

SYSTEMATICS AND BEHAVIOR
OF SOME
NORTH AMERICAN WOODPECKERS,
GENUS *PICOIDES* (AVES)

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LESTER L. SHORT
Curator, Department of Ornithology
The American Museum of Natural History

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INTRODUCTION

THE RELATIONSHIPS AND BEHAVIOR of woodpeckers have interested me for more than 15 years. The genus *Picoides* (which includes *Dendrocopos* of many authors, but my generic usage follows that of Bock and Short, ms) contains more species than do the other genera of North American woodpeckers. From an evolutionary viewpoint, interest in this genus is enhanced by the fact that as many as four species (more than in any other North American genus) may occur sympatrically. The species of *Picoides* are more or less similar in size, and are intricately patterned, mainly in black and white. (Fig. 1 shows some of these patterns for certain New World species of *Picoides*.) Thus, it seemed profitable to initiate field studies of interactions among some of these woodpeckers.

During field work in Baja California in 1964,

at one locality, I saw together two of the most similar species of *Picoides*, Nuttall's Woodpecker (*Picoides nuttallii*), and the Ladder-backed Woodpecker (*P. scalaris*). I later discovered certain puzzling specimens in museum collections that suggested the possibility of hybridization between these species. To investigate interactions between these woodpeckers I planned field studies in California and Baja California, Mexico. These studies were conducted in November, 1966, and January to May, 1967. Museum studies of specimens and other data have taken place since 1964. The present report includes and discusses the results of these studies.

METHODS AND MATERIALS

Comparative studies of specimens were conducted using standard museum procedures.



FIG. 1. Head and outer tail patterns of certain New World species of *Picoides*. For each species is shown: head pattern (rear view); side of head; and three outer retrices. Head patterns are of females, but distribution of red on head of males is shown as area between two lines extending above head in side view. Species at top, from left to right are: *P. nuttallii*, *P. scalaris*, *P. pubescens*, and *P. villosus*. At bottom from left to right: *P. mixtus* (*P. lignarius* is almost identical), *P. borealis* (note only one mark indicates site of tiny red area in males), *P. albolarvatus*, and *P. stricklandi*. Head patterns from a side view are drawn to scale, but other diagrams are not. The patterns are representative, as variation of course occurs.

Measurements obtained included wing length (chord), tail length, bill length (gonys, see below), and other measurements described below. Statistics were computed where sample sizes warranted, usually for samples of five or more specimens.

I made field observations with 8 by 40 field glasses. Moving pictures and tape recordings augmented observational data acquired in the field. I used a Bolex 16 mm. camera with various telephoto lenses. I analyzed the film frame by frame with a model 224A LW Photo-optical Data Analyzer kindly lent me by Walter Bock. To obtain recordings I used a Uher 4000 L Report Tape Recorder, operated at 7.5 inches per second together with a Uher MD 514 Dynamic microphone mounted in a 24-inch parabolic reflector. Representative vocalizations were analyzed with a sound spectrograph using both narrow and wide band filters.

Approximately 2000 specimens were examined during the course of the study; about 1200 adults formed the major basis for comparisons. Among these are 102 specimens of various species of *Picoides*, including many mated pairs, obtained during these investigations. Specimens were examined from the collections of the institutions listed below:

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia

B.M., British Museum (Natural History), London
C.A.S., the California Academy of Sciences, San Francisco

C.M., Carnegie Museum, Pittsburgh

F.M.N.H., Field Museum of Natural History, Chicago

L.A.M., Los Angeles County Museum

M.C.Z., Museum of Comparative Zoology at Harvard College

M.N.H.S.D., Museum of Natural History, San Diego

M.V.Z., Museum of Vertebrate Zoology, University of California, Berkeley

O.C., Occidental College, Los Angeles

O.S.M., Ohio State Museum, Columbus

S.D.S.C., San Diego State College collection

U.C.L.A., University of California at Los Angeles

U.K.M.N.H., University of Kansas Museum of Natural History, Lawrence

U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor

U.S.N.M., United States National Museum, Smithsonian Institution

U.U., University of Utah collection, Salt Lake City
Z.P., Zion National Park collection, Springdale, Utah.

ACKNOWLEDGMENTS

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DISTRIBUTION AND ECOLOGY

Picoides nuttallii AND *P. scalaris*

NUTTALL'S AND LADDER-BACKED WOODPECKERS

THESE WOODPECKERS are almost completely allopatric in California (figs. 2, 3). Known points of contact in that state are in the Kern Basin, Kern County, and in Morongo Valley, San Bernardino County. In other areas the two species breed within 1 to 3 miles of each other, as for example: in the northeastern San Bernardino Mountains between Cushenbury Spring and Whiskey Spring, and between Cactus Flat and Horsethief Basin; in the eastern San Jacinto Mountains between Live Oak Spring and Lower Live Oak Canyon; and possibly in San Diego County in Upper San Felipe Valley and east of Banner. The situation, however, differs in northwestern Baja California, where these species are sympatric, at least in some localities, over an area about 100 miles long (north-south) and 25 miles wide (fig. 4).

In central and northern California Nuttall's Woodpeckers are characteristic of, if not confined to, oak woodland (fig. 5). Of this species throughout its California range Grinnell and Miller (1944, p. 245) noted: "There is some attachment of this species to deciduous trees other than oaks, especially where latter are wanting or scarce." Oaks become increasingly scarce, especially at lower elevations, as one proceeds southward in California. I have found Nuttall's Woodpeckers present wherever oaks, particularly large live oaks, grow in southern California and northern Baja California. In the latter areas, however, the species is also a characteristic bird of the riparian willow-cottonwood-sycamore woodlands. Its abundance in the latter woodlands in the southern part of its range suggests that a scarcity of oaks is not the only factor involved in its habitat preference. Rather the prevalence, indeed almost the restriction, of the Downy Woodpecker to riparian woodlands in northern and central California, its striking decrease southward, and its total absence from Baja California, correlate so well with the enhanced tendency of the Nuttall's Woodpecker to inhabit such woodlands as one proceeds southward that interaction between these woodpeckers appears to be a strong factor influencing

their distribution. Their hybridization also indicates that competitive interactions are likely between these closely related woodpeckers.

The aridity of the east slope of the southern California mountains limits contact between the Nuttall's and Ladder-backed woodpeckers in California. Thus, in only a few places do riparian woodlands extend from the mountains eastward into the desert. To my knowledge, these places include only the Mohave River north of the San Bernardino Mountains, and Morongo Canyon east of those mountains, although a few other sites may exist in San Diego County or elsewhere in southern California (possibly also in the Olancho region in east-central California). The reverse situation, an extension of the desert into Kelso Valley and over Walker Pass, is responsible for a *nuttallii-scalaris* contact in the Kernville region. In northern Baja California the barren character of the xeric eastern slopes of the mountains not only precludes contact between these woodpeckers, but also appears to limit the distribution of *scalaris*. Nuttall's Woodpecker reaches its southern limit in riparian woodland at Rancho Rosarito, Baja California (Short and Banks, 1965, p. 48), which is the approximate southern limit of large, riparian willows and cottonwoods in that region. South of that point the Ladder-backed Woodpecker alone of the genus *Picoides*, occupies both desert (habitats figured in Short and Banks, 1965, fig. 3; and Short and Crossin, 1967, fig. 6) and desert riparian (palms, dense low bushes, mesquites) habitats. (Two very different, unrelated woodpeckers, the Gilded Flicker [*Colaptes auratus*, *chrysoides* group] and the Gila Woodpecker [*Melanerpes uropygialis*], also occupy the Baja California deserts.)

The northern limit of the range of the Nuttall's Woodpecker is attained in southern Oregon (Ashland; Umpqua Valley?; Short, 1965b). The various oaks (*Quercus*) characteristic of much of California's woodlands diminish to the north. At that latitude barely any woodland persists in the form of the California Mixed Evergreen Forest (Küchler, 1964; oaks include *Quercus chrysolepis*, *Q. wislizenii*, *Q. douglasii*, *Q. garryana*, *Q. kelloggii*), which barely enters southwestern Oregon along the upper Rogue and Klamath

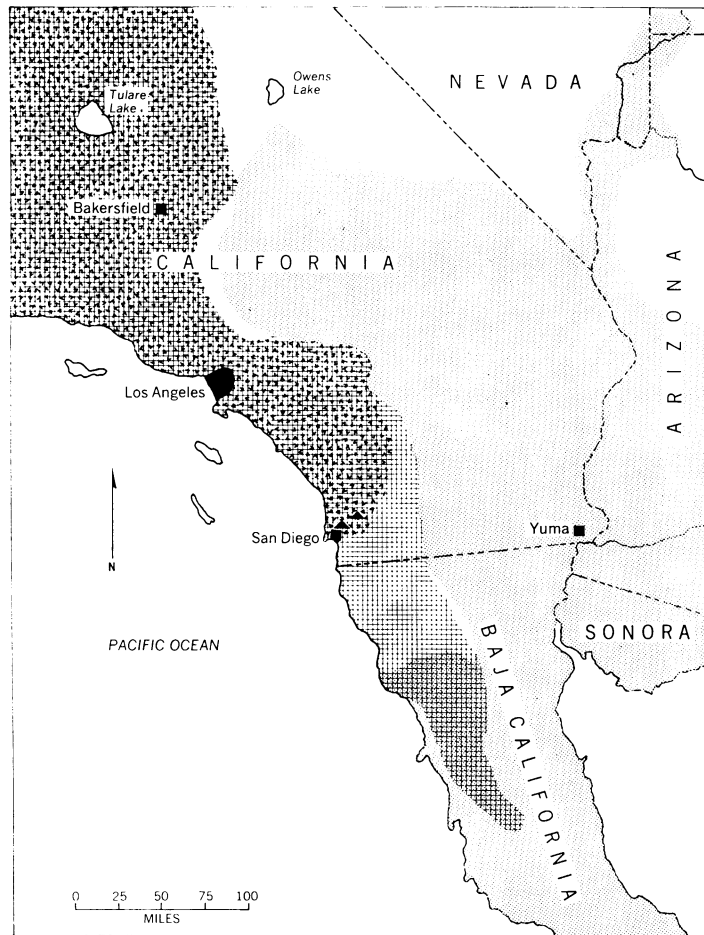


FIG. 2. Distribution of three woodpeckers in southwestern North America. Stippling denotes range of *Picoides scalaris*. V-shaped marks show area of sympatry of *P. nuttallii* and *P. pubescens* in California. Cross-hatching shows range of *P. nuttallii*. Triangles near San Diego mark localities of two hybrids of *P. nuttallii* \times *P. pubescens* (see text). Note that *nuttallii* and *scalaris* have complementary distributions except for overlap area in Baja California shown by stippling and cross-hatching.

ivers. North of there, coniferous forests predominate, and woodlands other than evergreen forest lack oaks. An exception is the Oregon Oakwoods (Küchler, *op. cit.*), which occupy a small area of south-central Oregon and contain but one species of oak, the Oregon white oak (*Quercus garryana*), but the Nuttall's Woodpecker does not inhabit this woodland. Faced with a lack of oak woods at the northern limit of its range, *nuttallii* might be expected to switch habitats and occur in riparian woodland. It does not, however, and the Downy Woodpecker instead

occupies riparian woodland in Oregon, and northward and eastward from there.

The Ladder-backed Woodpecker inhabits the desert regions of southwestern North America from western Oklahoma and Texas through southern New Mexico and Arizona to southwestern Utah, southern Nevada, and southeastern California. It occupies virtually all of Baja California. Within the United States its habitat includes the Chihuahuan and Sonoran deserts. It does not occur above the western fringes of the desert in California, where *nuttallii*

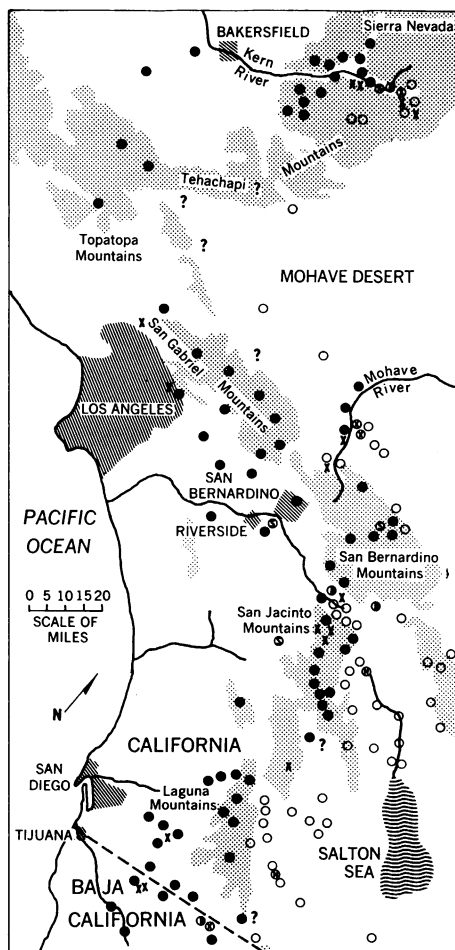


FIG. 3. Details of distribution of *P. nuttallii* and *P. scalaris* in California and northern Baja California (see fig. 2 for their general ranges). Localities for *nuttallii* are shown by darkened circles; those for *scalaris* by open circles. Half-black circles are localities where both occur together. Circles enclosing an X indicate hybrids, and an X without a circle indicates an introgressant or possible hybrid specimen. Records from outside normal ranges of the two species are shown by circles enclosing an S (*scalaris*) or N (*nuttallii*). Only records near possible area of contact between these species are shown (see also fig. 4). Descending lines indicate urban areas, and stippling denotes mountains. Irregular lines mark major streams.

replaces it, but in the absence of that species it occurs at higher elevations (up to 6000 feet) in the Little San Bernardino Mountains and the Argus Mountains (Grinnell and Miller, 1944).

In mainland Mexico it may breed up to or even above 7000 feet (Davis, 1965).

Within California, the Ladder-backed Woodpecker seems unable to invade the riparian habitats occupied by Nuttall's Woodpecker. Near Onyx, east of Kernville, the Ladder-back occurs adjacent to lush riparian willow-cottonwood vegetation (fig. 6). Occasional individuals enter this woodland, and hybridization has resulted. However, no pairs were found in the riparian trees, and the species was not observed in these trees during the breeding season. Rather, they occurred only in shrub desert dominated by Joshua trees (*Yucca brevifolia*; see fig. 7). The Mohave River Valley contains a rich, if somewhat discontinuous, cottonwood-willow woodland penetrating the desert to beyond 16 miles north of Victorville. Nuttall's Woodpeckers are common throughout the riparian vegetation, but no Ladder-backs were found. Sparse and low Joshua trees occur in the desert about the riparian woods near Victorville, but they are apparently insufficient to sustain a Ladder-back population. Ladder-backed Woodpeckers do occur within 3 miles east of the river, and the few hybrids taken near Victorville attest to the fact that Ladder-backs wander sporadically into the riparian woodland and occasionally mate with Nuttall's Woodpeckers. The presence of Nuttall's Woodpeckers seems to be the only reason for the absence of Ladder-backs in these riparian, desert-edge woodlands. Certainly, Ladder-backs of the same subspecies (*cactophilus*) inhabit such situations elsewhere to the east (Providence Mountains, Colorado River Valley, various places in Arizona), often abundantly (Colorado Valley, personal observ.).

The arid east slopes of the San Bernardino Mountains show a gradation from lowland Mohave Desert vegetation, including Joshua trees, to upland Pinyon-Juniper Woodland (actually here better termed Pinyon-Joshua Tree-Juniper Woodland; Küchler, 1964). Grinnell (1908) described the avifauna and the vegetation in these mountains. Joshua trees provide eminently suitable nesting sites for the Ladder-backed Woodpecker in surroundings often lacking any other trees of sufficient diameter to permit excavation of a nesting cavity. Somewhat to my surprise, I found Joshua trees not restricted to the Mohave Desert, but commonly occurring in the San Bernardino Mountains at elevations over 6000 feet, and occasionally to 7000 feet (as

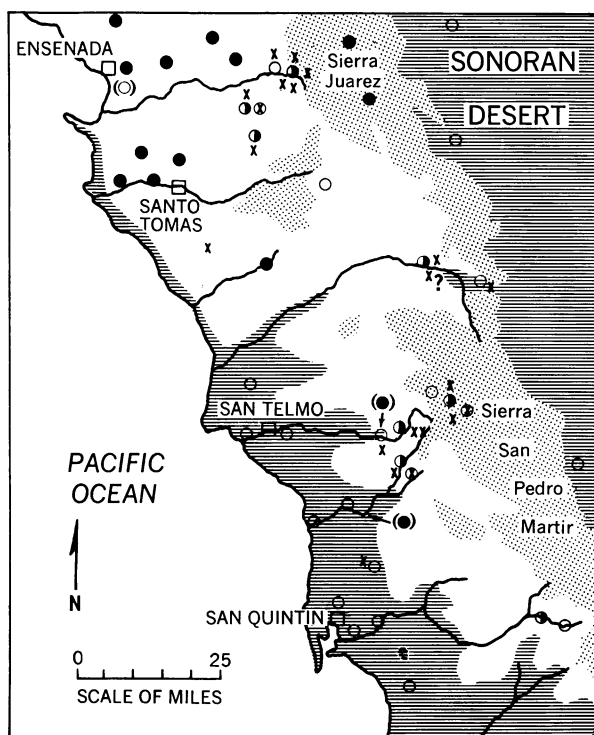


FIG. 4. Distribution of *P. nuttallii* and *P. scalaris* in northwestern Baja California. Occurrence of *nuttallii* is shown by darkened circles; that of *scalaris* by open circles. Half-black circles mark localities where both occur together. Circles enclosing an X indicate hybrids, and an X without a circle indicates an introgressant or possible hybrid specimen. Records from outside normal ranges of the two species are shown in parentheses. Towns are marked with squares, the Sonoran Desert by horizontal lines (its limits follow those of Short and Crossin, 1967); mountains over 3000 feet in elevation are stippled. Irregular lines mark major streams.

northwest of Rose Mine). Indeed, some of the finest specimens of Joshua trees (diameter to 91 cm.; estimated height 12 to 13 meters) I have seen were near their uppermost altitudinal limit. A diligent search of the pinyon-Joshua tree forests of the northeastern San Bernardino Mountains failed to disclose the presence of Ladder-backed Woodpeckers. A few Nuttall's Woodpeckers were encountered, mainly in pinyons, around Rattlesnake Mountain and Cactus Flat during November only. Woodpecker holes in trees in such areas were few, and could have been made by Flickers (*Colaptes auratus*), sapsuckers (*Sphyrapicus* sp.), Hair

Woodpeckers, or possibly even wintering Nuttall's Woodpeckers rather than Ladder-backed Woodpeckers. The uppermost elevation of occurrence of Ladder-backs coincided with the upper limit of pure stands of Joshua trees, and of the Cactus Wren (*Campylorhynchus brunneicapillus*), at Horsethief Flat (elevation about 4700 feet). Interestingly, the Ladder-back pair at this locality utilized scattered individual (about 12) sycamore and willow trees along a small stream, in addition to the Joshua trees (and associated vegetation), and scattered pinyons on the slopes above. This occurred in the absence of Nuttall's Woodpeckers (the nearest



FIG. 5. Oak woodland, habitat of Nuttall's Woodpeckers at Hastings Reservation, Carmel Valley in Central California.

individuals were found about 2 miles to the west, and about 1300 feet higher up in the mountains).

The western limit of the distribution of the Ladder-backed Woodpecker in southern California seems strongly influenced by at least: altitudinal factors, the birds occurring only in a few cases up to 5000 feet even when the habitat appears favorable and available; and, the presence of Nuttall's Woodpeckers in otherwise suitable riparian woodlands and perhaps in marginally suitable chaparral and oak woodland formations.

The ecological distribution of the Ladder-backed Woodpecker in Baja California differs somewhat from that in California. From the vicinity of Ensenada south to the Cape Region *scalaris* is found principally in the lush scrub-desert (Sonoran Desert) that comprises a vast portion of the peninsula. It occurs up to 5500 feet elevation in the Laguna Mountains at the southern end of the peninsula (Banks, 1967), but in the north it rarely reaches 4700 feet (Concepcion; Short and Crossin, 1967). Along the north-western coast, *scalaris* reaches its limit just north of the mouth of the Arroyo San Telmo in the region where larger agaves and yuccas diminish in the peculiar coastal scrub (succulent) desert. It seems likely that the species will be found to occur sparsely north to Punta Banda, just below

Ensenada (Short and Crossin, 1967). Continuous populations from the desert to the south feed into various arroyos north to the Arroyo San Telmo. North of there, grasslands, cultivated areas, and desert patches lacking large arborescent shrubs or trees occur in lower areas, and chaparral is found on the higher hills west of the granitic mass of the Sierra San Pedro Mártir. The Ladder-back does not occur in these habitats. However, small populations of this woodpecker are found in isolated riparian woods along various streams from Ojos Negros Valley southward along the western base of the mountains. In some such situations the Ladder-back occurs sympatrically with the Nuttall's Woodpecker, whereas in others one or the other of these species occurs allopatrically (see discussion elsewhere in this report, and also Short and Crossin, 1967). The occurrence of desert vegetation about some of these riparian woodlands, occupied by elements of the Sonoran Desert avifauna (Short and Crossin, *ibid.*), and their spotty distribution east of Ensenada and north of La Calentura Valley suggest that the desert may once have extended farther northward than it does at present.

There appears to be no barrier to the northward distribution of *P. scalaris* in Baja California, given its sympatry there with *P. nuttallii* unless: 1) their sympatry is very recent; and, or

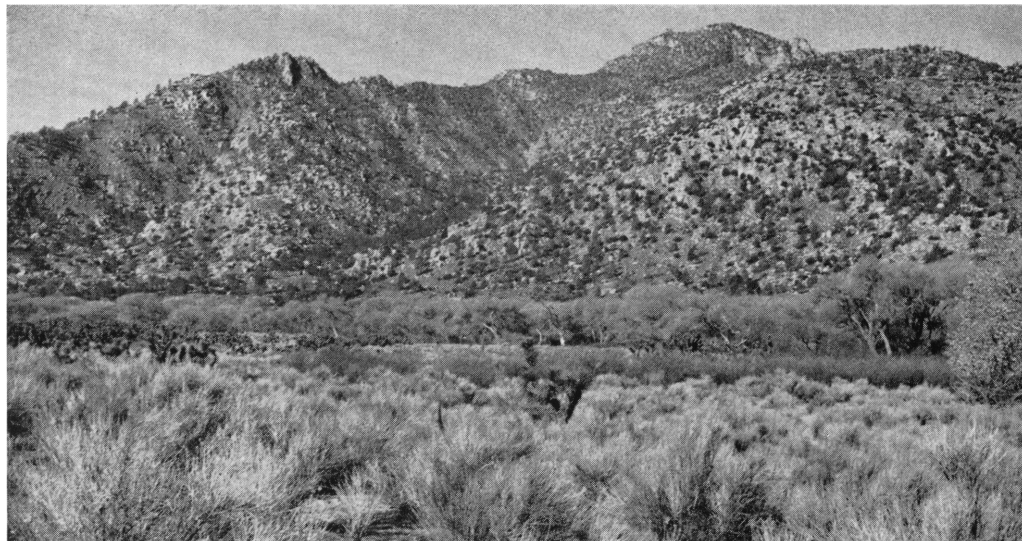


FIG. 6. Riparian habitat of Nuttall's Woodpeckers in sporadic contact with Ladder-backed Woodpeckers on South Fork of Kern River east of Onyx, California. Note approach of Joshua trees (left center) to riparian timber. Hybrid female A.M.N.H. No. 791507 was collected within $\frac{1}{4}$ mile of location. Photograph taken in November.

