scores of 145 males and their 145 female mates from this zone are plotted in Fig. 4. Kolmogorov-Smirnov tests were used to determine the proportion of typical parental specimens of each hybrid index category to be expected in the samples from the zone of overlap and hybridization based on the frequencies seen in the allopatric samples (Fig. 3). Proportions of allopatric and sympatric populations were not significantly different in 3 of 4 comparisons ($d_{max.}$ ranged from 0.077 to 0.117, $P > 0.2$), those for

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Fig. 2. Breeding distribution of Red-breasted and Red-naped sapsuckers in portions of Oregon, northern and central California, and in Nevada. The outline in southwestern Oregon, extreme western Nevada, and California describes the essentially continuous nesting range of *S. r. daggetti*, exclusive of populations in the mountains of southern California. Islands of forest and woodland in south-central Oregon, eastern California, and Nevada, containing the known breeding stations of *S. nuchalis* (circles), also are outlined. The histograms depict the hybrid index scores of specimens (black bars above the line) and of sight records (striped bars below the line) for nine large samples of the two species and their hybrids from eight restricted geographic regions.

Hybrid Index Scores of Sexes of Mated Birds
in Zone of Sympatry and Hybridization.

0   1   2   3   4   5   6   7   8   9   10   11   12

n= 145
MALES

47.6%   40.7%

S. r. daggetti   *S. nuchalis*

n = 145
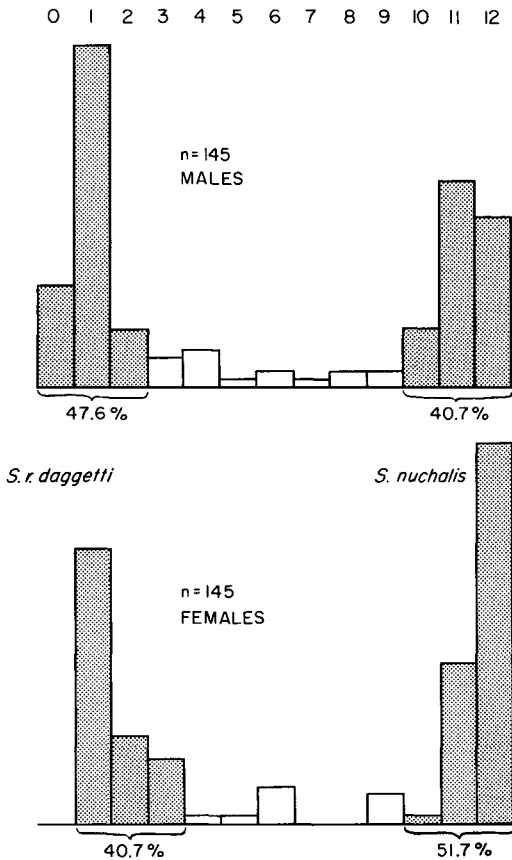FEMALES

40.7%   51.7%

Fig. 4.   Hybrid index scores of typical *daggetti* and *nuchalis* from the zone of sympatry and hybridization. This analysis includes only birds known to be mated and established for breeding. Shaded bars represent "pure" parental types of either species and clear bars are assumed to be hybrids.

female *daggetti* and for both sexes of *nuchalis*. However, in males of *daggetti*, allopatric and sympatric frequencies differed significantly ($d_{max.} = 0.290$, $P < 0.01$). The disagreement resulted from the relative numbers of specimens of hybrid index scores 0 and 1. Zero was a more common score in allopatric than in sympatric populations; the reverse was true for a score of 1. Although the meaning of this difference is unclear, we suspect that it is an artifact of collecting date. In general, specimens were taken later in the season in the zone of sympatry and hybridization than in the regions of allopatry,

simply because of the fortuitous scheduling of field trips. Thus, the sympatric specimens appear slightly more worn and, therefore, have slightly higher hybrid index scores than those from allopatry. Despite this single instance of nonconcordance, the frequencies of most categories were similar enough according to the Kolmogorov-Smirnov tests to justify the conclusion that the proportions of typical parental types within the zone of overlap and hybridization were correctly identified.