2) they are interacting and sympatry is possible only under certain conditions (e.g., the presence of some desert vegetation for foraging by *scalaris*) within the Sonoran Desert–Chaparral ecotone (Short and Crossin, 1967). Limiting the upward altitudinal occurrence of the Ladder-back may be a number of factors, perhaps including: 1) the prevalence of the Nuttall's Woodpecker in the chaparral, oak, and riparian woods within, and emanating from the Sierra San Pedro Mártir and the Sierra Juárez; 2) diminishing aridity and associated factors as one proceeds into the mountains from the west; and 3) the presence in the mountains of Hairy Woodpeckers, both in pine forest and, to a lesser extent, in riparian situations. The east slopes of the mountains lie in their rain shadow (Shreve, 1951) and they are very arid, perhaps providing too little vegetation for Ladder-backs except in a few ravines. At any rate the sparse population of Ladder-backed Woodpeckers limits their contact with the Nuttall's Woodpecker: also limited is the contact of *P. scalaris eremicus* with the more northern *P. s. cactophilus* (Short, 1968).

Mention must be made of the break between the Sierra Juárez and the Sierra San Pedro Mártir. The low area between these mountains (San Matias Pass) diminishes their rain shadow effect, and its low elevation (3200 feet) permits

the westward extension of a rather rich desert vegetation through the pass and westward down some 800 feet into the Valle de la Trinidad. This allows Ladder-backs to enter the valley from the east, and to make contact with Nuttall's Woodpeckers along the various streams bordering the valley to the north and south. Unfortunately the area has been highly modified by cultivation at its west end. Nevertheless, study of the Nuttall's–Ladder-backed woodpecker-contact in this area would be rewarding. I was prevented from doing work in the field there by a nearly disastrous late spring blizzard on April 14–15, 1967 that rutted the roads and dumped almost a foot of snow in the valley. I was unable to return later.

Picoides pubescens

DOWNY WOODPECKER

This species, familiar to Californians as the "Willow" Woodpecker, reaches the southern limit of its western North American range (see map, fig. 17, in Grinnell and Miller, 1944, p. 242) in San Diego County. Two hybrids of the Downy \times Nuttall's woodpeckers and two Downy Woodpeckers (now in the American Museum of Natural History) were obtained by Paul A. Dehnel during September and October, 1949, in the vicinity of San Diego (along the San Diego

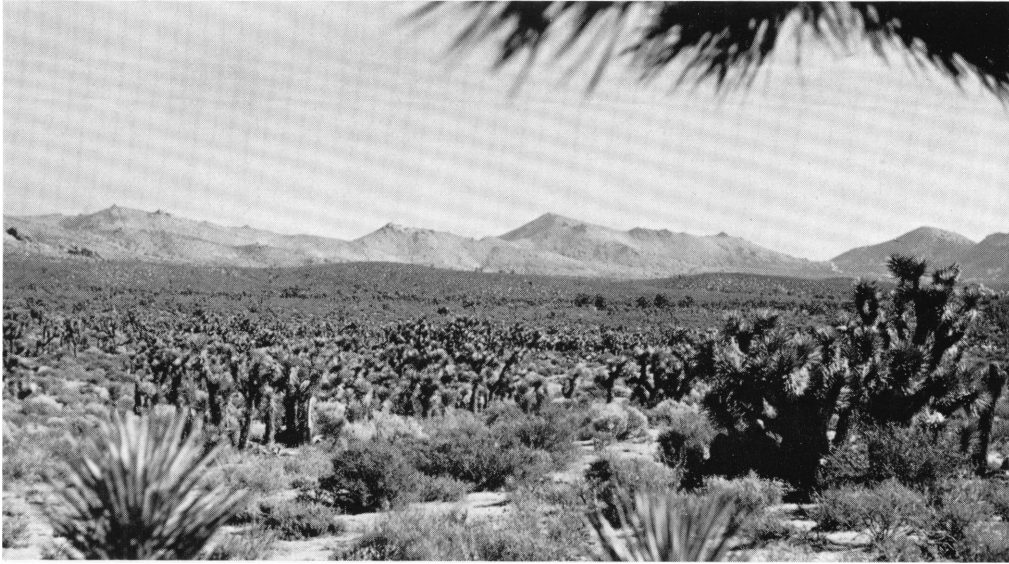


FIG. 7. Joshua tree desert, habitat of Ladder-backed Woodpeckers in Kelso Valley about 12 miles south of Weldon, California.

River at 2–3 miles northeast of Mission Fathers' Dam within San Diego, and along the same river at 2 miles northeast of Lakeside, just outside of San Diego). Although these could represent wandering, post-breeding birds, it is more likely that they were produced locally. Dehnelt also obtained 21 Nuttall's Woodpeckers from these two localities during the same period of time. Of the four more widely occurring species of *Picoides* discussed herein, the Downy Woodpecker is generally the least common even in its preferred habitat. Grinnell and Miller (1944, p. 243) aptly characterized the Downy Woodpecker as "markedly restricted to riparian softwoods, willow and cottonwood." In southern California this species is scarce in such situations west of the mountains, and is less able than the Hairy or Nuttall's woodpeckers to extend into apparently suitable habitat on the eastern side of the mountains. For example, I failed to find the Downy Woodpecker in extensive riparian woods southeast of Victorville, San Bernardino County, during November, 1966 and February, 1967, although both Hairy and Nuttall's woodpeckers occurred there (Grinnell and Miller, *op. cit.*, mentioned a specimen taken at Victorville; however, the species is now absent or decidedly uncommon there). The Downy Woodpecker apparently becomes more common north of the Los Angeles region. It occurs regularly and is

almost as common as the Hairy Woodpecker in riparian woodland along the South Fork Kern River near Weldon, Kern County. No individuals were observed away from riparian timber.

Picoides villosus

HAIRY WOODPECKER

This species occurs within and west of the nondesert mountains of southern California (see map, fig. 16 in Grinnell and Miller, 1944, p.239) and southward into northern Baja California. In the latter region it is found primarily in montane coniferous forests, and rarely occurs in riparian woodlands at lower elevations (the only record of its occurrence below an elevation of 4700 feet is that of a pair attempting to breed at San Jose, elevation 2200 feet, discussed by Short and Crossin, 1967, p. 292). As noted by Grinnell and Miller (*op. cit.*) the Hairy Woodpecker is principally a bird of higher elevations in southern California, but is prone to follow suitable habitat in the form of riparian woodland downward to lower elevations. Its habitats are diverse, including various types of coniferous forest, mixed forests, and riparian woodland. I have not observed this species in extensive stands of oaks, although it may occur sporadically in such woodlands. Occasionally I noted Hairy Woodpeckers in pinyon-Joshua tree woodland on the

eastern and northern slopes of the San Bernardino Mountains during November, 1966. I am uncertain whether it is this species or the Nuttall's Woodpecker that is responsible for widely scattered, small holes in Joshua trees in such pinyon-Joshua tree areas (e.g., at Cactus Flat, eastern San Bernardino Mountains). These holes may have been winter roosting sites of one or the other of these woodpeckers. The diversity of habitats utilized by Hairy Woodpeckers in both breeding and nonbreeding seasons enhances its dispersal and is doubtless partly responsible for its extensive range, although perhaps precluding its attaining the abundance of Nuttall's Woodpeckers in riparian woodland (where it is outnumbered by from 2 to 1 to as much as 5 to 1 by Nuttall's Woodpeckers) or White-headed Woodpeckers in high pine woodland. The additional presence of the Ladder-backed Woodpecker along with the Nuttall's Woodpecker in riparian woodlands of northwestern Baja California may limit further the downslope distribution of the Hairy Woodpecker at the southern end of its range. As elsewhere in its range (Arizona; Phillips, Marshall, and Monson, 1964; Mexico; Davis, 1965), the Hairy Woodpecker is essentially allopatric with the Ladder-backed Woodpecker, although they show an overlap in habitat preference (riparian woodland, as *scalaris* in northern Baja California and the Colorado River Valley and *villosus* in the South Fork Kern River Valley, valleys of the Great Plains, and elsewhere). The Hairy and Downy woodpeckers exhibit some ecological overlap in their broad area of sympatry in North America, but at the southern extreme of the range of the Downy in the West (southern California, Arizona) the latter becomes uncommon and is replaced in its preferred riparian habitat in lowlands by the Ladder-backed Woodpecker and the Nuttall's Woodpecker. It is significant that where the Nuttall's Woodpecker occurs in riparian woodland without the Ladder-back and

with few or no Downy Woodpeckers present, the Hairy also occupies this woodland, but where the Ladder-back occurs (with or without the Nuttall's Woodpecker) the Hairy is strictly an upland (usually coniferous forest) bird. However, in analyzing patterns of distribution one must not give undue weight to possible competitive exclusion as a causal factor. Although the Hairy Woodpecker becomes an upland bird precisely where the distribution of the Ladder-back commences, it remains so southward throughout Central America even where no other species of *Picoides* occur. The Flicker (*Colaptes auratus*), which has no close relatives in lowland Middle America, similarly becomes a highland bird in that region (Short, 1965a, p. 316). Indeed, as a group the New World species of *Picoides* are temperate zone birds. Only the xeric-adapted Ladder-back occurs in (dry) tropical areas, and therein perhaps is the key to the explanation of how *Picoides* traversed the Neotropics to reach temperate South America (*P. mixtus*, *P. lignarius*).

Picoides albolarvatus

WHITE-HEADED WOODPECKER

This species was observed commonly in the San Jacinto Mountains during November, 1966, but was not seen elsewhere. Its habitat has been noted by Grinnell and Miller (1944, pp. 246-248: see distributional map, fig. 18) as open coniferous forest, principally above 6000 feet. On November 12, eight individuals were observed 4 miles east of Kenworthy (elevation about 5800 feet) feeding in scattered, large Coulter pines (*Pinus coulteri*). Three Nuttall's Woodpeckers and a Hairy Woodpecker also were observed in the area; although they occasionally perched and even foraged in pines, their activities were confined to the vicinity of a stream bordered by low bushes, some deciduous trees, and open chaparral.

HYBRIDIZATION BETWEEN THE DOWNY AND NUTTALL'S WOODPECKERS

AMONG SPECIMENS EXAMINED in the collection of San Diego State College (specimens now in the American Museum of Natural History) were several Downy Woodpeckers and two peculiar, barred-back birds superficially the size of the Downy. These abnormal specimens proved to represent the second and third hybrids of *P. pubescens* × *P. nuttallii*, the first having been described by Ridgway (1887). Unfortunately the Ridgway specimen (U.S.N.M. No. 39456) is from an unknown locality; the "San Francisco" notation on the label could be more or less correct (both species occur in that vicinity), but the specimen may simply have been shipped to Ridgway from San Francisco after it was collected elsewhere in California. All three hybrids are shown in figures 8 and 9 (see also fig. 10).

DESCRIPTION OF THE HYBRIDS

The only previously known hybrid, the Nuttall's × Downy Woodpecker described by Ridgway (1887) is included in this discussion to complete the record. This male hybrid in characters is closest to *P. pubescens turati*, but its red nuchal patch and barred back are prominent *nuttallii*-like features (see tables 1 and 2). The facial and tail patterns and wing length are clearly intermediate. The bill (gonys) length tends to be intermediate. In other features the hybrid approaches or resembles *pubescens*.

The two female hybrids differ somewhat in their characteristics. A.M.N.H. No. 799792 resembles *pubescens* in its dark underparts, facial pattern, and narrow bill (tables 1 and 2), but is similar to *nuttallii* in tail pattern and in the extent of white in its wings. Its intermediacy is evident in most mensural characters, the small streaks on the sides, barring on the back (bars asymmetrical on lateral feathers, and barring restricted laterally on upper back), and the reduced barring on its secondaries. Hybrid A.M.N.H. No. 799790 resembles *P. pubescens* in bill width and tail barring, and resembles *P. nuttallii* in its wing-barring (including secondaries). This specimen is variously intermediate between the two species in other attributes. In bill length (gonys) it is intermediate, but

tends toward *pubescens*, whereas its wing and tail length are intermediate but approach *nuttallii*. Its face pattern is intermediate (auricular-nuchal connection almost obtains, and malar black with white traces). The pattern of the outermost rectrices is intermediate, as is the pale buff coloration of the breast, which grades into white both anteriorly and posteriorly. Other intermediate features are indicated in table 1.

Although information is lacking concerning the weight of the hybrids, their measurements (table 2) suggest that they are intermediate in size. Nuttall's Woodpeckers average about 50 per cent heavier (roughly 37 grams versus 25 grams) than southern California Downy Woodpeckers. The intermediacy of the hybrids in size is also suggested by simple comparison of the specimens (figs. 8 and 9), after allowing for differences in their preparation.

Observers in southern California should note carefully all Nuttall's and Downy woodpeckers, particularly where both occur together, to detect other hybrids of these species. The most useful characters for initial determination of such hybrids in the field are probably the combination of a barred back with restricted ventral markings and (perhaps) some buffy below. Other external features of hybrids are probably useful only when birds are in the hand, or in the unlikely event that both species can be observed and compared directly with a suspected hybrid.

DISCUSSION

The distribution and ecology of the Downy and Nuttall's woodpeckers, discussed above, suggest a pattern of replacement and ecological interaction between these species. The three instances of hybridization corroborate occurrence of this interaction, and suggest the very close relationship of these species. The Downy Woodpecker probably interacts similarly with the Ladder-backed Woodpecker. The latter species are virtually allopatric with narrow overlap in Texas and western Oklahoma, where they are more or less separated ecologically. Davis (1965, p. 558) stressed the probable interaction of *scalaris* and *pubescens* and invoked the absence

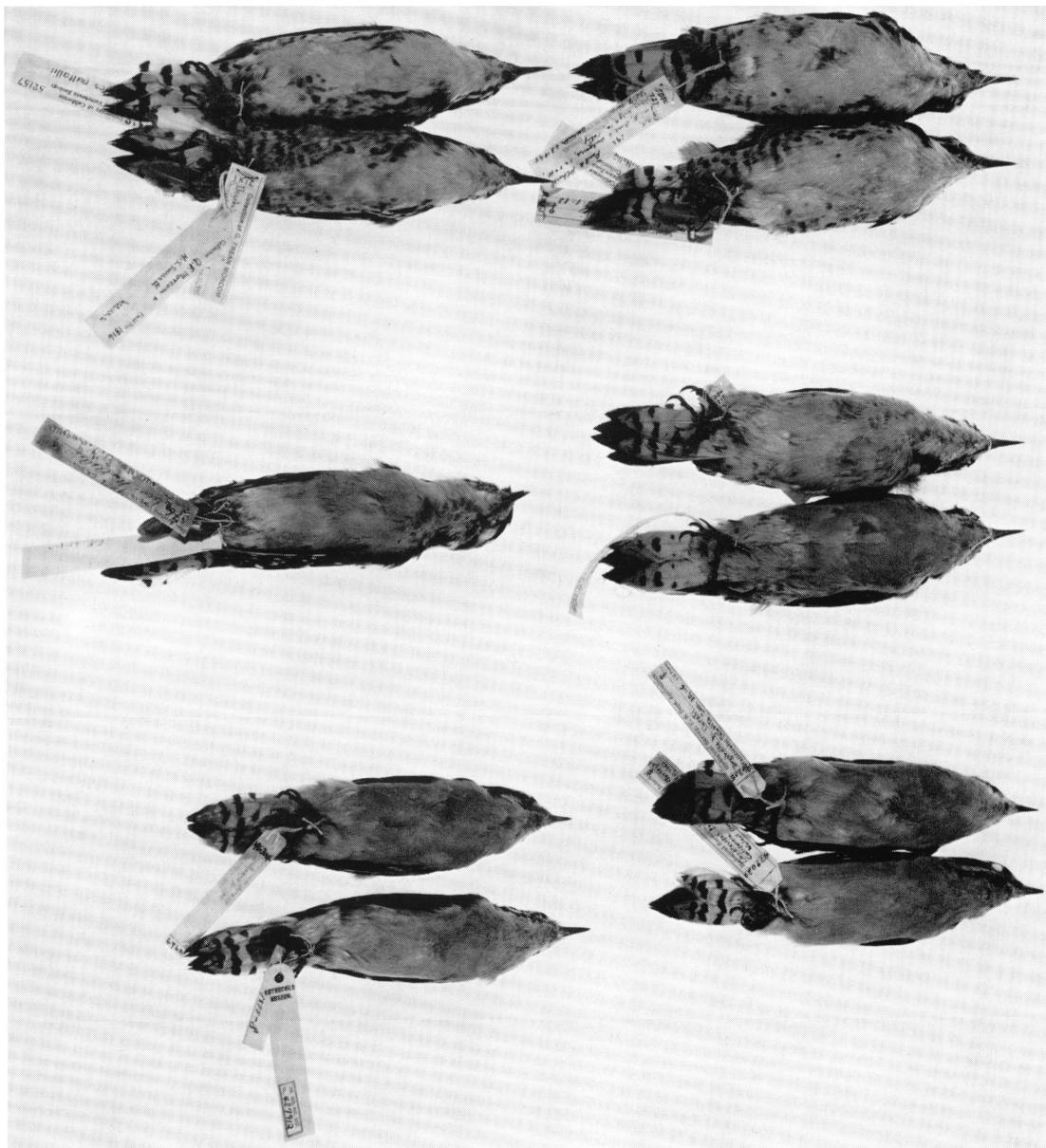


FIG. 8. Nuttall's Woodpeckers, Downy Woodpeckers, and their hybrids, ventral view. Birds at left are males, those at right females. Specimens of Nuttall's Woodpeckers, two of each sex, at top, hybrids in the middle, and two of each sex of Downy Woodpecker at bottom. Note particularly the condition of ventral markings, and over-all (dark versus white) coloration. Downy Woodpeckers are of the race *turati*. (See fig. 9 for dorsal view.)

of the latter species in Mexico as a factor in the much broader ecological distribution of *scalaris* there. I have noted that *nuttallii* tends to occur in riparian woodlands in southern California where *pubescens* diminishes in numbers. It must also be

emphasized that *scalaris* fails to occupy riparian situations in California where both *nuttallii* and *pubescens* frequent such habitat, but that it does inhabit (with *nuttallii* in some places) riparian woodland in northern Baja California, just south



FIG. 9. Nuttall's Woodpeckers, Downy Woodpeckers, and their hybrids, dorsal view. Same birds as figure 8. Birds at left are males, those at right females. Two of each sex of Nuttall's Woodpecker at top, hybrids in the middle, and two of each sex of Downy Woodpecker at bottom. Note particularly coloration of back (barred versus unbarred). Downy Woodpeckers are of the race *turati*.

of the range of *pubescens*, and riparian woodland in the desert region of Arizona where no other species of *Picoides* occurs.

The two recently collected hybrids were taken about 15 miles apart along the San Diego River, within two weeks of each other (September 17, October 1). I consider it possible, but not likely, that both were products of the same parents.

Two Downy and 21 Nuttall's woodpeckers were taken along the same river during September and October, 1949, by Paul Dehnel.

I was unable to study in this area in 1967, but various trips to San Diego County, and extensive field work in the foothills of the San Bernardino and San Jacinto mountains farther north failed to disclose any Downy Woodpeckers. This

TABLE 1

A COMPARISON OF SOME QUALITATIVE FEATURES OF *Picoides nuttallii*, *Picoides pubescens*, AND THEIR HYBRIDS

Character	<i>nuttallii</i>	Hybrid ♂	Hybrid ♀ No. 799792	Hybrid ♀ No. 799790	<i>pubescens</i> ^a
Nuchal patch	Broad, red in male; absent in female	Broad, red	Absent	Absent	Narrow, red in male; absent in female
Back color	Barred; black and white	Barred; black bars narrow	Barred; black bars narrow	Barred; black bars narrow	Unbarred; white
5th rectrix	1 complete bar	1 bar complete, 2nd nearly so	1 complete bar	2 complete bars	2 complete bars
6th rectrix	Mostly black	Mostly white	Mostly white; <i>nuttallii</i> pattern	Mostly black	Mostly white
Color below	White	Gray-buff wash	Gray-buff wash	Partial gray wash	Gray-buff wash
Markings below	Barlike spots on sides	Scattered fine spots	Several spots; bars	12 small spots on each side	Unmarked
Malar-auricular junction	Present	Almost connecting	Absent	Absent	Absent
Auricular-nuchal connection	Absent	Barely connecting	?	Almost connecting	Present
Malar patch	Black	Black and white	Black and white	Black; few white traces	Black and white

^a*Picoides pubescens turati* only.

TABLE 2

COMPARISON OF MEASUREMENTS (IN MILLIMETERS) OF *Picoides pubescens*, *Picoides nuttallii*, AND THEIR HYBRIDS^a

		Wing Length	Tail Length	Gonys Length	Bill Width
MALES					
<i>nuttallii</i>	Maximum	102.2	70.0	14.2	6.3
	Mean	101.63	67.58	13.31	5.86
	Minimum	99.7	64.7	12.0	5.7
Hybrid		95.3	59.3	12.7	5.1
	Maximum	93.3	59.2	12.1	5.4
	Mean	90.95	55.85	11.21	5.01
<i>pubescens turati</i>	Minimum	89.4	52.8	10.0	4.5
FEMALES					
<i>nuttallii</i>	Maximum	104.5	71.9	13.7	5.9
	Mean	102.60	68.89	13.13	5.61
	Minimum	100.7	66.2	12.8	5.4
Hybrid No. 799790		98.0	65.1	11.7	4.9
Hybrid No. 799792		95.4	63.6	11.6	4.8
<i>pubescens turati</i>	Maximum	92.4	61.1	11.2	5.0
	Mean	90.92	58.49	10.62	4.78
	Minimum	89.4	55.1	10.4	4.3

^aSamples include 10 males and nine females of *nuttallii*, taken in the fall near San Diego, California (whence came the hybrids), and 15 males and 10 females of *P. pubescens turati* taken in the fall and early winter in central and southern California.

species is unreported from Baja California (and all of Mexico). It seems clear that Downy Woodpeckers are only of sporadic occurrence in California south of Los Angeles and west of the mountains, and that in this region they are far outnumbered by Nuttall's Woodpeckers. Such circumstances are favorable for the occasional occurrence of mixed matings, such as those (or that) which produced the two hybrids.

The hybrids may be regarded as F_1 individuals. It is unknown whether such hybrids are fertile and can backcross with one, the other, or both parental species. The combination of characters in the hybrids, their general inter-

mediacy, and lack of indications of introgression in samples of Downy and Nuttall's woodpeckers, corroborate the view that the hybrids represent F_1 individuals, despite some variation among them. Little can be said regarding the genetics of the various features by which the two species differ, because of the small number of hybrids and their variability. It appears that most of their traits are controlled by multiple genetic factors. The hybrids suggest that genes responsible for the back-barring of *nuttallii* are generally dominant to those responsible for the white back of *pubescens*.

HYBRIDIZATION BETWEEN NUTTALL'S AND LADDER-BACKED WOODPECKERS

THE MORPHOLOGICAL ANALYSIS of hybridization between *P. nuttallii* and *P. scalaris* was difficult because of the generally close resemblance of these species and their great variability. Two morphologically distinct forms of *P. scalaris* meet and hybridize with *P. nuttallii*, and each interacts differently with the latter. Additional problems result from wear, fading, and plumage discoloration, all of which especially seem to affect the plumages of these woodpeckers. As a consequence of these difficulties it proved impossible to establish a "hybrid index" or character index (see Short, 1965a) to treat effectively the various color and mensural patterns of these species in all areas of contact and hybridization. My treatment of the morphology of hybrids and possible hybrid and introgressant individuals is admittedly subjective, but I have endeavored to evaluate each feature and the sum of the features of every individual before designating a specimen as a "hybrid." If I have erred in rendering determinations, the error is apt to be an understatement of the occurrence and effects of hybridization, for I have chosen standards that might minimize, but could not exaggerate the actual occurrence of interbreeding. One of the hybrids is illustrated with the parental species in figure 10. The differences between *nuttallii* and *scalaris* are also shown in figure 1 and summarized in table 3.

INDIVIDUAL VARIATION

The various categories of individual variation (Mayr, 1942, 1963) include age, sexual, and seasonal variation. I do not propose to discuss diverse details of age variation, for I treat herein only adult birds. However, a few points are worthy of consideration. Juveniles of both *P. nuttallii* and *P. scalaris* differ from the adults in the distribution of red on their heads. Juvenal males of both species have the entire crown covered with broadly red-tipped feathers with white central spots; their napes are black, however. This pattern is essentially that of adult males of *P. scalaris*, but without their red nuchal patch. Thus, in contrast to adult males, juvenal males of the two species are alike in their pattern

of red head coloration. Juvenal females of both species differ from adult females in possessing a red crown patch. This patch is restricted to the center of the crown. The rear of the crown is black, like the nape, forming a larger black area than is present in juvenal males. The anterior crown is black spotted with white in juvenal females. The red crown patch of juvenal females of *nuttallii* tends to be smaller than is that of *scalaris*. Despite some variation in extent of this patch, the sexes of birds in the juvenal plumage usually can be distinguished in both species. The major effects of the distribution of red coloration on the heads of these birds are: less

TABLE 3
SUMMARY OF DIFFERENCES BETWEEN
Picoides nuttallii AND *Picoides scalaris*^a

Character	<i>nuttallii</i>	<i>scalaris</i>
Male crown	Black (may have white spots)	Red spots on white spotting ^b
Nasal tufts	White, contrasting with crown ^b	Dusky, grading with crown
Malar stripe	Black	Black and white
Ear coverts	Broad; black	Narrow; black
Sides of neck	Broad, black angular mark, connects with back	Narrow black area; no connection
Eye stripe	Narrow white	Broad white
Wings	Blackish; less spotted	More spotted and barred; whiter
Upper back	Black	Black and white barred
Back	Barred; black bars broader	Barred; white and black bars equal
Outer tail	Bars few, at tip only	Fully or mainly barred
Rectrix 6	Mainly black; unbarred	Mainly white; barred with black
Ventral color	White ^b	Buffy ^b
Sides of breast	Large bar-spots	Smaller, fine spots
Bill	Short	Longer

^aSee text for variation and details.

^bEspecially subject to wear, discoloration, or other modifying factors.

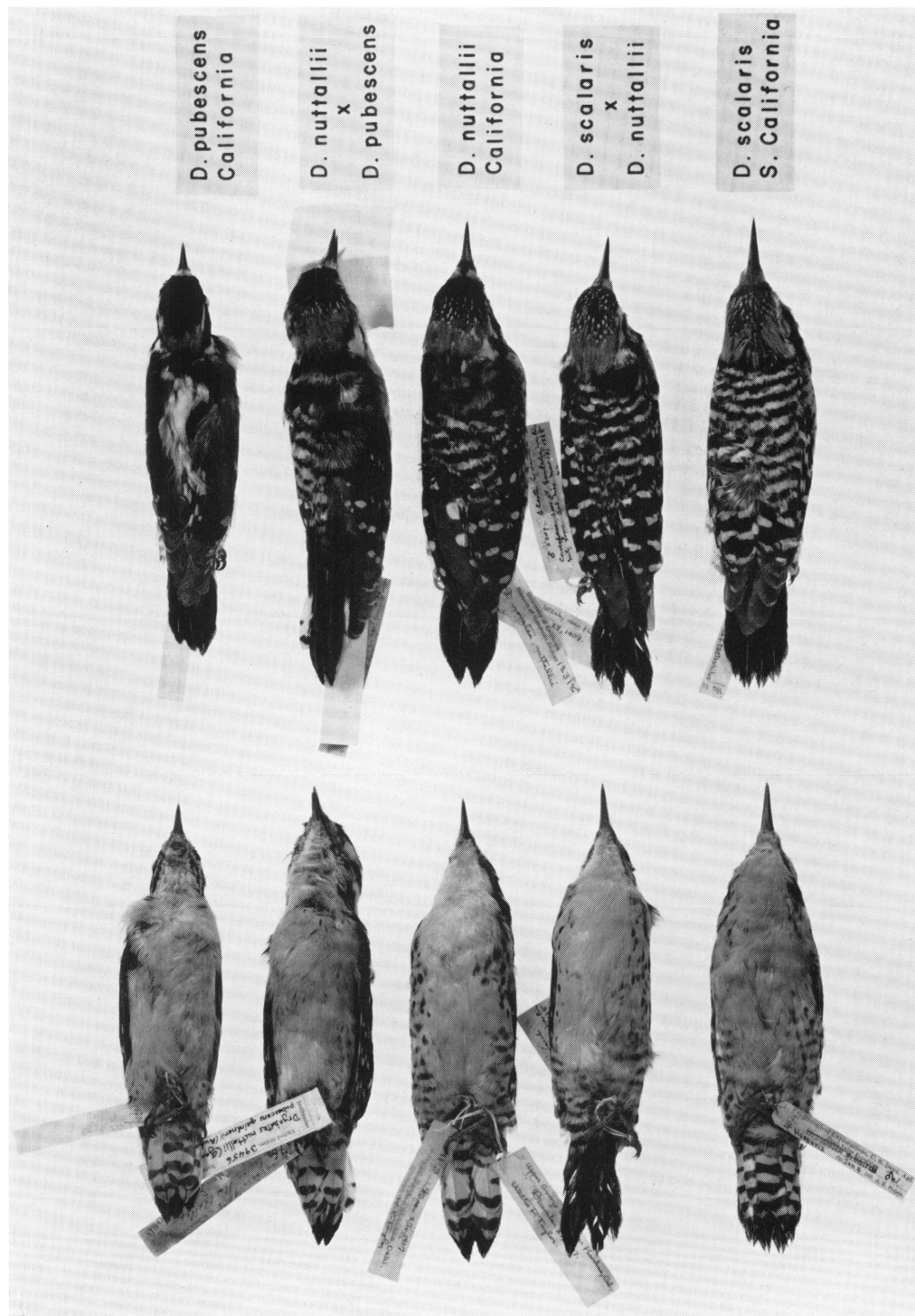


FIG. 10. Three species of woodpeckers and their hybrids. Shown are male woodpeckers in dorsal view (right) and ventral view (left). All birds are from California. Note particularly over-all coloration and markings in ventral view, and color and barring in dorsal view. Variable extent of red on crown and nape is visible in dorsal view, red appears as pale gray. Also note gradation in bill size from *pubescens* through the hybrids and *nuttallii* to *scalaris*.

difference between the species in juvenal compared with adult plumages because of the similarity of patterns of the juvenal males; and, within each species the juvenal male and female and adult male and female plumages are rendered distinct. Pattern differences suggest that these woodpeckers may discriminate between sexes and between age groups. The juvenal crown pattern is retained for about two months following fledging.

Although the juvenal plumage is otherwise very similar to the adult plumage, certain minor differences render juveniles of the two species more alike than are adults. Juveniles of the Nuttall's Woodpecker are tinged with buffy and grayish ventrally, unlike the clear white underparts of the adults. Thus they appear rather like Ladder-backed Woodpeckers in this respect. Traces of the dusky-tinged white of the underparts also are found in the nasal tufts of *nutallii* juveniles. This fact, and the spotting of the forehead running into the nasal tuft area, make the nasal tufts less sharply set off from the crown in *nutallii* juveniles, so that their nasal tufts approach those of *scalaris* in color. Otherwise, juveniles are colored like adults but have the usual (in woodpeckers) softer, fluffier plumage and duller, browner color of areas pigmented by melanins.

SEXUAL VARIATION

Differences in color between juvenal males and females are noted above. Adult females differ from males by lacking the red nuchal (*nutallii*) or nuchal-crown patch (*scalaris*) of males. Average differences between the sexes in color characters utilized in the analysis of hybridization are discussed below. Males of both species are larger, with generally greater meas-

urements (tables 4-9; see also Short, 1968, pp. 2-4) than females, as is the case in woodpeckers. One exception to this generalization is that females of *nutallii* tend to have longer tails than have males. This instance of reversal in a sexually dimorphic feature actually is not uncommon among woodpeckers as I have noted elsewhere (Short, 1970b). Other than the reversal of the sexes in tail length, the major features of sexual variation are the rather large bill length difference (more pronounced in *scalaris*), and the size (weight) difference in *scalaris*.

As shown in table 4, weights in the sexes of the Nuttall's Woodpecker are nearly alike. Males average from one-half to one-and-one-half grams heavier than females. Weights of males and females so closely approximate each other that samples of females from mated pairs, even excluding females with very large ova, may average heavier than their mates. On the contrary, male Ladder-backed Woodpeckers are considerably heavier than females and only occasionally does a breeding female with large ova or an egg in the oviduct outweigh its mate. The relatively limited data from 67 Nuttall's Woodpeckers and 37 Ladder-backed Woodpeckers indicate that males of the two species (only southwestern *scalaris*) weigh about the same; and that females of Nuttall's average only about a gram lighter than males, whereas female Ladder-backed Woodpeckers are considerably (about one-eighth) lighter than males of both species and female Nuttall's Woodpeckers. The difference in weight between the sexes of Ladder-backed Woodpeckers parallels their difference in bill length, and greatly exceeds the rather small wing length difference (table 4) between them. The data in table 4 suggest that Selander and Giller (1963, pp. 261, 263) have placed undue

TABLE 4
PERCENTAGES BY WHICH MALES EXCEED (+) OR FALL SHORT (—) OF FEMALES
IN VARIOUS MENSURAL CHARACTERS^a

Form	Weight	Wing	Tail	Gonys	Tarsus	Bill Width
<i>nutallii</i>	+2%	+0.5%	−1.5%	+10%	+5%	+2.4%
<i>s. cactophilus</i>	+16%	+2.5%	+0.8%	+15% ^b	+4%	+7%
<i>s. eremicus</i>	+10%	+2.7%	+1.5%	+13% ^b	+4%	+3%

^aPercentages were obtained by dividing mean difference between sexes by lesser mean (usually female mean), and averaging percentages obtained for various samples of each form.

^bFor comparison, the value for *P. s. lucasani* is +18%.

TABLE 5
NONOVERLAP OF BILL LENGTH (GONYS) BETWEEN SEXES OF THREE WOODPECKERS

Form	Total Range (mm.)	Range Nonoverlap %	Individual Nonoverlap %	Coefficient of Difference ^a	Joint Nonoverlap ^a %
<i>P. pubescens turati</i>	2.6	30	8	0.36	—
<i>P. nuttallii</i>					
Northern California	4.3	39	15	0.93	82
Southern California I	4.2	44	14	1.21	89
Southern California II	3.7	28	8	0.84	80
Baja California	4.9	50	15	0.83	80
<i>P. scalaris</i>					
<i>eremicus</i> (S)	5.7	60	49	0.96	83
<i>eremicus</i> (N)	5.0	73	71	0.88	81
<i>cactophilus</i> (E)	6.0	75	64	1.29	90
<i>cactophilus</i> (W-A)	6.0	85	84	1.53	94
<i>cactophilus</i> (W-B)	6.7	85	74	1.50	93
<i>lucasanus</i>	5.6	76	79	1.81	97

^aSee Mayr (1969, p. 190); samples used for these two columns are from December–March.

Symbols: I, area away from contact with *scalaris*; II, area in proximity to contact with *scalaris*; (A), western southern California; (B), Colorado River Valley; (S), (N), (E), (W), compass directions. Nonoverlap indicated is minimal because samples were drawn from all seasons (see text).

TABLE 6
SEASONAL MEAN VARIATION IN THREE MENSURAL FEATURES OF MALE WOODPECKERS^a
(Measurements are in Millimeters)

Form	Aug.–Nov.	Dec.–March ^b	April–July ^b	Per cent Change ^b
WING LENGTH				
Northern <i>nuttallii</i>	103.12	—1.63	—0.37	—1.9
Southern <i>nuttallii</i>	102.20	—0.30	(+0.01)	—0.3
<i>s. cactophilus</i> A	106.28	—0.71	—0.68	—1.3
<i>s. cactophilus</i> B	102.45	(+0.69)	—0.71	—0.7
<i>s. eremicus</i>	105.42	—0.18	—1.16	—1.3
TAIL LENGTH				
Northern <i>nuttallii</i>	66.12	—0.91	—1.47	—3.6
Southern <i>nuttallii</i>	66.05	—0.63	—0.72	—2.0
<i>s. cactophilus</i> A	65.40	—0.66	—0.88	—2.4
<i>s. cactophilus</i> B	62.58	—0.81	—1.65	—3.9
<i>s. eremicus</i>	70.40	—0.71	—1.56	—3.2
GONYS				
Northern <i>nuttallii</i>	13.68	+0.09	+0.29	+2.8
Southern <i>nuttallii</i>	13.70	+0.13	+0.33	+3.4
<i>s. cactophilus</i> A	16.31	+0.37	+0.13	+3.1
<i>s. cactophilus</i> B	14.82	+0.09	+0.50	+3.9
<i>s. eremicus</i>	17.86	—0.13	—0.52	—3.6

^aSample sizes 8 (*eremicus*) or more.

^bChanges in mean are indicated, with their direction (+, —), from column to column, whereas per cent column indicates over-all change from August–November to April–July.

Symbols: A, southern California (excluding Colorado River area) sample; B, Arizona sample.

TABLE 7
SEASONAL MEAN VARIATION IN THREE MENSURAL FEATURES OF FEMALE WOODPECKERS^a
(Measurements are in Millimeters)

Form	Aug.-Nov.	Dec.-Mar. ^b	April-July ^b	Per cent Change ^b
WING LENGTH				
Northern <i>nutallii</i>	101.78	-0.27	-0.34	-0.6
Southern <i>nutallii</i>	102.02	-0.14	-0.58	-0.7
<i>s. cactophilus</i> A	103.18	(+0.13)	-1.23	-1.2
<i>s. cactophilus</i> B	101.43	-0.84	-0.34	-1.2
<i>s. eremicus</i>	102.39	(+0.04)	-0.59	-0.6
TAIL LENGTH				
Northern <i>nutallii</i>	66.51	-0.66	-1.26	-2.9
Southern <i>nutallii</i>	67.33	-0.63	-1.16	-2.7
<i>s. cactophilus</i> A	—	64.21	-1.72	(-2.6)
<i>s. cactophilus</i> B	62.35	-0.73	-1.25	-3.2
<i>s. eremicus</i>	68.28	(+0.28)	-0.95	-1.4
GONYS				
Northern <i>nutallii</i>	12.53	+0.04	+0.64	+5.4
Southern <i>nutallii</i>	12.99	(-0.43)	+0.14	+1.0
<i>s. cactophilus</i> A	14.70	-0.26	-0.07	-2.2
<i>s. cactophilus</i> B	12.64	+0.28	+0.16	+3.5
<i>s. eremicus</i>	15.51	+0.31	(-0.04)	+1.7

^aSample sizes 8 (*eremicus*) or more.

^bChanges in mean are indicated, with their direction (+, -), from column to column, whereas per cent column indicates over-all change from August-November to April-July.

Symbols: A, southern California (excluding Colorado River area) sample; B, Arizona sample.

emphasis on sexual dimorphism in bill length of *P. scalaris*. Rather than having a disproportionately shorter bill, the small females of this species actually have, for their size (as indicated by weight), disproportionately longer wings, legs, and tail. This is discussed below.

Female Nuttall's Woodpeckers have, on the average, longer tails than do males. Tails of the female Ladder-backed Woodpeckers closely approach in length those of the male, despite the considerably smaller size of the female. The tail length difference between the sexes in *nutallii* is small, but significant (Short, 1970b), especially considering the slightly smaller size of the females. The wings, tarsi, and bill width of female Ladder-backed Woodpeckers are shorter in relation to those of the male than is the tail of females. Within southwestern *scalaris*, the average tail length of females particularly approached or exceeded that of males in several April to July samples. The sexes appear to exhibit differential wear during the year, probably correlated with their feeding habits (see discussion below).

Data for bill length (gonys) are presented in tables 8 and 9 (*nutallii*), in figure 11, and in Short (1968; *scalaris*); they are summarized with

regard to sexual differences in tables 4 and 5. Female Nuttall's Woodpeckers tend to have shorter and slightly narrower bills than do males. In this species the relative sexual difference in bill length far exceeds that observed for weight, wing length, tail length, bill width, and tarsal length. The difference is greater in the Ladder-backed Woodpecker, although it roughly corresponds to the size difference between the sexes as indicated by their weights. The non-overlap between the sexes is shown for various samples in table 5. The range of variation for each sex is about the same in the two species. However, the total (both sexes combined) range of variation in length of gonys of *scalaris* is greater, because the sexes show less overlap. Various measures of nonoverlap are provided in the table, including the Coefficient of Difference and its corresponding Joint Nonoverlap (from Mayr, 1969, p. 190), the nonoverlap in range (i.e., the proportion of the total range comprised of the ranges of both sexes combined that fall outside their range of overlap), and the actual nonoverlap of individuals (i.e., that proportion of the total individuals of both sexes combined that fall outside their range of overlap).

TABLE 8
ANALYSIS OF MEASUREMENTS (IN MILLIMETERS) OF MALE NUTTALL'S WOODPECKERS
TAKEN FROM DECEMBER THROUGH MARCH

Sample	Mean ± 2 SE ^a	Range	SD ^a	N
WING LENGTH				
Northern California	101.49 \pm 0.48	97.1–106.5	1.75	54
Southern California A	101.90 \pm 0.60	98.5–105.2	1.72	32
Southern California B	102.71 \pm 0.48	98.8–106.0	1.75	52
Baja California	101.73 \pm 0.99	99.9–104.1	1.40	8
TAIL LENGTH				
Northern California	65.21 \pm 0.54	61.6–70.0	1.85	48
Southern California A	65.42 \pm 0.74	62.1–70.8	2.05	31
Southern California B	65.81 \pm 0.55	60.8–70.2	1.97	51
Baja California	66.04 \pm 1.20	63.5–68.7	1.71	8
BILL LENGTH (GONYS)				
Northern California	13.77 \pm 0.18	12.3–14.9	0.62	51
Southern California A	13.83 \pm 0.21	12.9–15.0	0.58	32
Southern California B	13.87 \pm 0.16	12.1–15.0	0.59	51
Baja California	13.90 \pm 0.28	13.3–14.5	0.40	8
BILL WIDTH				
Northern California	5.98 \pm 0.12	5.1–6.8	0.43	49
Southern California A	5.83 \pm 0.14	5.1–6.5	0.37	26
Southern California B	5.87 \pm 0.11	5.1–6.7	0.40	46
Baja California	6.03 \pm 0.20	5.7–6.5	0.29	8
BACK BAR DEPTH ^b				
Northern California	4.92 \pm 0.14	3.2–6.7	0.69	101
Southern California A	5.25 \pm 0.16	4.0–7.0	0.64	65
Southern California B	5.19 \pm 0.14	3.8–7.0	0.72	91
Baja California	5.10 \pm 0.21	3.6–6.6	0.71	46

^aSE indicates standard error of the mean; SD, standard deviation from the mean.

^bBirds taken throughout the year.

Symbols: A, samples from southern California representing birds from areas away from *P. scalaris* range; B, samples from California representing birds from areas near *P. scalaris* range.

The first mentioned of these measures is based on the mean difference between the sexes divided by their combined standard deviations: it roughly indicates (Joint Nonoverlap column) the proportion of individuals of each sex which do not overlap in bill length a like proportion of individuals of the other sex. The other two measures indicate absolute nonoverlap of individuals, or of the range. It is clear from these data that the sexes of the Ladder-backed Woodpecker overlap in bill length much less than do the sexes of the Nuttall's Woodpecker. Total nonoverlap of the sexes, and of the two species may prevail at localities within the region of sympatry, at least during March and April. Data from April specimens representing two localities in northern Baja California where these species occur together are as follows: female *nuttallii* (N=5)—12.4 to 13.2 mm.; male

nuttallii (N=3)—13.5 to 14.4 mm.; female *scalaris* (N=4)—15.5 to 16.4 mm.; and male *scalaris* (N=6)—17.2 to 18.6 mm. The bill length difference between individuals of 10 mated pairs of *nuttallii* collected in March and April averaged 1.36 mm.; males were longer-billed in nine instances and the bill of one female equaled that of her mate. Six mated males of *scalaris* taken in the same months exceeded their mates in bill length by an average of 2.93 mm.