Eighty-eight percent of the males and 92% of the females are either typical *daggetti* or typical *nuchalis* (Fig. 4). Thus, only 10% of all mated birds are hybrids. Oddly, 7% more *daggetti* males than females and 11% more *nuchalis* females than males were involved in these matings from the zone of overlap. However, this difference only approaches statistical significance ($\chi^2_1 = 2.55$, $0.100 < P < 0.250$). It is of interest that more males (11.7%) than females (7.6%) of the mated birds are presumed hybrids. Scott et al. (1976) also report an excess of male intermediates between *S. r. ruber* and *S. nuchalis* in their zone of sympatry and hybridization between Kersley and Bouchie Lake, British Columbia. Although hybrid males may have a slight advantage over hybrid females in obtaining mates, the reason for the excess is unclear in either instance. However, John Endler (pers. comm.) has suggested that the excess of males may result from the operation of Haldane's Rule (Maynard Smith 1975), in which hybrid breakdown results in greater mortality of the heterogametic sex (females in birds).

Finally, we compared allopatric (Fig. 3) and sympatric (Fig. 4) frequency distributions for both species with the sexes combined (Kolmogorov-Smirnov test). The distributions were significantly different ($d_{max.} = 0.165$, $P < 0.005$).

MATE PREFERENCE IN THE ZONE OF
SYMPATRY AND HYBRIDIZATION

Mate selection in a zone where diverse phenotypes interact sympatrically can provide crucial evidence bearing on gene exchange, reproductive isolation, hybrid fitness, and the systematic status of closely related forms. For *daggetti* and *nuchalis*, we have such data for 145 nesting pairs from the principal zone of interaction in south-central Oregon and northeastern California. The mate preferences of these 290 individuals are illustrated in a matrix of

hybrid index scores for the sexes of individual pairs (Fig. 5). These data are categorized by mating type in Table 1. Most pairs (110 = 75.9%) mated in a positively assortative manner, i.e. typical *daggetti* mated to typical *daggetti* or typical *nuchalis* mated to typical *nuchalis*. In most pairs involving a hybrid, the hybrid individual backcrossed with one of the pure parental types (24 matings = 16.6%). Hybrid individuals paired with other hybrids only rarely, in 2 cases (1.4% of the matings). Most interestingly, 9 of the matings (6.2%) were interspecific. These are shown in Fig. 5, either in the upper left corner (8 matings of typical *nuchalis* females with typical *daggetti* males) or in the lower right corner (1 pairing of a typical *nuchalis* male with a typical *daggetti* female). This asymmetry will be discussed later.

Because of the large number of cells in Fig. 5, for purposes of statistical testing we collapsed the data into a 4 × 4 contingency table consisting of hybrid index scores 0–3, 4–6, 7–9, and 10–12. These categories maintain the separation of typical *daggetti* (scores 0–3) from typical *nuchalis* (scores 10–12) and from matings involving F_1 hybrids, backcrosses, and recombinants (scores 4–6 and 7–9). The data are very highly associated or nonrandom ($\chi^2_9 = 100.094$, $P < 0.005$). As would be expected from an examination of Fig. 5, the four corner cells of the contingency table contributed heavily to the very high total χ^2 value (18.96, 18.06, 25.09, and 23.01).

FITNESS OF HYBRIDS

Information on the survival of hybrid offspring, their relative success in eventual mating, and their production of young is central to interpretations of the status of hybrid zones and of the evolutionary significance of these zones to the taxa in question. Although such data are essentially lacking for the present example of hybridization in *Sphyrapicus*, certain useful inferences on hybrid fitness can be gained from further analysis of the phenotypes of mated adults (Fig. 5, Table 1). Twenty-eight hybrids (9.7% of the total population) were recorded. These fell into two groups: (1) probable F_1 hybrids, or those individuals with hybrid index scores of 5, 6, or 7; and (2) various recombinants resulting from backcrossing. Ten individuals were presumed to be F_1 hybrids and the remaining 18 hybrids were presumed to be re-
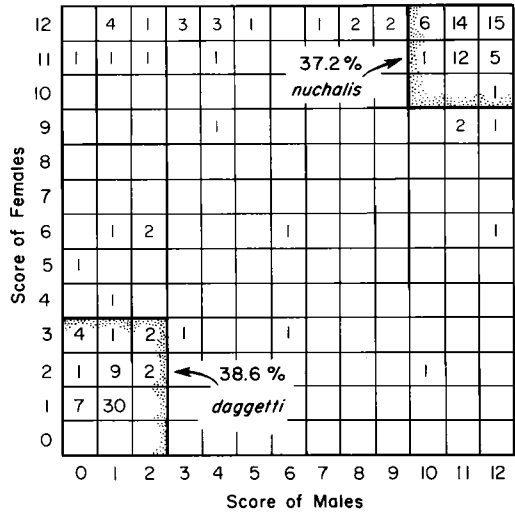