Thus the sexes of Nuttall's Woodpecker differ little in weight and wing length, females have slightly longer tails than those of males, and males have a somewhat wider bill, longer tarsi, and a considerably longer bill than do females. Because of their longer tail and slightly shorter wings the tail/wing ratio is greater (by about 1 per cent) in females than in males. Female Ladder-backed Woodpeckers, varying some-

TABLE 9
ANALYSIS OF MEASUREMENTS (IN MILLIMETERS) OF FEMALE NUTTALL'S WOODPECKERS
TAKEN FROM DECEMBER THROUGH MARCH

Sample	Mean \pm 2 SE ^a	Range	SD ^a	N
WING LENGTH				
Northern California	101.51 \pm 0.58	97.0–107.2	1.96	46
Southern California A	101.37 \pm 0.76	98.0–104.5	2.14	32
Southern California B	102.17 \pm 0.56	98.7–106.4	1.94	47
TAIL LENGTH				
Northern California	65.85 \pm 0.70	60.0–71.1	2.35	45
Southern California A	66.60 \pm 0.86	63.0–72.3	2.45	32
Southern California B	66.88 \pm 0.60	61.2–70.3	2.02	45
BILL LENGTH (GONYS)				
Northern California	12.57 \pm 0.20	11.0–13.9	0.67	45
Southern California A	12.56 \pm 0.16	11.5–13.4	0.47	31
Southern California B	12.95 \pm 0.15	11.7–14.2	0.52	46
BILL WIDTH				
Northern California	5.70 \pm 0.12	4.8–6.6	0.39	44
Southern California A	5.72 \pm 0.16	5.0–6.5	0.43	27
Southern California B	5.88 \pm 0.13	4.9–6.7	0.46	46
BACK BAR DEPTH ^b				
Northern California	4.90 \pm 0.16	3.5–6.2	0.64	59
Southern California A	4.89 \pm 0.16	3.8–6.8	0.63	62
Southern California B	4.89 \pm 0.13	3.6–6.6	0.60	82
Baja California	4.69 \pm 0.20	3.8–5.9	0.59	35

^aSE indicates standard error of the mean; SD, standard deviation from the mean.

^bBirds taken throughout the year.

Symbols: A, samples from southern California representing birds from areas away from *P. scalaris* range; B, samples from California representing birds from areas near *P. scalaris* range.

what with the race involved, have a slightly shorter tail, shorter wings, moderately shorter tarsi, a narrower bill, a much shorter bill, and they weigh considerably less than do males. The tail/wing ratio in *scalaris* is about the same in both sexes, with female samples averaging slightly greater ratios.

SEASONAL VARIATION

Seasonal variation involves the effects of molt, wear, discoloration, and growth. Plumage areas or features the colors of which are particularly affected include back barring, the underparts, and facial region. Occasional individuals have apparently "bleached" out parts of the black areas of the plumage, as the tail, or part or all of the back. Whether this is the result of a deficiency in pigment production, contamination of the plumage by some material in the environment, or a combination of these and the action of sunlight is unknown. Discoloration of the

underparts and especially the face occurs in many cases especially in spring birds. Occasionally the nasal tufts of *nuttallii*, which are usually white, are so discolored as to look like the brownish white nasal tufts of *scalaris*. I have noted such tendencies in birds collected as they were feeding amid cottonwood buds in the spring. Discoloration of the underparts and facial region may be caused by fluids from freshly excavated holes. This discoloration is most notable in spring and summer birds.

Wear greatly affects the appearance of the birds. Late spring and early summer individuals exhibit a frayed and bedraggled plumage. The strongly contrasting white and black *nuttallii* seems less affected by wear than is *scalaris*. In fact, by virtue of the presence of a dusky brown edging of the flank feathers in fresh plumage, Nuttall's Woodpeckers actually look "dirtier" in the fall and more distinctly white ventrally and on their faces later in the winter and spring. In fresh plumage the Ladder-backed Woodpecker

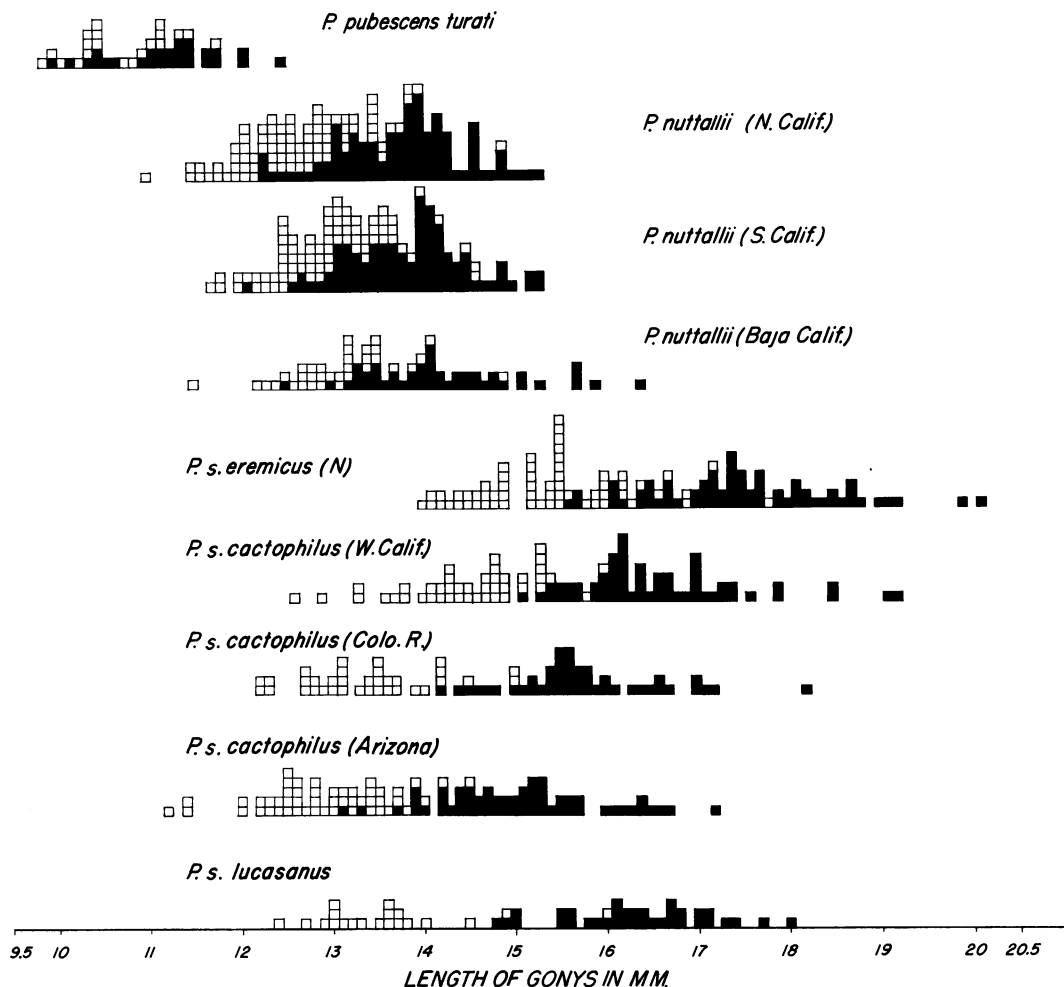


FIG. 11. Histogram of bill length (gonys) in three species of southwestern woodpeckers. Each black square denotes a male, each open square a female. Note variation within samples and overlap between samples of sympatric populations (i.e., *P. pubescens turati* and *P. nuttallii* from California; and *P. s. eremicus* and *P. nuttallii* from Baja California). Overlap between, and variation within, samples is at a maximum because adult specimens taken throughout the year are included (see seasonal variation discussion in text).

is buffy white, rather than white on its face and underparts. As a result of wear plus the effect of fading, this species becomes whiter below from fall to spring. However, discolorations frequently replace the dusky tone so that the spring birds do not appear white, or else the underparts have a blotched white and dusky appearance in late spring. In both species wear of the back feathers causes reduction of the broad white terminal bar (there is actually a very narrow, terminal black bar, which, however, is rapidly lost in fresh-plumaged birds). As a result, these woodpeckers gradually appear

blackier dorsally through the year, and blackest in their most worn plumage of June and July.

The color of the crown is severely affected by wear, perhaps especially during the excavating of nesting or roosting cavities. Those females of both species that have white-spotted crowns (fresh-plumaged adults, especially of *nuttallii*, often have at least a trace of crown spotting) tend to lose this spotting. Only those with very large spots still have them by spring. Males of *nuttallii*, too, often have white spotting on the black forecrown, and this spotting diminishes with wear during the year. Most severely

affected are the crowns of male Ladder-backed Woodpeckers. In fresh fall plumage males appear to have a fully red crown and nape. Actually, the nape region and areas lateral and anterior to it extending forward over the eyes have black-based, broadly red-tipped feathers, whereas the main portion of the anterior crown has black-based feathers with angular white spots at their centers and narrow red tips. Through wear, the red tips become narrower in depth; the barbs in this part of the feathers seem to wear rapidly, so that the red is restricted to the shaft. Greater wear may altogether eliminate the red tips, so that the forecrown is black spotted with white. Such worn birds may have but a ring of nuchal red actually narrower than the nuchal band of male Nuttall's Woodpeckers.

Other effects of wear will be noted in the discussion of characters involved in hybridization.

Seasonal variation in some mensural characters is presented in tables 6 and 7. It is clear that owing to wear the wings and tail diminish in length, especially in the late spring (breeding period). A noteworthy fact is that the tail wears proportionally more than do the wings, a fact responsible for a lessening of the tail/wing ratio throughout the year in both sexes of both species. Also, particularly in *scalaris*, the tail of males appears to wear more than that of females. This is especially true of *P. s. cactophilus* from Arizona, for late spring females of that population frequently exceed males in tail length.

Less expected perhaps is the indication (tables 6 and 7) that bill length varies seasonally, usually increasing from fall to spring. This suggests that there may be spurts in growth, perhaps correlated with seasonal changes in use of the bill (discussed below). That the bill differs significantly in length from season to season can be demonstrated by Student T-test analysis of the larger samples. For instance, late spring males of *nuttallii* from northern California (N=26) show a mean length of gonys of 14.06 mm., compared with 13.77 mm. for winter males (N=51). An "F" value of 6.85 indicates that the difference is highly significant. Comparing differences in bill length between the sexes, I noted that Coefficients of Difference were seasonally variable in *P. scalaris* with no pattern, but that all high values (above 0.83) for *P. nuttallii* were obtained from winter and fall samples. All low C.D.'s (below 0.70) came from spring and fall samples. Thus, sexual overlap in

bill length of Nuttall's Woodpeckers appears least in the winter months, somewhat greater in fall, and greatest in spring. Correlated with the general increase in bill length from fall to spring is an increase in bill width, especially in *nuttallii*, for which the spring male samples exhibited both the greatest bill length and broadest bills among the various seasonal samples from all geographical areas.

SEXUALLY ABERRANT VARIANT WOODPECKERS

During the course of the investigation, two unusual variant Nuttall's Woodpeckers were obtained at Valladares, Baja California. One female (A.M.N.H. No. 791451) possessed two ovaries instead of the normal, single ovary. The female was taken on April 24 with her mate. The left ovary measured 9 by 4 mm., with ova to 1.5 mm. The right ovary measured 4 by 2 mm., and the ova were not enlarged but granular. Hence, although enlarged, the right ovary was not as advanced as the left, and it probably would not have produced functional eggs. It is significant that the smaller ovary was the right one, normally that lacking in adult female birds. The female had a brood patch and weighed 40.4 grams. Its plumage was normal for females of this species. The apparent mate of this female weighed 39.4 grams, and had enlarged testes (8 by 6 mm.) and a full brood patch. It, too, was normal in coloration.

The second variant (A.M.N.H. No. 791448) was a female-plumaged hermaphrodite, collected on April 25; no other birds were nearby, although it presumably was mated with a male. Its ovary, positioned slightly left of the body midline, was much enlarged and contained three ruptured follicles. Its oviduct too was enlarged, and it had a full brood patch. Presumably it had laid at least three eggs. Dorsal to the ovary and in normal position were two slightly enlarged testes equal in size (3.5 by 3 mm.). Unfortunately its body was not saved for more detailed study. The bird weighed 41.0 grams, and its plumage is that of a normal female *P. nuttallii*.

Although one cannot implicate hybridization as a factor in the occurrence of these variants, it must be noted that Valladares is a locality from whence comes a hybrid. Indications are that *P. scalaris* once occurred at Valladares together with *P. nuttallii*, or that *nuttallii* replaced *scalaris* there. Hence, introgression or hybridization

could have been involved in the production of these aberrant birds. I also recall taking a female-plumaged, but gonadally male Flicker (*Colaptes auratus*) from a hybrid zone in Arizona (Short, 1965a, pp. 386–387). Thus the three sexually aberrant woodpeckers out of the more than 1000 specimens of picids that I have collected came from areas of hybridization. Both aberrant Nuttall's Woodpeckers from Valladares could have been siblings, the offspring of parents one of which was itself aberrant.

GEOGRAPHIC VARIATION

I have already (1968) presented an analysis of geographic variation in southwestern *Picoides scalaris*. The major point resulting from this analysis is the considerable difference between peninsular Baja California populations (*P. s. eremicus*, *P. s. lucasanus*) and those populations to the north and east (*P. s. cactophilus*, including "mojavensis" and "yumanensis"). Essential features of *eremicus* compared with *cactophilus* are its proportionally longer tail and correlated greater tail/wing ratio, its blacker back, and its less-barred outer rectrices. Other features are given in the article cited above. As noted in the discussion of individual variation, *eremicus* and *cactophilus* differ to a minor extent in many ways, so that it was impossible to treat the two together in comparing *scalaris* with *nuttallii*. I believe that these differences reflect the former geographic isolation of the peninsular Baja California populations from *cactophilus*; the latter is now engaged in a tenuous (if existent) secondary contact with *eremicus* about the north end of the Sierra Juárez (Short, 1968, p. 9). Perhaps the best measure of the distinctness of peninsular populations from *cactophilus* as a result of their isolation and divergence is the difference in the way they interact with *P. nuttallii*.

In *nuttallii*, geographic variation is slight and does not approach that found even among diverse populations of the subspecies *P. s. cactophilus*. Among the tendencies noted are for southern California and Baja California *nuttallii* to differ from northern *nuttallii* in: longer wings; longer tail; narrower bills in males, broader bills in females; broader black back bars; fewer and smaller white markings in the wings; and more variable rectrix patterns (see tables 18 and 19). Some of these tendencies will be treated below in the discussion of possible introgression. The comparisons in which the above tendencies were

detected involved three seasonal samples of each sex from each of northern California (total N=103 males, 80 females), southwestern California (66 males, 72 females), and central southern California (localities immediately adjacent to range of *scalaris*; N=91 males, 82 females), and three seasonal samples of males and one (April to July) of females from Baja California (48 males, 27 females). Only some of the mensural data are included in tables 8 and 9. Use of the Student T-test for comparing the larger samples indicated that some differences between northern and southern California samples were highly significant ($P=0.99$ or more; wing length, one instance; bill width, one instance; back bars, three instances). The concordance in the direction of the differences (all eight north to south tail length comparisons, seven of eight wing length comparisons, six of eight back bar comparisons, and southern males narrower-billed and southern females broader-billed in all comparisons for each sex), combined with close approaches to significance (two or three cases for each feature) further corroborate the existence of these tendencies. When additional specimens become available, it will be possible to demonstrate other such tendencies, as well as to substantiate more fully those noted here.

MORPHOLOGICAL COMPARISON OF NUTTALL'S AND LADDER-BACKED WOODPECKERS

The limits of variation in *P. nuttallii* and *P. scalaris* must be established to make possible the recognition of hybrids. In general the two species are distinct in many features, but some variant individuals of each approach or attain the condition of the other in one to several of these characters. It is the purpose of the present analysis to define the limits of variation in the characters by which the two species differ. This is best accomplished by a comparison of the features by which *scalaris* and *nuttallii* differ where they are not sympatric. Field observations indicated that random interbreeding of the two forms was not occurring. Hence introgression was presumed to be less than massive and not likely to have strong effects on populations of the two species away from their areas of contact (the question of introgression away from areas of contact is discussed below). The critical populations for this comparison are therefore: 1) *nuttallii* from southern California, which is allopatric

with *scalaris*, although they are sporadically in contact; 2) *scalaris* from south central California (sporadically in contact with *nutallii*—this is the “*mojavensis*” portion of *P. s. cactophilus*; see Short, 1968); and 3) *scalaris* from that part of northern Baja California south of the overlap area with *nutallii* (i.e., the southern portion of *P. s. eremicus*).

MENSURAL CHARACTERS

In terms of nonoverlap of characters essential for the discrimination of intermediate (hybrid) individuals, perusal of the various tables and data presented for individual and geographic variation shows that Nuttall's and Ladder-backed woodpeckers overlap in essentially all mensural features. Even where mean differences are greatest, there is overlap of extreme individuals. Only in bill length (gonys) is there non-overlap among some samples of the two species (the data suggest that at localities where the two species occur together they usually do not overlap), but the gap does not exceed 1 mm. Thus, mensural data are not useful in determining intermediate (hybrid) birds, but only in establishing limits that serve to indicate whether measurements of putative hybrids fall within or outside the range of one or the other species. Perusal of tables 6 and 7 will indicate the mensural characteristics of each form. Briefly, compared with *scalaris*, *nutallii* has: slightly shorter wings (about as in Arizona *P. s. cactophilus*); a tail averaging almost as long as in *P. s. eremicus* and longer than that of *cactophilus*; a shorter bill (much shorter than that of *eremicus* and western *cactophilus*, but approached by Arizona *cactophilus*); a narrower bill; and slightly shorter tarsi. Additionally, the tail/wing ratio of *nutallii* averages from 0.63 to 0.65 in various samples, closely approaching that of *P. s. eremicus* (0.65 to 0.67), and considerably greater than the average for *P. s. cactophilus* (0.59 to 0.62; see Short, 1968).

CROWN COLOR

The crown color of males has been discussed above. Briefly, males of *scalaris* have a red nuchal patch and red-tipped, white-spotted crown feathers, whereas males of *nutallii* have a broad red nuchal stripe (adult females lack red in the crown). Fall and winter males of *scalaris* appear entirely red from their nasal tufts to the nape,

but worn spring and summer birds may have the red so reduced (or lacking) anteriorly that the crown does not appear red. I established a character index in which the black, or white-spotted black crown of *nutallii* scored 0, and the red crown of *scalaris* scored 2. Intermediate conditions scored 0+ (red extending somewhat forward), 1 (crown lightly spotted with red), and 1+ (crown red, but red tips narrow or red incomplete). This system presents difficulties in spring and summer, when allowance must be made for some excessively worn males of *scalaris* (red reduced or lacking, hence “intermediate”), and for early fall males of *nutallii*, which may be molting (new, red-tipped nuchal feathers grow in from the hindcrown posteriorly, hence may score 0+ or even 1). All males of central southern California *P. s. cactophilus*, and of southern *eremicus* scored 2 in crown color (table 10). Six per cent (8 of 133) of males of *nutallii* from southern California scored 1, and 18 (mainly fall birds) scored 0+. Thus, only 1+ is unrepresented in these samples. I interpret these data as follows: a crown color score of 1+ may be expected in some hybrids of the two forms; males resembling *scalaris* generally, but with a crown color below 2 may be hybrids (backcross products) or introgressants; and, males resembling

TABLE 10
CROWN COLOR SCORES OF MALE WOODPECKERS

Sample	Scores				
	0	0+	1	1+	2
<i>nutallii</i>					
Northern California	98	2	1	0	0
Southern California	133	18	8	0	0
Baja California	42	4	1	0	0
Totals	273	24	10	0	0
<i>nutallii</i> introgressants ^a	9	0	4	1	0
Hybrids	0	0	2	3	0
<i>scalaris</i> introgressants ^a	0	0	0	1	3
<i>scalaris</i>					
<i>cactophilus</i> W.	0	0	0	0	59
<i>cactophilus</i> E.	0	0	0	1	139
<i>eremicus</i> N.	0	0	1	0	27
<i>eremicus</i> S.	0	0	0	0	38
Totals	0	0	1	1	263

^aIntrogressants include possible and probable introgressants and backcross hybrids.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nutallii* and S., from area south of sympatry.

TABLE 11
NASAL TUFT SCORES OF MALE AND
FEMALE WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nuttallii</i>					
Northern California	178	4	0	0	0
Southern California	277	17	3	0	0
Baja California	72	7	2	0	0
Totals	527	28	5	0	0
<i>nuttallii</i> introgressants	14	5	0	0	0
Hybrids	0	2	5	1	0
<i>scalaris</i> introgressants	0	0	2	1	14
<i>scalaris</i>					
<i>cactophilus</i> W.	0	0	7	5	88
<i>cactophilus</i> E.	0	0	16	1	246
<i>eremicus</i> N.	0	2	3	2	39
<i>eremicus</i> S.	0	0	2	0	69
Totals	0	2	28	8	442

^aSamples as described in table 10 for crown color.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nuttallii* and S., from area south of sympatry.

nuttallii generally, but with a crown color score of 1 might represent hybrids or introgressants, particularly if they are winter, spring, or summer birds.

NASAL TUFTS

The nasal tufts of *nuttallii* typically are white, sharply contrasting with the black crown. Those of *scalaris* are dusky white, and they gradually blend into the black crown feathers (fig. 1). These conditions were scored 0 and 2, respectively, in a character index. Intermediate conditions scoring 0+, 1, and 1+, are highly subjective, especially for worn birds. Birds scoring 0+ have white nasal tufts slightly blending with the crown. A score of 1 designates dusky-tinged, white nasal tufts blending moderately with the crown, whereas 1+ indicates a condition slightly more white and contrasting than in *scalaris*. Conditions of wear and discoloration make *nuttallii*-like birds more difficult to assess for the color of the nasal tufts than are *scalaris*-like birds. The scores for both sexes presented in table 11 show that, although the bulk of *nuttallii* (94 per cent, southern California) score 0, and most (88 to 98 per cent) *scalaris* from central southern California and Baja California (south-

ern *eremicus*) score 2, extreme variants of the two overlap (2.5 per cent, 12 of 468 birds of both species) with a score of 1. Most of the individuals scoring 0+, 1, and 1+ are very worn or discolored. If one discounts such birds, the actual overlap is negligible and intermediates not excessively worn or discolored may be readily distinguished. No sexual differences were detected with regard to nasal tuft color.