Fig. 5. Matrix of mating preference among 145 mated pairs of Red-breasted and Red-naped sapsuckers in the zone of sympatry and hybridization. The small squares in the lower left and upper right corners of the diagram encompass the scores of mates judged to be either pure *daggetti* or pure *nuchalis*. Because of sexual dimorphism within *S. r. daggetti*, typical females range from 0 to 3 but typical males range from 0 to 2.

combinants. [Some backcross matings would be expected to produce phenotypes with hybrid index scores ranging from 5 to 7, but at a low frequency, especially if 3 or more pairs of genes are involved in the control of the traits upon which the scores are based (see p. 5)].

It is of immediate interest to determine if the number of F_1 hybrids present (10) is in agreement with the expected number of surviving offspring derived from the frequency of interspecific crosses occurring (9) in the sample from the zone of overlap and hybridization. Unfortunately, data on the relative survival of young from either normal conspecific crosses or from interspecific matings are unavailable. Although Howell (1952) presented data from a few interspecific nests that suggested that F_1 fledging success was fully comparable to that from conspecific pairings, a much larger sample is necessary to prove this point. Furthermore, we lack information on the welfare of surviving F_1 offspring approximately 1 yr after

TABLE 1. Types of matings represented by 145 nesting pairs of *Sphyrapicus* in zone of sympatry and hybridization.

Taxa	Number of pairs	Percent of total	Type of mating
S. r. daggetti × *S. r. daggetti*	56	38.6	Conspecific
S. nuchalis × *S. nuchalis*	54	37.2	Conspecific
♀ hybrid × ♂ *S. r. daggetti*	5	3.5	Backcross
♂ hybrid × ♀ *S. r. daggetti*	2	1.4	Backcross
♀ hybrid × ♂ *S. nuchalis*	4	2.8	Backcross
♂ hybrid × ♀ *S. nuchalis*	13	8.9	Backcross
F_1 hybrid × F_1 hybrid	2	1.4	Hybrid
♀ *S. nuchalis* × ♂ *S. r. daggetti*	8	5.5	Interspecific
♂ *S. nuchalis* × ♀ *S. r. daggetti*	1	0.7	Interspecific
Total	145	100.0	

hatching, when they are competing for mates and attempting to raise young of their own. In the absence of such information, we can infer relative production of offspring and their survival from the proportions of the various phenotypic classes observed in our sample of 290 birds.

As a working null hypothesis, assume that the 9 interspecific pairs fledged as many young as conspecific pairs and that the proportion of these young surviving to breed 1 yr later was comparable to that from typical matings. Assuming an average clutch size of 4.5 eggs, a reasonable figure for a variety of species of picids (Cody 1971: 501), and 25% survival of young from these 40.5 eggs to the first year of breeding [a figure based on long-term demographic studies by Walter D. Koenig of the Acorn Woodpecker (*Melanerpes formicivorus*), the only species of woodpecker for which such survivorship data are available], then 10.125 offspring would be expected from 9 normal pairs of sapsuckers. Considering the many sources of imprecision in estimates such as these, this figure is remarkably similar to our finding of 10 F_1 hybrids, and the null hypothesis cannot be rejected. Thus, based on these figures, there is no evidence for either F_1 hybrid inferiority or superiority.

The interspecific matings account for only 10 of the total of 28 hybrids observed. The remaining 18 hybrids evidently resulted from backcrosses and intermating of hybrids. Thus it also is useful to estimate the total number of hybrids expected from the number of backcrosses (24) and hybrid matings (2) actually observed (Table 1). Because parental phenotypes are produced in addition to hybrids in both backcross and hybrid matings, calculation of

expected numbers of different phenotypes is more complex than for interspecific matings, in which all offspring are assumed to be intermediate F_1 individuals. The calculation of expected numbers of hybrid and recombinant phenotypes vs. parental phenotypes, for either backcross matings or matings of F_1 hybrids, also requires estimates of the number of gene pairs involved. Earlier, we estimated that six pairs of genes control degree of redness of the head and breast in these sapsuckers.

For backcross matings, the formula 0.5^n, where n represents the number of gene pairs, can be used to compute the expected proportion of parental phenotypes. For six gene pairs, 1.56% of the offspring would be expected to be parental phenotypes for backcrosses to pure parents homozygous at all six loci (character states 0 and 12). An additional 0.292% of the offspring from backcrosses to character states 1 and 11 (heterozygous at a single locus), also assumed to be pure parents in this study, would represent parental phenotypes. Thus, most (98.15%) of the offspring would be hybrid or recombinant phenotypes.

For F_1 hybrid matings, the formula 0.25^6 is appropriate for the calculation of the expected proportion of either extreme parental phenotype, again assuming that six gene pairs control the red color difference between *daggetti* and *nuchalis*. Thirteen phenotypic classes would be expected. Each parental phenotype therefore would occur at a proportion of only 0.0244%. It is clear that under the assumption of six gene pairs, for either backcrosses or hybrid matings, the expected fraction of parental phenotypes in the offspring is so low that it safely can be ignored in our calculations. Even if only three pairs of genes control the trait, only 17.2% of

backcross offspring and 3.125% of offspring from F_1 hybrid matings would be expected to represent the parental phenotypic classes. The question, therefore, is whether the figure of 18 hybrids or recombinants produced by 26 backcross and hybrid matings is comparable to what might be expected from an equivalent number of conspecific matings. Again assuming a clutch size of 4.5 eggs, 117 eggs would be expected from these 26 matings. At a survival rate of 25% for the first year, 29.25 1-yr-olds would be expected in the population. Our figure of 18 hybrids and recombinants is, therefore, low compared to expectation. Furthermore, it also is lower than expected when we realize that we have calculated the number of surviving offspring expected for only a single year. Hybrid and recombinant matings would produce phenotypes that would be represented for several years in the population. This is in contrast to the interspecific crosses that annually produce only one phenotypic class of offspring, the F_1 hybrids. Therefore, the representation of phenotypes of hybrids and recombinants in the sample of 290 individuals is much lower than expected. This suggests that survival, and thus fitness, of hybrids is reduced after 1 yr of age.

Finally, the apparent greater mortality of female than of male hybrids, possibly resulting from Haldane's Rule, is further evidence for hybrid breakdown.

Discussion and Conclusions

Models proposed to explain hybrid zones.—Moore (1977) reviewed three alternative hypotheses offered to explain hybrid zones in vertebrates. In (1) the "ephemeral zone hypothesis," hybridization after secondary contact leads either to complete reproductive isolation (speciation) or to merger (swamping) of the populations. Speciation is probable if the populations have diverged sufficiently so that the parental phenotypes are more fit than the hybrids; fusion is probable if the reverse is true. Sibley (1957) illustrated both of these outcomes with ingenious diagrams. In (2) the "dynamic equilibrium hypothesis," the standard interpretation of hybrid zones (Mayr 1963: 378–379), a balance occurs between gene flow into the hybrid zone, from the extensive areas of allopatry of the parental forms, and selection against hybrids. Bigelow (1965), who has championed this view, felt that introgression of genes from one form

into the other would be suppressed by steep gradients of selection on each side of the narrow hybrid zone and that the development of mechanisms opposing hybridization might be countered by the influx of parental types into the comparatively narrow zone of overlap. Barton (1979a, b, 1980) has developed this hypothesis in detail. In addition (3), Moore (1977) offered a hypothesis that envisions the superior fitness of hybrid phenotypes over those of either parent in ecologically intermediate hybrid zones. Finally, Endler (1977) proposed models that allow for differentiation in parapatry by contiguous populations positioned along environmental gradients.