COLOR OF MALAR STRIPE

The malar stripe is typically black in *nuttallii* and black liberally flecked with white in *scalaris* (no sexual difference in malar pattern was observed). An all-black malar was assigned a score of 0, and when one or two white spots were present, 0+. A few more white spots produce a condition given a score of 1. A fully white-sprinkled malar scores 2, whereas less than the normal spotting scores 1+. About 13 per cent of the specimens of *nuttallii* from southern California score 0+ or 1. Few *P. s. eremicus* (southern sample, 3 per cent) have less than fully white-flecked malar stripes, but 18 per cent of the western *cactophilus* sample score 0+, 1 and 1+ (table 12). Thus, about 8.5 per cent of the individuals of the two species in these three

TABLE 12
MALAR COLOR SCORES OF MALE AND
FEMALE WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nuttallii</i>					
Northern California	165	12	4	0	0
Southern California	266	26	9	0	0
Baja California	74	5	1	0	0
Totals	505	43	14	0	0
<i>nuttallii</i> introgressants	10	5	4	0	0
Hybrids	3	4	0	1	0
<i>scalaris</i> introgressants	0	0	4	4	9
<i>scalaris</i>					
<i>cactophilus</i> W.	0	1	13	4	82
<i>cactophilus</i> E.	0	0	17	6	238
<i>eremicus</i> N.	0	0	8	4	45
<i>eremicus</i> S.	0	0	2	0	68
Totals	0	1	40	14	433

^aSamples as described in table 10 for crown color.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nuttallii* and S., from area south of sympatry.

TABLE 13

AURICULAR (EAR COVERT) PATTERN SCORES IN
MALE AND FEMALE WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nuttallii</i>					
Northern California	164	7	10	0	0
Southern California	244	39	15	0	0
Baja California	71	6	3	0	0
Totals	479	52	28	0	0
<i>nutallii</i> introgressants	10	5	4	0	0
Hybrids	0	1	5	1	1
<i>scalaris</i> introgressants	0	0	3	2	12
<i>scalaris</i>					
<i>cactophilus</i> W.	0	0	8	1	89
<i>cactophilus</i> E.	1	0	8	7	246
<i>eremicus</i> N.	0	1	5	0	50
<i>eremicus</i> S.	0	0	1	0	70
Totals	1	1	22	8	455

^aSamples as described in table 10 for crown color.Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nutallii* and S., from area south of sympatry.

samples overlap with scores of 0+ and 1, rendering this trait nondiagnostic for the identification of hybrids. However, it may be used in combination with other characters to indicate hybridity. It is not normally subject to modification by wear or discoloration which affects other characters.

AURICULAR (EAR COVERT) PATTERN

A broad, black patch occupies most of the posterior auricular or ear covert area in *P. nuttallii*, and this condition is scored 0. In *P. scalaris* the black area is narrow, nearly forming a stripe (rather than the angular patch of *nutallii*), which condition scores 2 (see fig. 1). The gradient stages from the condition of *nutallii* to that of *scalaris* are scored 0+, 1 (intermediate) and 1+. Five per cent of the individuals in the three samples of *nutallii* and *scalaris* overlap with a score of 1 (table 13). Of *P. nuttallii* 82 per cent scored 0, whereas 91 per cent of western *P. s. cactophilus* and 98 per cent of southern *P. s. eremicus* scored 2. Seasonal variation and discoloration present no problem in considering this feature, which is helpful in discriminating hybrids. The sexes appear not to differ in their auricular pattern.

SIDES OF NECK

The pattern of black on the sides of the neck is generally distinctive in these species, *nutallii* having a large black mark that usually connects with the black of the hindcrown and upper back just anterior to the wings and with the malar stripe, and *scalaris* having a narrow black mark usually isolated from both the malar and the back (fig. 1). As with other characters, the condition found in *nutallii* scores 0 and that of *scalaris* scores 2, with variously intermediate scores of 0+, 1, and 1+ going from the condition typical of *nutallii* toward that of *scalaris*. Although wear poses no problem with this feature, the mode of preparation of specimens severely limits its usefulness. Specimens prepared with the head very close to the body have the neck region obscured, and it is almost impossible to satisfactorily appraise them for this character. Scores of 1 and 1+ were attained by 24 per cent of western *P. s. cactophilus* and by 4 per cent of southern *eremicus* specimens (table 14). About 12 per cent of southern California *nutallii* specimens scored 0+, 1, and 1+. The overlap at scores of 1 and 1+ involves 8 per cent of these combined samples. Two points are noteworthy concerning this variation. The mode of preparation

TABLE 14

NECK PATTERN SCORES OF
MALE AND FEMALE WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nutallii</i>					
Northern California	155	12	14	0	1
Southern California	261	27	10	1	0
Baja California	73	5	3	0	0
Totals	489	44	27	1	1
<i>nutallii</i> introgressants	13	4	2	0	0
Hybrids	0	2	4	1	1
<i>scalaris</i> introgressants	0	0	3	3	11
<i>scalaris</i>					
<i>cactophilus</i> W.	0	0	19	5	76
<i>cactophilus</i> E.	1	1	22	5	233
<i>eremicus</i> N.	2	0	10	6	39
<i>eremicus</i> S.	0	0	4	0	67
Totals	3	1	55	16	415

^aSamples as described in table 10 for crown color.Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nutallii* and S., from area south of sympatry.

of the specimens hampers proper evaluation of *nutallii*-like birds more than of *scalaris*-like birds, simply because the larger black area of the neck of *nutallii* is more readily obscured than is the small, discrete mark of *scalaris*. The second point is that *P. s. eremicus* tends to have an even smaller black mark on the neck than has *P. s. cactophilus*. The usefulness of this feature for determination of hybrids is somewhat impaired by the slight overlap shown by the two species, and by the partly obscured pattern in poorly prepared specimens. I detected no sexual difference in this character.

EYE (SUPERCILIARY) STRIPE

Like the neck pattern, the eye stripe is difficult to assess because of variation in preparation of specimens. A score of 0 is assigned to the narrow white eye stripe of *nutallii*, which is often restricted by black posteriorly, and 2 is assigned to the broad white stripe of *scalaris*. Only one intermediate stage is recognized, scoring 1, because of the difficulty in assessing this character (due to the vagaries of specimen preparation). About 10 per cent of southern California *P. nuttallii*, 9 per cent of *P. s. cactophilus* from central southern California and 3 per cent of

southern *P. s. eremicus*, score 1, representing an overlap of 9 per cent of their combined total (table 15). This character is thus difficult to utilize in appraising putative hybrids. The pattern of variation in superciliary pattern does not vary sexually.

WING MARKINGS

In general Ladder-backed Woodpeckers have more white wing markings and broader white markings than have Nuttall's Woodpeckers, but they overlap considerably. Various measures of wing markings were used in studying this feature. Markings on the greater and lesser wing coverts were scored (e.g., few or no markings, versus many markings, with intermediate categories) as were other characters discussed above. All samples of *scalaris* showed higher scores (more spotting) than did samples of *nutallii*, but the variation encountered was considerable and resulted in complete overlap. The overlap is largely due to variation in *scalaris*, for no individuals of *nutallii* attain the average condition of spotting found in *scalaris*. Another measure used was a count of the number of white bars (or spots) reaching the outer edge of the outer vane of the eighth primary. Various samples of *nutallii* averaged about five spots on this primary. Samples of *P. s. eremicus* averaged 4.57 to 4.60, whereas samples of *P. s. cactophilus* showed greater variability and more spotting than *nutallii* (average 5.37 to 5.64). Although the bars were not measured, it was clear that *scalaris* (both races) has broader bars than those in *nutallii*; the bars of the latter are more frequently reduced to spots. Variation is too great to allow utilization of this character in analyzing hybrids.

UPPER BACK COLOR

Contributing to the markedly blacker appearance of *P. nuttallii* is a broad black band on the upper back (connecting with the hind neck and anterior to the white and black back barring); this band is narrow or absent in *scalaris* (fig. 10). Scores were assigned ranging from 0 for the full band of *nutallii*, through 0+, 1 (intermediate) and 1+ to 2, the latter marking the condition found in *scalaris*. This character is affected somewhat by wear, but much more important is the mode of preparing the skin, which can obscure completely even a fully developed band. Nuttall's Woodpeckers score 0 to 1, with 21 per

TABLE 15

WIDTH OF SUPERCILIARY STRIPE AS SCORED FOR
MALE AND FEMALE WOODPECKERS^a

Sample	Scores		
	0	1	2
<i>nutallii</i>			
Northern California	158	24	0
Southern California	266	32	0
Baja California	71	10	0
Totals	495	66	0
<i>nutallii</i> introgressants	13	6	0
Hybrids	0	7	1
<i>scalaris</i> introgressants	0	4	13
<i>scalaris</i>			
<i>cactophilus</i> W.	0	9	91
<i>cactophilus</i> E.	0	9	253
<i>eremicus</i> N.	0	7	51
<i>eremicus</i> S.	0	2	69
Totals	0	27	464

^a Samples as described in table 10 for crown color.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nutallii* and S., from area south of sympatry.

TABLE 16
UPPER BACK COLOR SCORES IN MALE AND FEMALE
WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nuttallii</i>					
Northern California	139	21	22	0	0
Southern California	237	31	34	0	0
Baja California	68	6	7	0	0
Totals	444	58	63	0	0
<i>nuttallii</i> introgressants	8	7	3	1	0
Hybrids	2	2	3	1	0
<i>scalaris</i> introgressants	3	1	8	0	5
<i>scalaris</i>					
<i>cactophilus</i> W.	3	3	39	10	45
<i>cactophilus</i> E.	0	3	57	29	174
<i>eremicus</i> N.	0	2	19	4	29
<i>eremicus</i> S.	0	0	20	6	45
Totals	3	8	135	49	293

^aSamples as described in table 10 for crown color.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nutallii* and S., from area south of sympatry.

cent scoring 0+ and 1. More variable is the Ladder-back, three individuals of which even have the fully developed band typical of *nutallii*. *Picoides s. cactophilus* from central southern California is most variable, with but 45 per cent of the sample scoring 2; the remainder score from 0 to 1+ (table 16). The southern sample of *P. s. eremicus* is less variable, with 63 per cent of the birds scoring 2, and the remainder scoring 1 and 1+. Thus *cactophilus* overlaps completely with *P. nuttallii*, whereas about 28 per cent of *eremicus* overlap with 11 per cent of *nutallii* specimens scoring 1. This feature thus is of supplemental use only with California birds, although it is more useful in analyzing possible hybrids from Baja California. The sexes appear similar in this feature in *nutallii*, but in *scalaris* the males tend to exhibit a back band more frequently, and it is larger than in the females.

BACK BARRING

The back barring of the Nuttall's Woodpecker tends to be dominated by black because of its wide black bars. Ladder-backed Woodpeckers tend to have broader white bars and hence appear whiter backed (fig. 10). The next to the outermost black bar of a randomly selected

feather in the middle back region was measured in depth along the feather shaft for each specimen. Feather wear is rarely sufficient to affect this bar, but it does affect, in many cases, the white bar distal to it, and invariably affects the terminal black bar. The latter is very narrow and frequently is lost by winter. Thus, it is possible to measure the penultimate black bar of specimens taken throughout the year, and to pool the seasonal samples for this feature. The depth of this back bar averaged 4.92 to 5.25 mm. in males and 4.69 to 4.90 mm. in females of *P. nuttallii* from various areas (tables 8 and 9). The black back bars of *P. scalaris* are narrower than are those of *P. nuttallii*, but there is racial and intraracial variation (Short, 1968, pp. 2-5). Intraracial variation in *P. s. cactophilus* is clinal, such that Colorado River Valley birds are very narrowly barred (means from 2.99 to 3.36 mm.), but to the east (Arizona), the west (central southern California) and the north (southwestern Utah), specimens have on the average broader black bars (means from 3.33 to 3.64 mm.). More broadly barred is *P. s. eremicus* with means of 4.51 mm. (males) and 4.50 mm. (females). The latter race thus approaches *nutallii* more than does *P. s. cactophilus*. Thus, there is great overlap between *P. nuttallii* and *P. scalaris eremicus*, and considerable (about 1 mm.) overlap between *nutallii* and *P. s. cactophilus*. Back barring is of secondary importance in evaluating putative hybrids of these species within California, and it is of no consequence for this purpose in Baja California. The sexes appear alike in back barring.

PATTERN OF OUTER THREE (LARGE) RECTRICES

The outer tail patterns of the Ladder-backed and Nuttall's woodpeckers are generally distinctive. The Ladder-back has a barred pattern, but the Nuttall's Woodpecker has a mainly white outer tail pattern with few and partial black bars (figs. 1 and 12). As in the case of many other characters, there is considerable variation which hampers its assessment. I have illustrated the normal and extreme patterns in figure 12. The variability of *scalaris* is greater than that of *nutallii*, and the greatest variability in the former is found in *P. s. eremicus*. I devised a character index for inner and for outer vanes of rectrices 3, 4, and 5. Scores assigned were 0 for the *nutallii* condition to 2 (inner vane of rec-

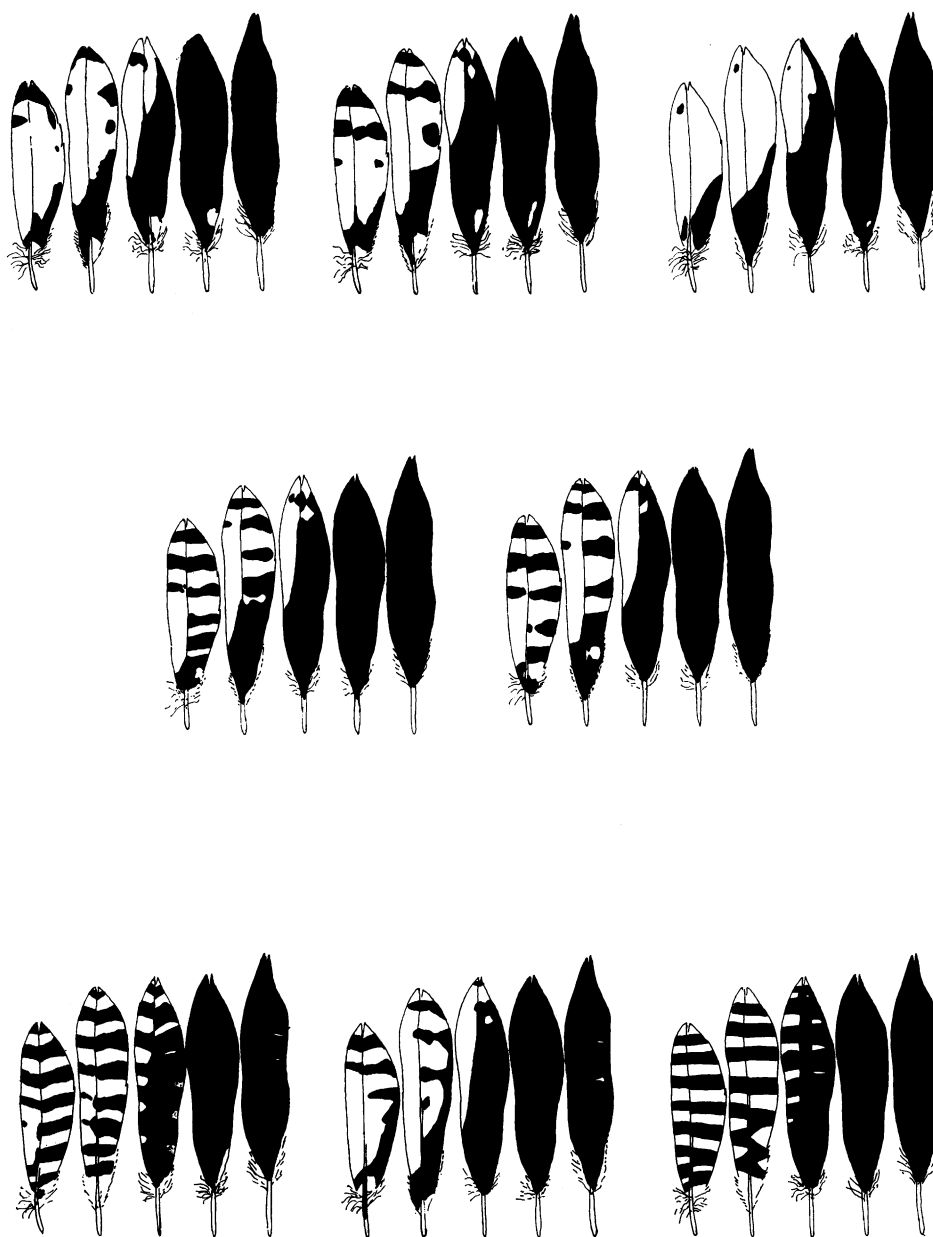


FIG. 12. Tail patterns of *P. nuttallii* (top row), *P. scalaris* (bottom row) and their hybrids (middle row). Rectrices 1 to 5 are shown for the left side of tail only. Shown for *nuttallii* are typical pattern at the left followed by extreme barred and then extreme unbarred patterns. Hybrids illustrated are A.M.N.H. No. 791507 (left) from near Onyx, California and A.M.N.H. No. 791485 from Rancho Escondido, Baja California. Patterns of *scalaris* include typical (at left) followed by extreme white pattern of *P. s. eremicus*, and typical pattern (right) of *P. s. cactophilus* (see text).

trices 3 and 4) or 4 (outer vane of rectrices 3 and 4, and both vanes of rectrix 5) for the condition found in *scalaris*. Because of the considerable overlap in most of these characters, evident from

a perusal of table 17, I shall not discuss the factors involved in their specific scores. Scores designated for the outer and inner vanes of rectrix 5 are as follows:

VANE	SCORE				
	0	1	2	3	4
Outer	0-2 bars	1 1/2 bars	3 bars	4 bars	5 bars
Inner	traces of 1 to 3 bars; 1 or 2 are complete	2 bars, 3rd partial but strong	3 full bars	4 partial or complete bars	5 or more bars, may merge

The results of scoring patterns for both vanes of rectrices 3 and 4 are contained in table 17. Variability of pattern is greatest in *scalaris* in the outer vane of both rectrices, whereas *nuttallii* is more variable in the inner vane of these rectrices. The great variability in outer vane patterns in *scalaris* is largely attributable to variation in *P. s. eremicus*. For example, 70 per cent of the *eremicus* specimens score below 3 in the pattern of outer rectrix 3, but only 27 per cent of *cactophilus* do so (for outer rectrix 4 the percentages are, respectively, 81 per cent and 42 per cent). The overlap in patterns between the two species does not permit determination of a hybrid on the basis of these characters. However, they are of use in the analysis of hybridization, and especially introgression. As an example, although *nuttallii* is variable and completely overlaps *scalaris* in scores for the inner vane of rectrix 4, only one specimen out of 350 of *P. s. cactophilus* deviates from a score of 2 by scoring 1; this suggests that individuals otherwise like or nearly like *cactophilus*, which score below 2 in this character may be introgressant birds.

The outer vane of rectrix 5, which I thought at first might be important in the analysis of hybrids, proved to be very variable also (table 17). Only 12 per cent of the Nuttall's Woodpeckers deviated from 0, scoring 1 and 2 (latter only 6 birds), but 80 per cent of *P. s. eremicus* and 30 per cent of *P. s. cactophilus* scored within the range of *nuttallii*. This variation involves a reduction of the barring of the outer vane in *scalaris*, and variants showing such reduction resemble the condition found in hybrids between "typical" individuals of *nuttallii* and *scalaris* (fig. 12).

The least variable and hence most useful of this character complex is the pattern of the inner

TABLE 17
CHARACTER SCORES FOR RECTRIX PATTERN IN
MALE AND FEMALE WOODPECKERS^a

Sample	Scores				
	0	1	2	3	4
OUTER RECTRIX 3					
<i>nuttallii</i> total	555	5	1	0	0
<i>nuttallii</i> introgressants	14	5	0	0	0
Hybrids	4	1	0	1	1
<i>scalaris</i> introgressants	5	3	6	1	2
<i>scalaris</i> total	33	46	78	97	220
INNER RECTRIX 3					
<i>nuttallii</i> total	414	132	11	—	—
<i>nuttallii</i> introgressants	5	9	4	—	—
Hybrids	1	2	4	—	—
<i>scalaris</i> introgressants	0	0	17	—	—
<i>scalaris</i> total	2	7	470	—	—
OUTER RECTRIX 4					
<i>nuttallii</i> total	562	4	0	0	0
<i>nuttallii</i> introgressants	15	3	1	0	0
Hybrids	6	0	1	0	0
<i>scalaris</i> introgressants	3	6	2	3	1
<i>scalaris</i> total	58	76	93	100	153
INNER RECTRIX 4					
<i>nuttallii</i> total	421	133	12	—	—
<i>nuttallii</i> introgressants	8	8	3	—	—
Hybrids	1	1	5	—	—
<i>scalaris</i> introgressants	0	2	15	—	—
<i>scalaris</i> total	0	7	470	—	—
OUTER RECTRIX 5					
<i>nuttallii</i> total	492	59	6	0	0
<i>nuttallii</i> introgressants	5	10	2	1	0
Hybrids	2	3	0	1	0
<i>scalaris</i> introgressants	1	3	4	4	4
<i>scalaris</i> total	9	73	98	91	198
INNER RECTRIX 5					
<i>nuttallii</i>					
Northern California	152	27	3	1	0
Southern California	176	95	26	1	0
Baja California	43	20	14	3	0
Totals	371	142	43	5	0
<i>nuttallii</i> introgressants	4	4	7	4	0
Hybrids	1	1	0	1	4
<i>scalaris</i> introgressants	0	0	0	4	12
<i>scalaris</i>					
<i>cactophilus</i> W.	0	0	0	3	96
<i>cactophilus</i> E.	0	0	5	1	245
<i>eremicus</i> N.	0	0	5	7	42
<i>eremicus</i> S.	0	2	4	22	38
Totals	0	2	14	33	421

^aSamples as described in table 10 for crown color, except that only combined totals for *nuttallii*, and for *scalaris*, are given for most rectrices.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nuttallii* and S. from area south of sympatry.

vane of rectrix 5, which is more completely treated than are the other features in table 17. As in the case of the inner vanes of the other rectrices *P. nuttallii* is more variable than *P. scalaris*; 17 per cent of northern California, and 42 per cent of the southern California and Baja California specimens of *nuttallii* score above 0. *Picoides scalaris*, especially *P. s. cactophilus*, is less variable. Only 3 per cent of the individuals of *cactophilus* from central southern California deviate from a score of 4. Thus, in southern California the overlap in pattern of the inner vane of rectrix 5 involves only 1 per cent of the individuals of both species, namely those scoring 3. In contrast there is overlap in this pattern among 21 per cent of the individuals (those scoring 2 and 3) of both species where they overlap geographically in Baja California. This character is useful in appraising possible hybrids in California. It is less useful for Baja California specimens, although it is a helpful trait for study of possibly introgressant individuals. No sexual differences in pattern were noted in these species.