Although the results of allopatric vs. parapatric differentiation cannot be distinguished, certain characteristics of the overlap-hybrid zone described here in *Sphyrapicus* allow us to discuss the merits for this example of the various hypotheses. Three features of the sapsucker hybrid zone are pertinent to the choice of a working hypothesis. First, at least in the short term, the zone is certainly not ephemeral; hybrids have been known for over a century (Howell 1952). Nonetheless, a zone that generates hybrids for a century could still be ephemeral over a millenium. Second, although parental phenotypes predominate in the hybrid zone, F_1 hybrids seem to enjoy equivalent viability, and their occurrence is in proportion to the frequency of interspecific matings. We interpret this as evidence that F_1 hybrids are neither selected for nor against (although some of their genes and recombinants may be). F_2 hybrids and recombinants, however, do seem to be at a disadvantage. Whether they are at enough of a disadvantage to prevent introgression is unknown. Third, the zone of interbreeding straddles a steep environmental gradient between coastal warm-wet and interior (continental) cool-dry climates (Johnson 1978), which is reflected in the biota present. These features of the hybrid zone in *Sphyrapicus* would seem to rule out a short-term ephemeral-zone model. Moore's hybrid-superiority model also seems poorly suited to these data; there is no evidence from which to conclude that hybrid individuals are of greater fitness than parental types.

We are left with the dynamic-equilibrium model (stable-zone hypothesis), the assumptions of which are in general agreement with all of the foregoing data. In the sapsucker ex-

ample, the "ecotonal" nature and position of the hybrid zone on a climatic gradient, rather than enhancing the fitness of hybrids as expected by Moore's model, seem instead to permit coexistence of parental phenotypes in a region compatible with the needs of both parental types and their hybrids.

Temporal change in the hybrid zone.—Data on spatial change in hybrid zones are relatively scarce (Selander 1971). Scott et al. (1976) describe the incursion of *nuchalis* into an area of British Columbia where only *S. ruber* had nested approximately 25 yr earlier. In the present study we have documented the invasion of *daggetti* eastward into the Warner Mountains, Modoc County, California, where *nuchalis* was overwhelmingly the predominant form in 1910. The time of arrival of substantial numbers of *daggetti* in the Warner region is unknown, but by 1964 both species commonly occurred at several sites (Johnson 1970). The apparently greater numbers of hybrids and of backcross recombinants in the recent Warner sample (Fig. 2) perhaps indicates an increased breakdown of premating isolating mechanisms because of the invasion of *daggetti* into the formerly exclusive domain of *nuchalis*. Nonetheless, despite the apparent increase in hybridization in the Warner region, the two species clearly maintain their integrity. Thus, this documented change in distribution may be regarded as evidence against the arguments that there is no selection one way or the other and that the ultimate result of the interbreeding will be complete blending of the two forms. The factors responsible for the eastward expansion of nesting range in *daggetti* are unknown.

Nuchalis also apparently has changed its breeding distribution near the southern portion of the zone of contact with *daggetti* in the present century. The former species was not found in the White Mountains, Mono County, California during the extensive vertebrate surveys there in 1917. Yet in 1954, a substantial population of *nuchalis* was nesting along Cottonwood Creek at 2,896 m (Miller and Russell 1956).

Premating isolating mechanisms.—Because mating in the zone of sympatry is strongly assortative according to phenotype rather than random, we may assume that some feature of behavior or plumage acts to reduce the numbers of matings between *daggetti* and *nuchalis*.

Neither Howell (1952) nor we discovered any differences in display or voice between the two forms; if such exist, they must be subtle. However, it is important to note than no detailed behavioral study of either form has ever been conducted. Presumably, then, the striking plumage differences of *daggetti* and *nuchalis* serve as the principal premating isolating mechanisms.

Howell (1952: 273) observed that in mixed matings, either of *S. r. ruber* (or of *S. r. daggetti*) and *nuchalis* or of birds of variously intermediate stock, the male of the pair was the redder individual in all but one instance. This intriguing finding led him to 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*." Our data can be examined in the light of Howell's findings. Of 9 interspecific matings of pure parental phenotypes, the male was *daggetti* and the female was *nuchalis* in 8 instances (Fig. 5, Table 1). Weisser (1973) also reported an interspecific pair of sapsuckers at Lee Vining Creek, Mono County, California where the male was *daggetti* and the female was *nuchalis*. Furthermore, in 8 additional matings involving typical female *nuchalis* and males of scores 3–5, the male was redder. Finally, in 5 examples in which a typical female *nuchalis* was mated to a male with a score of 7–9, again the male was redder. In 5 backcrosses of a hybrid mated to a pure *daggetti*, the redder bird was the male. One mating of hybrids, each with a score of 6, was equivocal. However, in 2 backcrosses (male 6 × female 3, male 12 × female 6) the female was the redder mate. In sum, of 36 matings, apart from those involving typical conspecifics, in 33 the male was redder, 1 was equivocal, and in 2 the female was the redder individual. Thus, Howell's hypothesis is strongly supported (Sign test, $P < 0.001$). Parenthetically, it is of interest to note that in the related species *S. varius*, in which the male has a red throat and the female a white throat, again the male is the redder sex.