PATTERN OF RECTRIX 6

The outermost rectrices of woodpeckers are much shorter than the others, and they often bear a pattern differing from those of the other rectrices. This is true of the Nuttall's and Ladder-backed woodpeckers, some of the many patterns of which are depicted in figure 13. Well over 100 variant patterns were observed, and these comprised 93 major patterns. I categorized these into nine groups, as follows:

GROUP	PATTERN	INCLUDED NUMBER OF PATTERNS
A	Basic black	9
B	Nuttall's white variant	6
C	Modified black	11
D	Barred black	9
E	Intermediate black barred	14
F	Black barred	9
G	Modified barred	10
H	Ladder-back barred variant	18
I	Basic barred	7

The analysis of the patterns is summarized in tables 18 and 19. It is evident that groups A and B form the major patterns of *P. nuttallii*, except for the Baja California population. Although a few California specimens of *nuttallii* exhibit patterns of group I, the major pattern group typical of *P. scalaris*, the Baja California sample contains individuals with patterns of groups C,

D, E, F, and G, as well as A and B (but not I). At least some of this variation may be the result of introgression.

Among forms of *P. scalaris*, the peninsular Baja California populations of the races *eremicus* and *lucasanus* are more variable than are continental samples of *P. s. cactophilus*. Furthermore, variation in the peninsular populations is clinal, with the southern sample (*lucasanus*) showing the fewest number of patterns, and the northern sample (northern *eremicus*) showing the most patterns. As a result of this variation there is little overlap in patterns between *nuttallii* and *scalaris* except for the sympatric Baja California populations of *P. nuttallii* and *P. scalaris eremicus*. In the Baja California samples from the area of sympatry 29 per cent of *nuttallii* overlap in pattern with 44 per cent of *P. s. eremicus*, and thus 35 per cent of the individuals of both samples (combined) overlap in their outer rectrix patterns. Patterns of groups H and I are the most typical patterns of *P. scalaris* throughout the range of this species. In *P. s. cactophilus* only two of 193 specimens exhibit patterns of groups other than H and I. Even in the highly variable peninsular populations these pattern groups are found in the majority (68 per cent of *lucasanus*, 75 per cent of southern *eremicus*, and 56 per cent of northern *eremicus*) of individuals. No sexual differences in pattern were detected.

Of the nine pattern groups two (B, C) are found exclusively in *P. nuttallii*, and one (H) exclusively in *P. scalaris* (tables 18 and 19). It is noteworthy that the basic pattern group of each species (A of *nuttallii*, I of *scalaris*) is found in one or a few specimens of the opposite species. This may reflect introgression or the effects of residual genes (see below). Five of the eight pattern groups observed in *P. nuttallii* are found only in the Baja California sample. These five include an exclusively *nuttallii* pattern (C) not noted in *nuttallii* from farther north, and four patterns (groups D, E, F, G) found also in *P. scalaris*. Within *scalaris*, four pattern groups (G, H, I, and A) are represented by individuals of *P. s. cactophilus*. Six pattern groups (D, E, F, G, H, I) are represented by individuals of the peninsular races *lucasanus* and *eremicus*, including three groups (D, E, F) not observed in *cactophilus*, nor in other races of *P. scalaris*, but found also in the Baja populations of *P. nuttallii*. The significance of this fact will be discussed below.

The nonoverlap of California specimens of *P.*

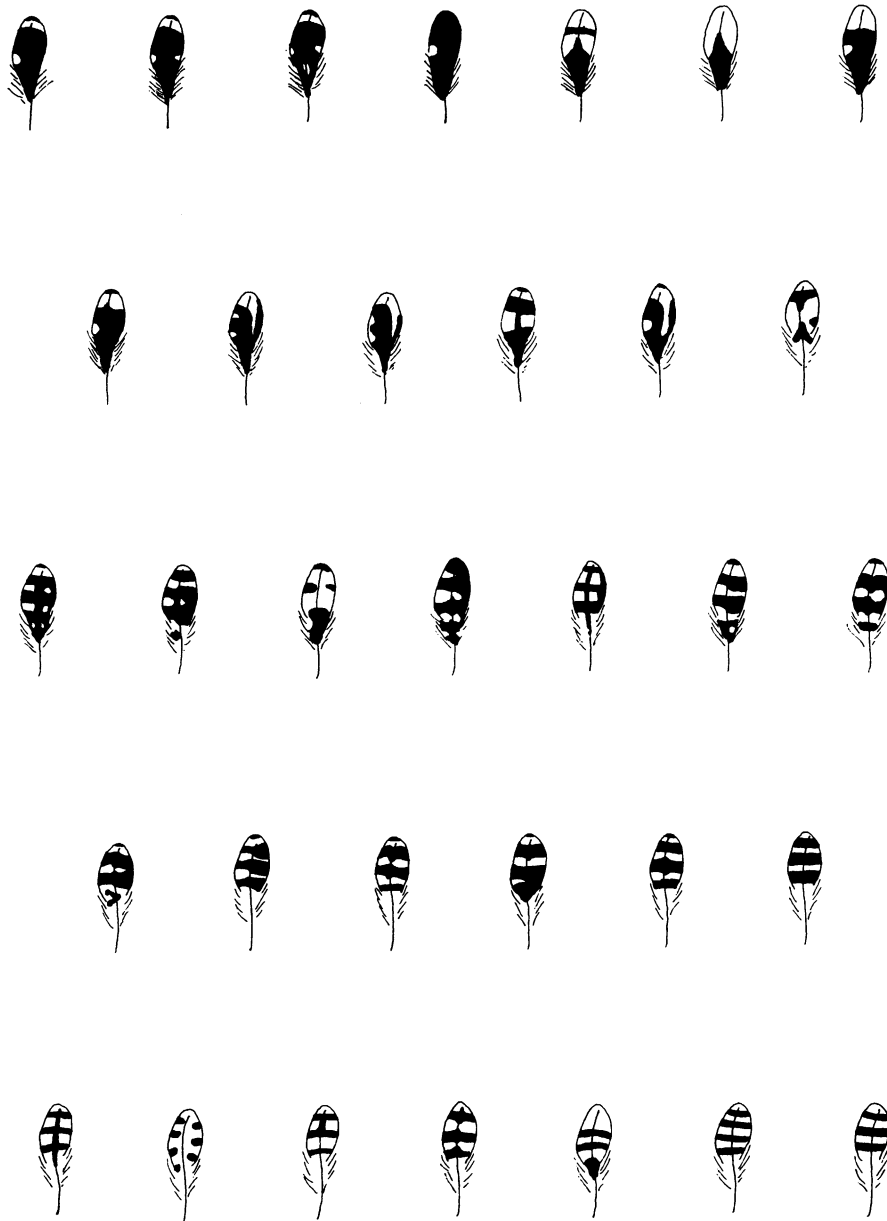


FIG. 13. Outer (6th) rectrix patterns of *P. nuttallii*, *P. scalaris*, and hybrids. Top row, *nuttallii* patterns, typical ones at left. Second row down, introgressant *nuttallii* patterns. Middle row, patterns of hybrids. Second row from bottom, introgressant *scalaris* patterns. Bottom row, patterns of *scalaris*, typical ones at right. Some of introgressant and hybrid patterns are also found in phenotypically pure birds of one or the other species (see text).

nuttallii and *P. scalaris cactophilus* in outer rectrix patterns of groups C, D, E, and F, is important for the discrimination of their hybrids. The great variability and overlap in outer rectrix patterns of northern Baja California populations of

nuttallii and *scalaris* render their patterns of only secondary importance in discriminating hybrids of *P. nuttallii* and *P. s. eremicus*. Such hybrids would be expected to exhibit generally patterns of groups D, E, and F.

TABLE 18

NUMBER OF MALE AND FEMALE WOODPECKERS EXHIBITING VARIOUS PATTERNS OF THE OUTER RECTRIX^a

Sample	N	A	B	Pattern Groups						
				C	D	E	F	G	H	I
Northern <i>nutallii</i> , A	132	69	62	0	0	0	0	0	0	1
Southern <i>nutallii</i> , P	130	95	28	0	0	0	0	0	0	7
Baja <i>nutallii</i> , S	65	36	1	9	10	7	1	1	0	0
"Hybrids" ^b , S	44	5	0	7	3	9	4	10½	3½	2
Northern <i>eremicus</i> , S	45	0	0	0	1	4	8	7	9	16
Southern <i>eremicus</i> , A	28	0	0	0	0	1	2	4	8	13
<i>lucasanus</i> , A	31	0	0	0	0	0	3	7	8	13
<i>cactophilus</i> , P (W)	104	1	0	0	0	0	0	1	18	84
<i>cactophilus</i> , A (E)	90	0	0	0	0	0	0	0	7	83

^aSymbols following samples indicate their status with respect to other species; A, allopatric; P, parapatric; S, sympatric. (E), (W) are compass directions.

^bIncludes introgressant individuals, see text.

VENTRAL COLORATION

The color of the underparts is white in *nutallii* and buffy white in *scalaris* (scored 0 and 2, respectively), although exceedingly variable seasonally as discussed above. Intermediate scores of 0+ (buffy traces, mainly white), 1 (mixed buffy and white), and 1+ (buffy with some white) were assigned. The results (table 20) of scoring for ventral coloration reflect the considerable variability of both species, and, more importantly, the effects of seasonal variation. More than half of the individuals of *nutallii* that score 0+ and 1 are buff-tinged fall specimens (see above sections on individual

variation). Also, about 40 per cent of the specimens of *scalaris* scoring less than 2 are worn, late-spring and summer birds. These facts generally restrict the usefulness of this character to the analysis of possible hybrids among winter, early spring, and less worn late-spring birds. The data in table 20 indicate certain important points. Regardless of intraracial variation, the peninsular Baja California *P. s. eremicus* is buffier below and less white than is *P. s. cactophilus*. Even allowing for seasonal variation there is virtually no overlap in color of underparts between the sympatric Baja California populations of *P. nutallii* and *P. scalaris*. Certainly a buff-bellied

TABLE 19

NUMBER OF RECTRIX 6 PATTERN TYPES IN MALE AND FEMALE WOODPECKERS^a

Sample	<i>N</i>	A	B	C	Pattern Groups			G	H	I	Total Patterns
					D	E	F				
Northern <i>nuttallii</i> , A	132	8	6	0	0	0	0	0	0	1	15
Southern <i>nuttallii</i> , P	130	8	5	0	0	0	0	0	0	3	16
Baja <i>nuttallii</i> , S	65	4	1	8	7	6	1	1	0	0	28
“Hybrids” ^b , S	44	3	0	7	3	8	3	10	4	2	40
Northern <i>eremicus</i> , S	45	0	0	0	1	4	6	2	8	2	23
Southern <i>eremicus</i> , A	28	0	0	0	0	1	2	3	6	5	17
<i>lucasanus</i> , A	31	0	0	0	0	0	2	4	5	3	14
<i>cactophilus</i> , P (W)	104	1	0	0	0	0	0	1	4	5	11
<i>cactophilus</i> , A (E)	90	0	0	0	0	0	0	0	5	5	10
Number of Patterns ^c	—	9	6	11	9	14	9	10	18	7	93

^aSymbols as in table 18.

^bIncludes introgressant individuals; see text.

^cNumber of distinct patterns comprising each pattern group; thus, under Total Patterns, there are 93 distinct patterns for all groups.

TABLE 20
SCORES OF COLOR OF UNDERPARTS IN
MALE AND FEMALE WOODPECKERS^a

Sample	Scores				
	0	0+	1	1+	2
<i>nuttallii</i>					
Northern California	159	21	1	0	0
Southern California	214	70	19	1	0
Baja California	63	16	2	0	0
Totals	436	107	22	1	0
<i>nuttallii</i> introgressants	7	5	6	0	0
Hybrids	0	3	3	0	2
<i>scalaris</i> introgressants	0	1	6	2	9
<i>scalaris</i>					
<i>cactophilus</i> W.	1	5	25	9	60
<i>cactophilus</i> E.	1	5	37	9	209
<i>eremicus</i> N.	0	0	2	2	43
<i>eremicus</i> S.	0	0	5	2	64
Totals	2	10	69	22	376

^aSamples as described in table 10 for crown color.

Symbols: W., *cactophilus* from central southern California and E., from southeastern California and Arizona; N., *eremicus* from area of sympatry with *nuttallii* and S., from area south of sympatry.

winter or spring Baja California specimen, otherwise *nuttallii*-like in appearance, should be considered a possibly introgressant individual, and likewise so too should any fall or winter white-bellied but otherwise *scalaris*-like bird from that same area. In California, however, this character is of secondary importance in distinguishing hybrids or possibly introgressant individuals. The sexes appear not to differ in this character.

VENTRAL MARKINGS

Both Nuttall's and Ladder-backed woodpeckers exhibit spotting and barring of the abdomen and sides (fig. 10). Although the pattern of barring of the posterior flanks, sides, and abdomen is virtually identical in these species, the black barring tends to be heavier (broader bars) in *nuttallii*. More importantly, the spotting of the sides of the breast normally differs in the two species. The spots tend to be small, but long and droplet-shaped in *scalaris*. They are often asymmetrical, being longer on one side of the feather shaft and highly reduced on the other vane, thus accentuating the droplet-like shape of the spots. Occasional birds are more heavily spotted, however. In *nuttallii* the spots are larger, about as long as broad, and they

appear more densely arranged and barlike. Nevertheless, variation, especially in *scalaris*, is considerable and the species overlap. I was unable to devise a suitable set of character index scores for the analysis of this character. About 10 per cent of the individuals of *nuttallii* examined have atypically small spots resembling those of *scalaris* (but in only a few of these are the spots actually droplet-like). Also, about 23 per cent of the specimens of *scalaris* have heavy spotting approaching or equaling the condition found in *nuttallii*. Such heavily spotted specimens are more prevalent in *P. s. eremicus* than in *P. s. cactophilus*. This character is not useful in diagnosing hybrids, because of the variation exhibited and the difficulty of describing and evaluating more or less intermediate conditions of spotting. However, it is a useful secondary character for the appraisal of introgression (see below). I detected no difference between the sexes in the ventral markings.

DESCRIPTION OF THE HYBRIDS

Eight birds appear to be hybrids, five representing *P. nuttallii* × *P. scalaris cactophilus*, and three *P. nuttallii* × *P. s. eremicus*. Various characters of these hybrids are summarized in table 21 (see also fig. 10), and characters of the parental species are summarized in table 3. Five of the hybrids are males and three are females.

The crown color of males, a diagnostic feature, was relied upon strongly in discriminating hybrids. The five males vary in this character, partly due to differential wear, for the birds represent different seasons. None has the fully red crown of *scalaris* (two variants from this normal condition in table 21 are worn birds), whereas three score 1+ with red crown color exceeding that found in *nuttallii*. The other two score 1, which is attained by only 6 per cent of 307 males of *nuttallii*. The least amount of red is found in C.A.S. No. 45217. In this specimen the red is asymmetrical in occurrence; there is more red on the left extending forward to the eye, and less red not reaching the eye on the right. Male A.M.N.H. No. 61050 is in worn plumage, and the red tips of the crown feathers are limited but red extends forward at least to the level of the eyes. The other three males approach the fully red spotted crown of *scalaris*, but none has red on the foremost feathers of the forehead. Asymmetry in extent of the red is evident in the fresh-

TABLE 21
CHARACTER SCORES, PATTERNS, AND MEASUREMENTS (IN MILLIMETERS) OF
HYBRID NUTTALL'S \times LADDER-BACKED WOODPECKERS^a

Character	Specimen ^b and Sex							
	1M	2M	3F	4F	5M	6M	7M	8F
Crown	1+	1	—	—	1+	1+	1	—
Nasal tufts	1	1	0+	0+	1	1	1+	1
Malar	0+	0+	1	0+	1	1	2	1
Ear coverts	1+	2	1	1	1	0+	1	1
Neck	0+	0+	1	2	1	1	1+	1
Eye stripe	1+	1	1	1	1	0+	1	2
Upper back	0+	1	1	1+	1	0	0	0+
Inner rectrix 5	4	4	4	0	—	2	3	4
Rectrix 6	F	G	F	G	E	H	G	C
Ventral color	0+	2	1	0+	2	1	0+	1
Tail/wing ratio	(0.59)	0.63	0.64	0.64	0.67	0.62	0.65	0.66
Wing length	105.0	106.7	105.9	103.6	106.3	104.5	104.4	101.0
Tail length	(62.2)	67.3	68.1	66.8	70.8	64.5	68.0	66.9
Gonys	15.9	16.4	15.1	14.1	15.6	14.0	15.2	15.0
Bill width	6.5	6.7	7.3	6.7	6.2	6.2	6.3	6.0
Back bar	4.0	3.6	3.8	3.7	4.5	4.8	4.2	6.1

^aScores are rendered from 0 to 4, with and without plus signs. Patterns (C to H) are indicated for rectrix 6. Measurements are presented for the last five characters and contain decimal points. (See text.)

^bSpecimens are: 1, M.C.Z. No. 253442, 2, C.A.S. No. 45217, 3, A.M.N.H. No. 791507, 4, A.M.N.H. No. 791508, 5, M.V.Z. No. 46918, 6, A.M.N.H. 61050, 7, A.M.N.H. No. 791485, 8, C.M. No. 20027. Specimens 1 to 4 are from southern California, 5 to 8 from Baja California.

plumaged male M.V.Z. No. 46918, which exhibits red tips farther forward on the left than on the right. The five males thus tend rather toward *scalaris* in this feature; only C.A.S. No. 45217 approaches the condition found in *nuttallii*.

The nasal tufts of the hybrids vary, as might be expected, from nearly the pure white condition of *nuttallii* (female A.M.N.H. No. 471508), almost to the dusky brownish white tufts of *scalaris*, most closely approached by male A.M.N.H. No. 791485. The latter has slightly paler feathers at the base of the nasal tufts than do individuals of *scalaris*. Five birds attain the intermediate score of 1, matched by only 2½ per cent of the specimens of *nuttallii* and *scalaris*. Two birds, both females (one mentioned above) approach *nuttallii* with scores of 0+. Most of the hybrids exhibit a yellowish discoloration (see above) of the nasal tufts, rendering difficult the determination of their color.

Three of the hybrids exhibit only a few traces (score 0+) of white in an otherwise all-black malar stripe, thus approaching the condition found in *nuttallii*. Four birds score 1 and are hence intermediate in malar color. Male

A.M.N.H. No. 791485 exhibits a malar patch heavily marked with white, as in *scalaris*. Thus all but one hybrid score in the intermediate range 0+ to 1, attained by the fewest individuals of both species. Without exception, the hybrids' faces are whiter than that of *nuttallii*. This is due to the white in the malars of some hybrids and to the restricted black auricular patch and expanded white superciliary and sub-ocular stripes in others.

Five of the eight hybrids score 1 for ear coverts, two tend toward *scalaris*, and one tends toward *nuttallii*. A few *scalaris* and *nuttallii* variant specimens also attain the score of 1. The junction of the malar and ear covert patches is large and joined to the back across the sides of the neck in two hybrids (♂ M.C.Z. No. 253442, ♂ C.A.S. No. 45217; score 0+). In these specimens, however, the black region definitely is smaller than that of typical *nuttallii*. The other five specimens exhibit either a tenuous juncture of the auricular-malar patch with the back, or no such connection (A.M.N.H. No. 791508). The mode of preparation of these skins is such that I cannot be certain that there is a contact between these areas. However, this contact is

readily observable in most specimens of *nuttallii* despite a diversity in modes of preparation. It is evident that the main factor responsible for making it difficult to determine the occurrence and extent of the junction of the black back, malar, and auricular regions is the restricted black face pattern of the hybrids, which mainly score in the intermediate range as might be anticipated.

Most of the hybrids are intermediate or tend toward *scalaris* in eye-stripe color, but A.M.N.H. No. 61050 has restricted stripes approaching (score 0+) the condition of *nuttallii*. In the extent of the black upper back most hybrids are intermediate or tend toward *nuttallii*. This patch, usually reduced or wanting in *scalaris*, is smallest in two females (A.M.N.H. Nos. 791507, scoring 1, and 791508, scoring 1+). It is more extensive in the other hybrids, and closely approaches the condition of *nuttallii* in males A.M.N.H. No. 61050 and A.M.N.H. No. 791485. In noting the condition of this feature, I gave special consideration to the manner in which the skins were prepared, for foreshortened specimens are apt to have the black of the upper back covered by nuchal and middle back feathers.

The hybrids have from three-and-one-half to four-and-one-half bars on their eighth primaries. This character (number of bars) is not useful in appraising hybrids, but it was noted that the hybrids fall within the intermediate range between the generally broader bars of *scalaris* and narrower bars of *nuttallii*. The hybrids varied in the amount of spotting on their wing coverts from the sparsely spotted condition typical on *nuttallii* to the very spotted condition of many individuals of *scalaris*.

I have discussed (above) the wide variation in patterns of the outer three (large) rectrices in *nuttallii* and *scalaris*, especially in Baja California. Despite this variation the patterns of the hybrids can be described as intermediate. This intermediacy is generally shown in the southern California hybrid female A.M.N.H. No. 791507 (fig. 12), which is, however, *scalaris*-like in its pattern of the inner vane of rectrix 5. In fact, of the five hybrids of *P. nuttallii* × *P. scalaris cactophilus* only one, A.M.N.H. No. 61050 is intermediate (score 2) in the pattern of the inner vane of rectrix 5. Three of the others exhibit the condition found in *scalaris*, and one, the condition of *nuttallii*. None scores 3, the score at which overlap is least (1 per cent of all specimens) in the

southern California populations of the two species. When one considers the over-all patterns of the outer three rectrices, however, four of the five hybrids from southern California exceed variation in California populations of both parental species. Their variation includes mixtures of features not found in *nuttallii* or *scalaris*. Male hybrid M.C.Z. No. 253442 has the inner vanes of its outer three rectrices patterned as in *scalaris*; its outer vanes are *nuttallii*-like except that outer rectrix 3 scores 4, typical of *scalaris*. Male C.A.S. No. 45217 has *scalaris*-like inner vanes of these rectrices, but outer vanes so closely approaching *nuttallii* that the over-all pattern exceeds the variation in all *scalaris* and *nuttallii* specimens. Female A.M.N.H. No. 791507 (fig. 12) has a nearly *nuttallii*-like inner third rectrix, and *scalaris*-like inner fourth and fifth rectrices, but its outer vanes are essentially "pure" *nuttallii*. Male A.M.N.H. No. 61050 has outer vanes patterned like *nuttallii*, and exactly intermediate inner vanes. The variation of the inner vanes tends toward *scalaris* more than any specimen typical of *nuttallii*. Only A.M.N.H. No. 791508 matches one of the parental species, *nuttallii*.

One of the three Baja California hybrids lacks outer (large) rectrices. The other two (one, A.M.N.H. No. 791485, is illustrated in fig. 12) tend to be intermediate in their outer tail patterns, but both fall within the range of variant specimens of *scalaris*.

I consider the mixture of patterns shown in the southern California birds to be an effect of hybridization. Particularly significant is the variation among the rectrices in their outer and inner vane patterns. The patterns of the outer vanes of rectrices three to five tend to be closely correlated. Likewise, patterns of the inner vanes of these rectrices appear correlated. Although both *nuttallii* and *scalaris* exhibit variation between the patterns of the outer vanes and those of the inner vanes, only in hybrids does one find great variation among outer vane patterns of the three rectrices, or among their inner vane patterns. The genetic control of the patterns of the outer vanes thus seems to be independent of that of the inner vane patterns. Breakdown of such control within these complexes appears to be a feature induced by hybridization.

The patterns of the sixth rectrix (table 18) of the California hybrids include pattern groups F, G, and H. No California specimens of *nuttallii*

fall in these pattern groups. Only one of 193 specimens of *P. scalaris cactophilus* achieves a pattern of group G, but two hybrids (C.A.S. No. 45217, A.M.N.H. No. 791508) do so. Two hybrids (M.C.Z. No. 253442, A.M.N.H. No. 791507) have patterns of group F, thus exceeding variation in both *nutallii* and *scalaris* in California. One hybrid (A.M.N.H. No. 61050) exhibits a *scalaris* variant pattern of group H. Because of the greater variation in pattern of the sixth rectrix in both *nutallii* and *scalaris* populations in Baja California, they overlap widely in these patterns (see discussion above). Two of the hybrids (M.V.Z. No. 46918 and A.M.N.H. No. 791485) have patterns of groups F and G, respectively; both fall in the area of overlap, although these patterns more frequently occur in *scalaris* than in *nutallii*. Hybrid female C.M. No. 20027 has a pattern of group C, which is found in nine specimens (of 65) of *nutallii* from Baja California, but is lacking in California specimens of that species.

When allowance is made for the effects of wear and discoloring, the plumage of the underparts of the hybrids generally exhibits the buffy cast typical of *scalaris*. Two males (C.A.S. No. 45217, M.V.Z. No. 46918) show fully as much buffy cast as does *scalaris*. Male A.M.N.H. No. 61050 and females No. C.M. 20027 and A.M.N.H. No. 791507 are somewhat intermediate in this feature, due to the effects of hybridization and possibly plumage wear. All three of these birds exceed the variation found in comparably plumaged specimens of *nutallii* in showing some buffy coloration of the throat. The remaining two males and a female approximate the ventral coloration of extremely discolored, worn specimens of *nutallii*. Soap, water, and carbon tetrachloride removed some, but not all the discoloration from female A.M.N.H. No. 791508; the remaining buffy coloration may be due to hybridization, persistent discoloration, the unusual retention of some such coloration normally occurring in fresh (fall) plumaged *nutallii*, or to any combination of these factors.

In ventral markings, only two males among the hybrids are clearly intermediate. Male A.M.N.H. No. 61050 has the heavy posterior (flank) barring of *nutallii* but its anterior markings are all narrow and streaklike. Male A.M.N.H. No. 791485 is heavily barred posteriorly, but has narrow, droplet-like anterior markings. Three hybrids (male M.C.Z. No.

253442; females A.M.N.H. Nos. 791507 and 791508) fall within the range of variation of *scalaris*, although the male is at the heavily marked extreme of that species. The remaining three birds are *nutallii*-like in ventral markings, but male M.V.Z. No. 46918 has a few narrow, *scalaris*-like spots distributed medially on its breast.

The strong resemblance of *nutallii* and *scalaris* in mensural characters makes difficult the detection of hybrids. Nevertheless, certain facts emerge from comparison of the putative hybrids with appropriate (seasonally, geographically) samples of the parental forms. In wing length, five hybrids fall within the broad areas of overlap. Two, C.A.S. No. 45217 and A.M.N.H. No. 791507 fall outside the range of *nutallii* and within the range of *scalaris*. Another (A.M.N.H. No. 61050) has shorter wings than has *scalaris*, falling within the range of *nutallii*. Despite great overlap in tail length, M.V.Z. No. 46918 is outside the range of *nutallii*, and C.M. No. 20027 does not attain the low range of *scalaris*. Tail/wing ratios show that hybrid M.C.Z. No. 253442 falls below the range of *nutallii*, but the other four southern California hybrids are in the range of overlap in this trait. Four of the hybrids have bills too long for *nutallii*, two (A.M.N.H. Nos. 61050, 791485) have bills shorter than *scalaris*, one (A.M.N.H. No. 791508) falls within a narrow range of overlap, and one (M.V.Z. No. 46918) is intermediate in bill length. In bill width most hybrids fall within the area of overlap, but two (A.M.N.H. Nos. 791507 and 791508) exceed *nutallii* and are *scalaris*-like. Only one hybrid (C.A.S. No. 45217) has black back barring so narrow as to fall entirely outside the range of *nutallii*, whereas two (A.M.N.H. No. 61050, C.M. No. 20027) have bars too broad for *scalaris*. The remainder of the specimens fall within the range of overlap.

The hybrids thus combine various features of *nutallii* and *scalaris*. Some intermediacy is evident in those characters by which these species differ sufficiently to allow determination of intermediate states. However, overlap is so common that the intermediate condition of the hybrids is precluded. Rather, for most characters the hybrids are intermediate to the extent of falling within the overlap range. I believe there is a sufficient mixture of the characters of both species in five of the eight putative hybrids to preclude their being extreme variant individuals

of one or the other species. Three birds might be questionable in this regard. Male M.V.Z. No. 46918 is more *scalaris*-like than *nutallii*-like. Unfortunately its outer rectrices are lacking. It falls within the overlap range in so many characters that in this attribute alone it is unique so far as specimens of either species are concerned. It seems to depart sufficiently from *scalaris* in bill length and in reduction of red in its crown (it is a fall bird, hence crown color is easily evaluated) to indicate its hybrid nature. Female A.M.N.H. No. 791507 is *scalaris*-like over all, but it falls within the overlap range in many characters, its nasal tufts are very white (within the range of *nutallii*), and the patterns of its outer rectrices, and of rectrix 6 are clearly intermediate between *scalaris* and *nutallii*. Finally, male A.M.N.H. No. 61050 is very like *nutallii* in a number of characters, but its rectrix 6 pattern is a variant *scalaris* pattern, and it is intermediate in the pattern of its outer rectrices and in crown color. Hence, I include these three birds among the hybrids between *nutallii* and *scalaris*.

OTHER POSSIBLE HYBRIDS, BACKCROSS PRODUCTS, OR INTROGRESSANT INDIVIDUALS

In the absence of information regarding the genetics of hybridization between the Nuttall's and Ladder-backed woodpeckers, it is difficult to set limits on the variation of F_1 hybrids. If backcrossing occurs, and I believe that it does, then diverse variant individuals can be expected to occur to the extent that such backcrossing prevails. Backcross products, and even F_2 hybrid progeny, may closely approach parental phenotypes. Such individuals also may resemble introgressant birds that have only indirectly received genes of the other species (through gene flow, backcross and F_2 individuals breeding with genotypically pure individuals of the parental forms and thus passing along alien genes and gene combinations). I have picked 36 individuals (other than the eight hybrids) that resemble one species in most features, but also show some approach toward the other species. These birds do *not* include every such individual (see below on introgression). Two of the main reasons for selecting these birds were to include among them at least all definite hybrids not already designated as "hybrids," and to exclude all possible hybrids (F_1 , F_2) from the samples of the

parental forms to be used in the analysis of possible effects of introgression. I do not imply that each of the 36 birds is a hybrid, a backcross product, or an introgressant individual, but only that each exceeds the usual variation of one or the other species in a manner suggesting this as a possibility.

The 36 birds differ from the hybrids generally in these ways: 1) they show less mixture of traits of the two species, and rather a predominance of those of one species; 2) they less frequently score in the overlap ranges of those characters in which the species overlap; and, 3) they less often show intermediacy in characters in which the species do not overlap. Of the 36 woodpeckers, 17 tend toward *scalaris*; of these nine are designated as "probable introgressants," and eight showing fewer tendencies toward *nutallii* are designated as "possible introgressants." These terms are mere labels, as they may include hybrids, backcross products, truly introgressant birds, and simply extreme variant Ladder-backed Woodpeckers. The other 19 birds tend toward *nutallii* and include seven designated as "probable introgressants" and 12 designated as "possible introgressants." A significant fact is the disparity of the sexes in the two groups, for only four of the 17 birds tending toward *scalaris* are males, whereas males number 14 among 19 individuals tending toward *nutallii*. Localities from whence came most of these 36 birds (those for which locality data are available, and the localities of which fall in the areas mapped) are shown in figures 3 and 4.

In table 22 I have attempted to summarize the features in which the 36 specimens exceed the variation in one or the other species and tend toward the other species, and those in which the overlap range is attained. All 19 of the *nutallii* introgressants, and all but four of the 17 *scalaris* introgressants exceed variation of their respective species in at least one character (nine of the former and seven of the latter do so in two or more characters), in some cases being intermediate and in others falling within the range of the other species instead. Four of the *scalaris* introgressants do not exceed variation in *scalaris* in any one character. However, they fall within the range of overlap of the two species in four or five characters, including in each instance several characters in which they are at the extreme of the range of *scalaris*. That they fall within the

TABLE 22

POSSIBLE EFFECTS OF HYBRIDIZATION OR INTROGRESSION ON 36 "INTROGRESSANT" WOODPECKERS

Specimen	Locality	Unusual Traits Tending toward Other Species ^a
PROBABLE <i>nutallii</i> INTROGRESSANTS		
♂ A.M.N.H. No. 791515	Onyx, Calif.	Wing length; wing marks; upper back; rectrix 6
♂ M.V.Z. No. 19856	Isabella, Calif.	Crown; rectrix 6; wing marks; underparts
♂ A.M.N.H. No. 437984	Calif.	Wing marks; crown; rectrix 6; malar; 4 others
♂ A.M.N.H. No. 363667	San Jose, BC	Crown; malar; underparts; rectrix 6; 3 others
♂ A.M.N.H. No. 791477	E. Ensenada, BC	Bill length; outer rectrices; tail; malar; 3 others
♀ M.V.Z. No. 4017	Witch Creek, Calif.	Tail length; outer rectrices; rectrix 6; malar; 2 others
♀ A.M.N.H. No. 791444	San Jose, BC	Bill width; outer rectrices; eye stripe; malar; 5 others
POSSIBLE <i>nutallii</i> INTROGRESSANTS		
♂ M.V.Z. No. 11899	Riverside Co., Calif.	Bill length; wing length; back bars; underparts
♂ M.V.Z. No. 11900	Riverside Co., Calif.	Rectrix 6; wing marks; upper back; underparts; 2 others
♂ A.M.N.H. No. 791518	Weldon, Calif.	Rectrix 6; wing length
♂ A.M.N.H. No. 791519	Victorville, Calif.	Rectrix 6; wing length; back bars; malar; 5 others
♂ C.M. No. 20033	Carrizo Valley, BC	Outer rectrices; rectrix 6; neck; malar; 3 others
♂ C.A.S. No. 34988	Beaumont, Calif.	Crown; malar; underparts
♂ M.V.Z. No. 19844	Walker Pass, Calif.	Upper back; rectrix 6; bill width; 2 others
♂ M.V.Z. No. 1791	San Jacinto Mts., Calif.	Crown; rectrix 6; bill width; 2 others
♂ A.M.N.H. No. 791474	Concepcion, BC	Crown; back bars; wing length; malar; 2 others
♀ M.V.Z. No. 32538	Pasadena, Calif.	Outer rectrices; bill length; back bars; 3 others
♀ C.A.S. No. 34990	San Fernando, Calif.	Outer rectrices; bill length; bill width; 3 others
♀ C.M. No. 20035	Carrizo Valley, BC	Outer rectrices; wing length; wing marks
PROBABLE <i>scalaris</i> INTROGRESSANTS		
♂ A.M.N.H. No. 791495	S. Santo Tomas, BC	Wing length; crown; rectrix 6; malar; 3 others
♂ A.M.N.H. No. 791496	Las Cabras, BC	Upper back; wing length; rectrix 6; outer rectrices
♀ M.V.Z. No. 49834	V. de la Trinidad, BC	Bill width; nasal tuft; tail length; 2 others
♀ S.D. No. 17219	S. Matias Pass, BC	Bill width; tail length; wing marks
♀ M.C.Z. No. 253445	S. Santo Domingo, BC	Malar; rectrix 6; wing marks; 2 others
♀ C.M. No. 20026	Valladares, BC	Nasal tuft; outer rectrices; tail length; 3 others
♀ A.M.N.H. No. 791498	E. Ensenada, BC	Rectrix 6; tail length; upper back; underparts
♀ A.M.N.H. No. 791499	E. Ensenada, BC	Bill length; tail length; rectrix 6; upper back
♀ A.M.N.H. No. 791503	Concepcion, BC	Bill length; eye stripe; neck; underparts; 4 others
POSSIBLE <i>scalaris</i> INTROGRESSANTS		
♂ M.V.Z. No. 133900	Santa Rosa Mts., Calif.	Upper back; rectrix 6; wing length; underparts; 4 others
♂ S.D. No. 17200	V. de la Trinidad, BC	Bill length; bill width; eye stripe; rectrix 6; 5 others
♀ C.M. No. 49054	Hesperia, Calif.	Upper back; tail length; back bars; neck; 2 others
♀ A.M.N.H. No. 791497	E. Ensenada, BC	Bill length; upper back; wing marks; malar; 3 others
♀ A.M.N.H. No. 791502	SE. Ensenada, BC	Tail length; neck; underparts; wing marks; 2 others
♀ A.M.N.H. No. 791501	E. Ensenada, BC	Rectrix 6; tail length; upper back; bill width
♀ M.V.Z. No. 1706	Cabazon, Calif.	Wing length; tail length; malar; ear coverts; 5 others
♀ C.A.S. No. 26644	Cottonwood Spa, Calif.	Bill length; underparts; tail length; 2 others

^aCharacters listed in column 3 in order from those showing a condition matching the other species, through those in which the specimen is intermediate, to those in the overlap range (see text).

extreme range in several characters is significant and may indicate introgression.

Perusal of tables 10 to 20 will indicate that, for character after character, the "introgressants" (pooled "probable" plus "possible" introgressants), as a sample, tend away from

their respective species and toward the other species. The proportion of high-scoring *nutallii* introgressants is in every case greater, usually much greater, than in any sample of *P. nutallii*. Likewise, low-scoring *scalaris* introgressants generally comprise a much greater proportion of

that sample than do low-scoring individuals of any *scalaris* sample. Finally, taken together the introgressant and hybrid samples clearly bridge the gap between *scalaris* and *nuttallii* in character after character.

Some of these 36 specimens, probably most or all of those in the "probable" category and most of those in the "possible" category, are undoubtedly hybrids or introgressant individuals. It is not of great importance whether every one of these birds represents a hybrid, backcross product, or introgressant individual. The nature

of the variation in the two species and the rather subjective analysis of qualitative characters, especially, make it likely that at least a few such individuals have passed my scrutiny. Allowing only for the possibility that some or all the "probable introgressants" are actually hybrids, I find the total number of hybrids between *P. nuttallii* and *P. scalaris* is of the order of eight to 24 individuals (from among 44 possible hybrids, including the above-mentioned 36 birds and the eight definite hybrids).

INTROGRESSION, CHARACTER CONVERGENCE AND CHARACTER DISPLACEMENT

The occurrence of introgression, the flow of genes from one to another well-differentiated population as a consequence of successful hybridization (see Short, 1965a, p. 360), can be demonstrated in two ways. It may be assumed that (some) introgression occurs whenever hybridization involves backcrossing. Lacking knowledge of the mating success of hybrids and their ability to backcross, one is forced to utilize evidence drawn from variation within each form involved, and the spatial orientation of this variation with respect to the zone in which interbreeding takes place. In terms of variation in these forms, one can expect: 1) each form to exhibit traits of the other increasingly as one approaches their area of contact if they are interbreeding extensively, or have done so in the past (introgression); 2) the forms to differ more where they meet or are somewhat sympatric if little or no hybridization is occurring (character displacement); 3) perhaps occasionally, the forms to resemble one another more closely where they are sympatric rather than allopatric, if no hybridization is occurring, due to social mimicry (one type of character convergence; see Moynihan, 1968); or, 4) increased variation and approach of two species toward each other in some traits in their region of sympatry, if they are reproductively isolated, through the effects of similar selection pressures in the same environment (a second type of character convergence).

It was evident from field studies of *Picoides nuttallii* and *P. scalaris* that these species do not interbreed very frequently where they occur together, but that most matings are between

conspecific individuals. This rules out massive introgression, but it does not preclude the occurrence of widespread introgression in the past leaving effects that are detectable today. Thus, any one of the above four alternatives could apply in this situation.

Let us examine the available data, and then discuss the conclusion or alternatives they suggest. It is clear that obvious hybrids and even possible hybrids should be excluded from comparisons between and within the two species. I have excluded from consideration in this section the 44 individuals discussed above. These include eight birds regarded as hybrids, and 36 possible hybrids, although the latter almost certainly contain introgressant individuals also. To the extent that some nonhybrid individuals that show the effects of introgression comprise part of this "hybrid" sample, the present analysis will minimize any effects of introgression.

Picoides nuttallii

Many of the data are contained in the various tables (10 to 20). Comparing samples of *P. nuttallii* from southern California and Baja California with the northern California sample, we see that a tendency in the direction of *P. scalaris* is indicated for crown color, nasal tufts, ear coverts (not in the Baja California sample), color of underparts, outer rectrix pattern, and wing length. For example, two-thirds of the males of *nuttallii* comprise the southern California and Baja California samples for crown color, but these include more than 90 per cent of those

Nuttall's Woodpeckers scoring 0+ or more in this character (table 10). Similar results are obtained with the data from the other characters mentioned. Additionally, the Baja California population tends toward *scalaris* even more than does the southern California population in the pattern of rectrix 6 (table 18) and in the pattern of its outer rectrices (table 17). The data for rectrix 6 are particularly indicative, for about half of the Baja California sample have patterns not found in California *nuttallii*, although several of these are found in *scalaris*. Likewise, significantly more barring occurs in the outer tail feathers of Baja California *nuttallii*. This is shown especially by the inner vanes of the outer rectrices. For example, 14 per cent (25 of 184) of northern California *nuttallii* specimens, 28 per cent (83 of 301) of the southern California sample, and 46 per cent (37 of 81) of the Baja California sample score 0+ or more in the pattern of the inner vane of rectrix 4. Chi-square tests show that the number of northern California birds exhibiting higher scores is significantly less than the number of such southern California birds, and the number of Baja California high-scoring birds is significantly greater than the number of southern California woodpeckers with such scores (Chi-squares 11.90 and 19.53, respectively, giving P values greater than 0.99).

In contrast to the evidence suggesting convergence toward *scalaris* in some characters, I could find no indication in *nuttallii* of enhancement of differences between the two species. All of the data for the samples just discussed were compared in an effort to find such indications. In addition, I split the large southern California *nuttallii* sample into two subsamples, one from the western region away from the range of *scalaris*, and the other from the region within 15 miles of the range of *scalaris*. These were compared for all characters, and no significant differences were detected. In addition each was compared separately with the northern California sample. Generally, both samples differed from the northern sample to the same degree in the characters (discussed above) by which the combined southern sample has been shown to differ from the northern sample. The comparison of measurements of birds among the various seasonal and sexual subsamples did show more significant differences (in longer wings, longer tail, broader male back bars, broader bill of

females in southern California birds) between northern *nuttallii* and the southern sample from close to the range of *scalaris* than between the former sample and the southern sample from the area more distant from *scalaris*. Some of these differences suggest a tendency toward *scalaris*, but they also could reflect adaptation to higher altitudes (the area within 15 miles of the range of *scalaris* is largely mountainous and hence higher in altitude than the coastal area from which the other sample came). In any event I find no morphological evidence for character displacement in *nuttallii*.

Picoides scalaris

Within *P. scalaris* comparisons were made between: 1) a western sample of *P. s. cactophilus* from central southern California (west of the Salton Sea, essentially "*mojavensis*" discussed by Short, 1968) and eastern samples from the Colorado River Valley ("*yumanensis*," see Short, *op. cit.*), and from Arizona; and 2) a northern sample of *P. s. eremicus* and a southern sample of the same race (also the more southerly peninsular Baja California *P. s. lucasanus* was compared with these). The western *cactophilus* sample represents a population in limited contact with *P. nuttallii*, and the northern *eremicus* sample is drawn from a population sympatric with *nuttallii*. Hence both of these would be particularly subject to introgression and character displacement.

Many of the data used in the comparisons are contained in tables 10 to 20, and some have been presented elsewhere (Short, 1968). Tendencies toward *nuttallii* in the western *cactophilus* sample include these characters: nasal tufts, eye stripe, neck pattern, malar, upper back, and the patterns of rectrix 6. From almost twice as many (upper back, 43 per cent versus 23 per cent) to more than twice as many (rectrix 6, 19 per cent versus 8 per cent) individuals of western *cactophilus* tend toward *nuttallii* in their scores for these characters as do individuals of eastern *cactophilus*. Some of these differences are not significant because of the low percentages and relatively few individuals differing from the typical condition. However, the differences between the samples in nasal tufts and malar approach significance despite small percentages, and their differences in neck, upper back, and rectrix 6 are significant (probability more than

0.99 by Chi-square tests). The western *cactophilus* sample also tends toward *P. nuttallii* in tail/wing ratio. A significantly greater portion (Chi-square 10.04, *P* over 0.99) of western birds have tail/wing ratio over 0.62 than do eastern birds.

The northern sample of *P. s. eremicus* exhibits even stronger tendencies toward *nuttallii* in the same characters (except upper back), plus ear covert pattern, surpassing southern *eremicus* (and all samples of *cactophilus*) in the proportion of low-scoring individuals by just under two to one (rectrix 6, 45 per cent versus 25 per cent) to as much as 11 to one (ear coverts, 11 per cent versus 1 per cent). Most of the differences are difficult to test for significance because of the low incidence (generally 1 to 5 per cent) of *nuttallii* scores in the southern *eremicus* sample. However, testing the larger southern sample using the percentages of the smaller northern sample indicates that the differences are highly significant (standard statistical practice dictates that one test the smaller sample on the basis of the larger one, but considering the size of the differences involved and the fact that the samples are not widely disparate in size, the reverse procedure appears satisfactory). The only exception is in rectrix 6 pattern, but here the occurrence of more pattern types tending toward *nuttallii* in the northern sample indicates that there is indeed a tendency toward *nuttallii*. The northern sample exhibits 13 patterns of four groups other than H and I, whereas the southern *eremicus* sample shows only six patterns in three such groups, and the more southerly *lucasanus* sample contains six patterns of but two such groups (table 19).