However, because most *nuchalis* mate with their own kind, it cannot be simply a matter of the amount of red that determines mate choice. Howell agreed when he stated (1952: 273), "one can hardly expect mate selection between the races to apply so strictly. . . ." How, then, can these mixed matings be explained? To this end we offer the following speculative scenario that

incorporates both the "lust for red" and other factors into an explanation of interspecific pairing in these sapsuckers.

It is well established that *daggetti* arrives on the sympatric nesting areas ahead of *nuchalis* (Howell 1952, 1953). We speculate that the reddest males of *daggetti* dominate the less-red males, win the best territories quickly, and are the earliest to gain mates. However, because the sex ratio in both *daggetti* and *nuchalis* probably is biased toward males, the common condition in birds (Mayr 1939, Welty 1982: 170), some male *daggetti* that already hold territories would be unmated at the time the first *nuchalis* females arrive. Some of these paler male *daggetti* possess territories before any *nuchalis* males. A small percentage of female *nuchalis* choose established male *daggetti* as mates because of the superstimulus value of the extensive red. These available mates, although paler than many *daggetti*, are still redder than any *nuchalis* male, and if these *daggetti* males hold territories, this gives them the edge some of the time. Thus, most unmated birds in the summer should be males of *nuchalis*. This assumption receives support from the proportions of mated birds shown in Fig. 4, which reveals a shortage of male *nuchalis*. Furthermore, 3 unmated individuals of *nuchalis* taken during the breeding season at the localities marked "+" in Fig. 2, where *daggetti* is the commoner form, were males.

Postmating isolating mechanisms.—Factors that tend to reduce the success of interspecific crosses once they occur are not easily identified. All 9 of the interspecific nests, all backcross nests, and the single nest in which both parents were F_1 hybrids contained vigorous young. Whether these nests fledged fewer young than conspecific nests is unknown. Because 6.2% of all matings in the zone of sympatry and hybridization were interspecific, a significant crop of F_1 hybrids must enter the population after each reproductive effort. The fact that F_1 hybrids were neither more scarce nor more common in the breeding population than this degree of interbreeding would suggest implies average fitness for this group. In contrast, because F_2 hybrids and recombinants were less numerous than expected, postmating isolating mechanisms must be operating to reduce the number of young produced by F_1 and backcross matings. Although F_1 hybrids appear to be as fully viable

as normal adults of either species, they may be at a disadvantage in gaining mates. Being intermediate in appearance, these individuals may form pairs less successfully than birds of either parental phenotype (Mayr 1963: 106). However, because a significant number of interspecific matings occurs between even more dissimilar phenotypes, the plumage differences among hybrids and recombinants may not seriously influence their mating success. Another possibility is that partial sterility barriers exist in these viable hybrids. Although the data point to the likely presence of such barriers, a study of comparative reproductive success would be needed to shed light on this possibility.

Species limits.—We feel that conclusions on species status in hybridizing taxa such as those discussed here should rest primarily on three criteria: (1) the relative numbers of pure parental types vs. hybrids in the zone of sympatry and hybridization, (2) the degree of assortative mating vs. random mating demonstrated, and (3) the fitness of hybrid offspring. In view of the preponderance of pure parental types that are mating assortatively in the zone and because of the relatively infrequent hybridization and backcrossing, we conclude that the Red-breasted and Red-naped sapsuckers are best treated as biologic species. The inference of reduced fitness of otherwise viable F_1 hybrids also argues for species status of these taxa.

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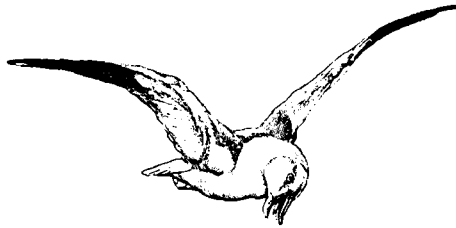
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