Thus, samples of *cactophilus* and especially of *eremicus* in proximity to, or sympatric with, *P. nuttallii* tend toward the latter in some traits. Although there is no detectable cline in this feature, it is worthy of emphasis here that the entire peninsular Baja California population of *scalaris* (races *eremicus*, *lucasanus*) differs from all of the many other races of *P. scalaris* and resembles *P. nuttallii* in tail/wing ratio.

Individuals of both populations of *scalaris* in contact with *P. nuttallii* have, on the average, longer bills than those in birds from farther east and south (in fact, these are the longest-billed populations of *scalaris*), thus diverging both from conspecific birds elsewhere, and from *nuttallii*. Mean bill length of samples of western

cactophilus averages about 1.5 mm. greater than means for Arizona samples (Short, 1968). All samples of northern *eremicus* have slightly greater means for bill length than in southern *eremicus*, and about 1.8 mm. greater than those for *lucasanus*. These tendencies are most evident on viewing a histogram (fig. 11). Additionally, western *cactophilus* specimens have longer wings by 2 to 3 mm. and wider bills by 0.5 to 1 mm. on the average than have birds from farther east. Thus, they tend away from *nuttallii* in these features. It is noteworthy that the Ladder-backed Woodpeckers in southern California (western *cactophilus*) live at no greater altitude or latitude than those inhabiting Arizona. The northern portion of *P. s. eremicus* does not tend away from *nuttallii* and from southern *eremicus* and *lucasanus* in wing length or bill width, but the outer rectrices of these birds tend to be more barred, especially on the inner vanes, than in birds from farther south. For example, only 22 per cent of the northern birds score 2 and 3 for inner rectrix 5 pattern, but 42 per cent of the southern sample score not only 2 and 3, but 1 as well. This difference is highly significant (Chi-square 8.9, *P* greater than 0.99).

CHARACTER CONVERGENCE AND DIVERGENCE

Thus, *scalaris* and *nuttallii* approach each other in some features, and diverge in others, where their ranges meet. In relation to the problem of character convergence, there appear to be several points that militate against social mimicry as a causal factor. It seems that selection favoring convergence of two species to facilitate their social interactions cannot commence operation until complete reproductive isolation precludes their interbreeding. If it does operate prior to that time it may counteract reinforcement of isolating mechanisms and increase hybridization. As the Ladder-backed Woodpecker does hybridize with the Nuttall's Woodpecker it would appear that hybridization must diminish and even cease before convergence due to social mimicry could take place. It is unlikely too that such convergence would affect *P. s. cactophilus* and *P. nuttallii* in California, where there is barely any contact and no overlap. Convergent characters of northern *P. s. eremicus* are clinal in their variation, scores typical of *nuttallii* generally diminishing to the south. I would expect these traits to be restricted more sharply

to the small area of sympatry between *eremicus* and *nuttallii*. One of the features affected by convergence, the pattern of rectrix 6, is inconspicuous, and it is very doubtful that it would function as a visual signal in social interactions. There is no question about the interaction of individuals of the two species, which even maintain exclusive territories against each other, and facilitation of social behavior is possible, but I rather regard their interactions as a result of their very close relationship, requiring at this point in time a reduction of their interactions and not their facilitation. Nevertheless, it is significant that variation exists within the two species ultimately to enable social mimicry, a case of which may involve the related, closely similar Downy Woodpecker and Hairy Woodpecker.

Can the observed convergence reflect the similar responses of the two species to the effects of selection in a similar environment? This is certainly possible, although it is not likely that this explains the observed variation in most of the characters. *Picoides nuttallii*, particularly, free from possible effects of competition from *P. pubescens* in southern California and Baja California, and there encountering more arid conditions than occur farther north in its range, might be expected to tend toward *scalaris*. However, I doubt that environmental conditions in the region where the range of *scalaris* approximates that of *nuttallii* differ sufficiently from those elsewhere in the range of *scalaris* (e.g., central Mexico, Arizona, mountains of southern Baja California) to account for a marked convergence toward *nuttallii*. Also if these variations are strictly environmentally correlated, it is difficult to understand why the convergent populations are so variable in the traits involved, that is, why have the normal frequency distributions for these characters not been narrowed about some optimum point as they have in populations elsewhere? Finally, there is the point that the convergence observed involves a number of color patterns. These are obviously visible to the birds, as well as to us, and it is likely that at least some involve features serving as recognition marks, or in other ways as elements of displays.

Granted that hybridization does occur between these woodpeckers, it is difficult to believe that the environmental correlates of the genes responsible for these patterns are so strong precisely in the area where the species meet, as

there and only there so to cause each species to approach the other. Rather, one would expect that if these correlates are strong, then populations of *nuttallii* and *scalaris* ought to show such variation elsewhere (wherever some similar conditions obtain), or that if they are not strong, then there should be divergence, not convergence in these characters where the two species meet, or that at least the differences that obtain elsewhere should be maintained in the region of contact.

Other populations of *scalaris* are indeed somewhat variable. The lower Colorado River Valley population of *P. s. cactophilus* has narrower back bars than other populations of that race (Short 1968; it is mensurally intermediate in some features between other Arizona populations and western California birds). The southwestern Utah population of *cactophilus* (Short, *op. cit.*) mensurally approaches the southwestern California birds, and is intermediate between the Colorado River and the central Arizona populations in back barring. Also, the Utah birds show a high incidence (42 per cent, nine of 21 birds) of 0 to 1+ neck pattern scores. This is the only instance of color pattern variation tending toward a *nuttallii* pattern away from the *scalaris-nuttallii* area of contact. This variation suggests, as might be expected, that mensural characters and back barring are plastic features easily influenced by environmental or other random factors. Despite the fact that one or another trait involving color pattern also may be so influenced, it is significant that by far the most variable populations of *scalaris* are those in contact with *nuttallii*. Thus, while I concede that local selection and intraspecific variation may strongly influence the features considered above, I do not believe that they account for convergence to the degree observed, and in all the characters in which it is observed in populations of *scalaris* in proximity to *P. nuttallii*.

Introgression, past and present, seems a factor likely to explain most of the convergence noted. When one considers that hybrids have been found despite the very tenuous contact between the two species in southern California, it is quite possible that greater contact and more frequent hybridization occurred in the recent past than at present. In Baja California, where hybrids are fewer despite greater contact of the two species in sympatry, they occur together in small, isolated, favorable sites. Recent increasing

aridity and the activities of man (see Short and Crossin, 1967, p. 285) probably have reduced favorable habitat for *scalaris* and *nuttallii* within the present area of sympatry. Thus, opportunity for hybridization and backcrossing was probably greater in the past.

The evidence pointing toward introgression follows. Populations of both species in proximity are more similar in several characters than they are elsewhere. In the characters in which convergence is shown, the populations in proximity are more variable than are populations more distant from the region of contact between *nuttallii* and *scalaris*. Such increased variability is a normal effect of hybridization and introgression. For example, the Baja California sample of *P. nuttallii* exhibits very great variability in the pattern of rectrix 6—indeed five pattern groups are represented among *nuttallii* populations only in that occurring in Baja California in sympatry with *scalaris* (tables 18, 19). Furthermore, four of these pattern groups are found also in *P. s. eremicus*. Rectrix 6 is tiny and well concealed by the tail coverts and rectrices, and hence its pattern is not visible to the birds. Some of the patterns of groups D, E, and F are clearly intermediate between those typical of *nuttallii* and *scalaris*, and since they are found nowhere else in the range of either species, hybridization seems the most reasonable explanation for their occurrence.

Within *P. nuttallii*, tendencies toward *scalaris* in the southern California and Baja California populations are featured by high scores in nasal tuft color (1), neck pattern (1+), color of underparts (1+), and by patterns of rectrix 6 (C, D, E, F, G) not found in northern California birds. Within *scalaris*, tendencies toward *nuttallii* in various characters are highlighted by low scores in nasal tuft color (0+), crown color (1), and by rectrix 6 pattern D in northern *eremicus*, and by malar color (0+) and by rectrix 6 pattern A (the major pattern group of *nuttallii*) in western *cactophilus*, not found elsewhere in this species. Additionally, within each race (*eremicus*, *cactophilus*) of *scalaris*, some scores or patterns tending toward, or also within, *nuttallii* are found exclusively in the populations in proximity to the range of *nuttallii*. Thus, convergence of the two species where they are in contact involves both a greater number of individuals exhibiting intermediate patterns or patterns like those of the other species, and a greater number of such

patterns exhibited by individuals of the populations in contact in comparison with conspecific populations away from the area of contact.

Based on the characters analyzed, I estimate the individuals affected by introgression (i.e., those showing indications of features of the other species) as comprising: a) below 8 per cent of the southern California population of *nuttallii*; b) perhaps 12 per cent of the Baja California population of *nuttallii*; c) about 10 per cent of the western population of *P. s. cactophilus*; and, d) from 15 to 30 per cent of the northern population of *P. s. eremicus*. Further studies probably will show these proportions to be greater than the above in populations from actual sites of contact between the two species, and less in populations removed from such sites (but included in my over-all samples). The available specimens are not sufficient in number to permit a finer breakdown of samples and more detailed analysis.

Not all characters show convergence. The introgression of genes responsible for these characters is influenced, of course, by natural selection. With limited hybridization and varying forces of selection operating on different characters, it is expected that introgression will be evident from but few characters, namely those controlled by genes, or whose genes are associated in combination with genes, not disadvantageous or markedly disadvantageous. Detectable introgression usually is but a small part of actual introgression, the effects of which may not greatly involve visible morphological attributes. Limited introgression may benefit species such as these woodpeckers. Those of their populations which are in contact are at the border of the species' ranges, where they encounter somewhat different environmental conditions than conspecific populations elsewhere. In addition they are confronted by severe competition and hybridization. In such a situation of stress, hybridization hampers the evolution of effective reproductive isolation, but it also enables each species to draw upon some genes and gene combinations of an alien gene pool confronted with the same local forces of selection and probably adapted to them in different ways. Under these circumstances advantageous genes may be more readily available through introgression than through gene flow from conspecific populations elsewhere—especially if gene flow from the latter is limited by the pattern of

distribution of the species. Without more data, it is difficult to establish precisely the amount of introgression and whether limited intraspecific gene flow is facilitating interspecific introgression.

Character displacement seems to be affecting *scalaris* alone, and it involves very few characters, namely bill length and outer rectrix pattern, which may (or could) be involved in competitive interactions and species recognition.

Thus, a combination of introgression and perhaps other factors resulting in convergence,

and character displacement seems to be occurring in these woodpeckers. The simultaneous occurrence of both divergence and convergence reflects different and possibly opposing types of selective forces operating on these interacting woodpeckers. The level of hybridization apparent today suggests that character displacement and reproductive isolating mechanisms are being enhanced, and that past hybridization may account for the present amount of detectable introgression.

THE SITUATION IN CALIFORNIA

The distribution of Nuttall's and Ladder-backed woodpeckers has been discussed earlier (see figs. 2, 3) and that information provides a convenient background for a more detailed discussion of the contact and occurrence of hybrids between these species. Five of their eight known hybrids come from the area of contact between *P. nuttallii* and *P. scalaris cactophilus* in California or barely across the Mexican border (Nachaguerro Valley, Baja California). Of the 36 other possible hybrids, backcross products or introgressant individuals, 19 come from California and the northern edge of Baja California. The latter include 15 birds tending toward *nuttallii* and four tending toward *scalaris* (this difference in numbers probably reflects the very limited collecting of *scalaris* close to the area of contact). All the hybrids come from known sites of contact (Kernville region, Victorville region, Nachaguerro Valley) between the two species. Most of the introgressants also are from near or in the zone of contact, but four *nuttallii* introgressants come from 12 to 20 miles from possible zones of contact (Pasadena, San Fernando, in Los Angeles County; 10 miles north of Beaumont in San Bernardino County; and Witch Creek in San Diego County), and one *scalaris* introgressant is from Cottonwood Springs in the Little San Bernardino Mountains. However, all hybrids and introgressants come from areas sufficiently close to the contact region as to be within the extreme range of a wandering individual of the other species, or of a hybrid originating in the contact region. Two areas where I studied these woodpeckers merit further discussion. Four of the eight hybrids (including all of the hybrids

from California) and six of the 36 introgressants come from these two areas.

THE KERNVILLE REGION

One area of contact between *scalaris* and *nuttallii* is in the upper Kern River region around Kernville, Lake Isabella, Walker Basin, and Walker Pass. In this region oak and chaparral of the lower mountain slopes surround a valley with a major stream bordered by lush riparian woodland. All of this forms habitat for *nuttallii*. Additionally, the extension of the Mohave Desert northward up Kelso Valley is such that desert vegetation, especially Joshua trees, barely reaches the upper South Kern River. One nearly dead Joshua tree marks a perhaps formerly more extensive growth at Weldon, within sight of the riparian woodland along the river. Joshua tree forests commence within a mile or so south of Weldon (upper Kelso Valley, fig. 7). East of Onyx, the South Kern River cuts sharply to the west after emanating from the mountains to the north. At the fork (Bloomfield Ranch, 4½ miles east of Onyx) is a small Joshua tree grove connected with a larger Joshua tree forest to the east (figs. 6, 14). This forest, situated in a basin, is in contact with scattered riparian groves of trees and with Joshua trees in scattered, large clusters extending east and south over Walker Pass and onto the Mohave Desert. Possible contact between the two woodpeckers in the South Kern Valley probably is enhanced by the partial isolation of the desert area in the valley from more extensive deserts to the east and south, and by the isolation of riparian woods



FIG. 14. Riparian habitat of Nuttall's Woodpeckers in sporadic contact with Ladder-backed Woodpeckers on South Fork of Kern River east of Onyx, California. Close-up of vegetation shown in figure 6, but photograph taken in March when trees were in fresh foliage. Scattered Joshua trees in foreground. Hybrid female A.M.N.H. No. 791507 was collected within one-quarter mile of this location.

from foothill woodlands by arid, often rocky lower slopes and cultivated fields around the bottomland. Also the artificial Lake Isabella bisects the riparian woodland, leaving the upper valley population of *nutallii* somewhat isolated.

Between Weldon and Bloomfield Ranch I collected (with the assistance of Fred C. Sibley) 17 *nutallii*, two introgressant *nutallii*, one hybrid, and two *scalaris* during March, 1967. The *scalaris* pair was obtained in the Joshua tree desert just east of Bloomfield Ranch, within one-half mile of where *nutallii* specimens were collected (a definite female *scalaris* was seen in the bottomland sympatric with *nutallii* in November, 1966). The female hybrid (A.M.N.H. No. 791507) was collected on March 21 as it foraged in trees bordering a field at the edge of the bottomland, immediately adjacent to a territorial pair composed of a female *nutallii* and a male probable introgressant *nutallii* (A.M.N.H. No. 791515). No mate of the hybrid was evident, although its ovary was enlarged (9 by 8 mm., ova to 3.5 mm.), and it had a brood patch. A possibly introgressant *nutallii* male (A.M.N.H. No. 791518) was collected farther west near Weldon (bottomland just east of Lake Isabella) on the same day. Altogether 17 Nuttall's Wood-

peckers were obtained during March at these two localities, which are about 5 miles apart.

Prior to my efforts, 14 specimens of *nutallii* had been collected in this region, about Weldon, Onyx, Lake Isabella, in the surrounding foothills, and in Walker Basin just to the south. One male hybrid (M.C.Z. No. 253442) was collected at Weldon in April, 1929. Older introgressant specimens include: 1) a possibly introgressant *nutallii* male (M.V.Z. No. 19844) collected at 4600 feet on the west slope of Walker Pass (an area now containing open Joshua tree-pinyon pine-juniper woods) in June, 1911; and, 2) a probable introgressant *nutallii* male (M.V.Z. No. 19856) taken at Isabella, now under Lake Isabella, in June, 1911. Of three old specimens of *scalaris* from the region, two were collected in Kelso Valley (Joshua tree desert, south of Weldon), and one (M.V.Z. No. 19839) was obtained in "tree yuccas" 5 miles east of Onyx, that is at Bloomfield Ranch, in June, 1911.

Thus, 31 *nutallii*, four introgressant *nutallii*, two hybrids, one introgressant *scalaris*, and five *scalaris* have been collected in this region over the years. With limited contact, limited hybridization and some introgression have occurred with no apparent change in the situation during

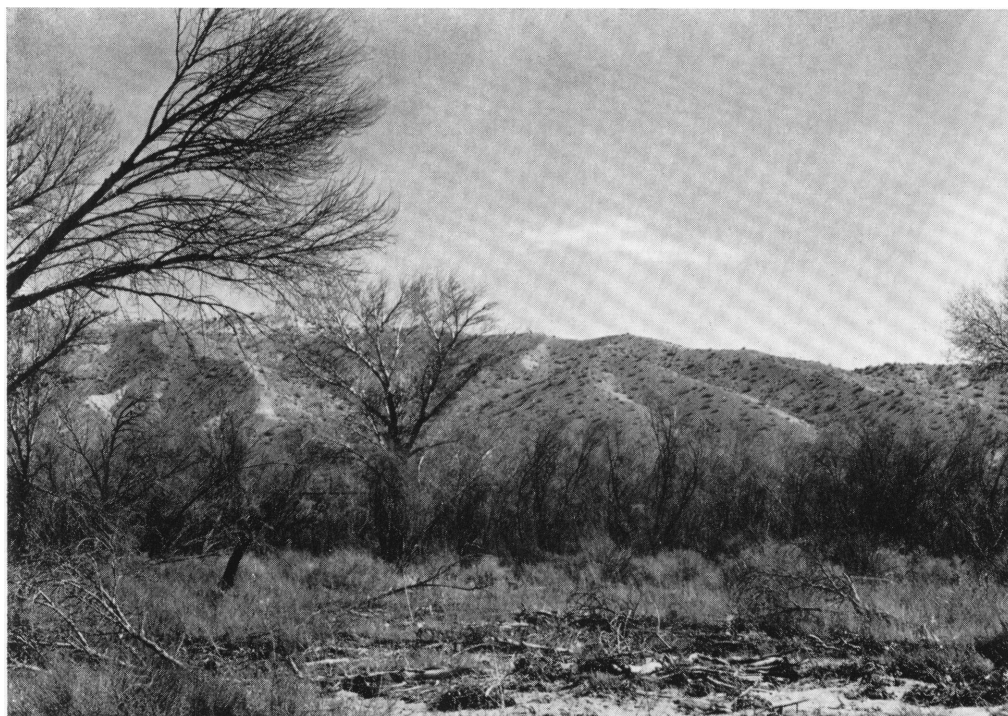


FIG. 15. Riparian habitat of Nuttall's Woodpeckers 16 miles north of Victorville, California, along Mohave River. Note barrenness of surrounding desert, from which *P. scalaris* is absent. Photograph taken in November.

that time. There are prospects of development of the Joshua tree desert in the basin east of Bloomfield Ranch for housing in the near future, which may eliminate the Ladder-backed Woodpecker, thus radically changing the contact between the two species in this area. In any event, they are in contact there today. Thus, in this region, alone of all the areas visited during my studies, four species of *Picoides* occur: *P. villosus*, *P. pubescens* and *P. nuttallii* sympatrically, and *P. scalaris* sporadically in contact with the other three.

THE VICTORVILLE REGION

This region includes the Mohave River from its point of departure from the San Bernardino Mountains south of Hesperia to about 16 miles north of Victorville (see fig. 15). At the present time riparian woodland occurs along the river at Hesperia, and from about 3 miles south of Victorville to about 16 miles north of that town. The arboreal vegetation is most dense and well developed just south of the "narrows" about a mile south of Victorville (fig. 16). To the north

from Victorville the woodland becomes narrower in extent, breaking up, with minor gaps to 16 miles north of Victorville. This woodland is completely isolated from that near Hesperia by about a 3-mile gap. Cultivated land borders the river within this gap north of Hesperia, and all riparian trees have been removed. Very widely scattered Joshua trees occur from Victorville to Hesperia, these being least common near the river (none enters the bottomland) and more common, though not clustered together, away from it. However, within a mile to the east and to the west are extensive groves of Joshua trees. North of Victorville the land along the river and back from it for several miles is exceedingly barren and devoid of Joshua trees or large shrubs of any kind (fig. 15). Even to the south of Victorville, the land surrounding the river bears little vegetation other than some grasses, very small shrubs and widely scattered Joshua trees. The barren nature of the desert around Victorville is not the result of recent changes, for Mailliard and Grinnell long ago (1905) pointedly commented about this.



FIG. 16. Riparian habitat of Nuttall's Woodpeckers where a hybrid (*nuttallii* × *scalaris*) was obtained just south of Victorville on Mohave River, California. Photograph taken in November.

During part of November, 1966, and February, 1967, I studied woodpeckers in this region, principally in the isolated riparian woodland in the vicinity of Victorville. I also studied in the northern outlying woodland 15½ miles north of Victorville. A survey of the desert surrounding the bottomland south of Victorville failed to disclose Ladder-backed Woodpeckers. Certainly the habitat close to the river could not support that species unless a substantial portion of its activity was centered in the bottomland. Otherwise, the Joshua trees are too widely scattered and the other vegetation too short to sustain the birds, especially in the nesting season. All the birds seen in the bottomland were Nuttall's Woodpeckers by appearance and vocalizations, with but one exception. The latter which proved to be a hybrid female (A.M.N.H. No. 791508), was obtained in the dense riparian timber southeast of Victorville while feeding in a grove of small ash trees in a wet area along the Mohave River. Its ovary was enlarged (6 by 4 mm.) but the ova were small, and its brood patch was not completely formed. A mate was not located although other (Nuttall's) wood-

peckers were observed nearby. One other bird (A.M.N.H. No. 791519, male) collected in this area is regarded as a possible introgressant *nuttallii*. The remaining six birds that I collected phenotypically resemble *nuttallii*.

The recently collected material (six *nuttallii*, one introgressant *nuttallii*, one hybrid) contrasts with the older material, which includes two specimens of *nuttallii*, one hybrid, one introgressant *scalaris*, and no fewer than 12 of *scalaris*. The hybrid male (C.A.S. No. 45217) was taken on December 26, 1904, apparently in the bottomland south of Victorville, by Mailliard and Grinnell (1905). These authors called attention to the intermediacy of this specimen between *nuttallii* and *scalaris*, and, prior to the present report, this was the only indication that the two species hybridize. All of the other three specimens taken by those authors, presumably in the bottomland, are typical of *scalaris*. One other specimen of *scalaris*, taken in September, 1921, is known from "Victorville." The other eight specimens of *scalaris* come from the desert 3 to 6 miles east of Victorville (three specimens) and the vicinity of Hesperia (five specimens). Also

from the vicinity of Hesperia is a possibly introgressant *scalaris* female (C.M. No. 49054) taken in 1916.

It would be fitting to regard the occupation of the upper Mohave River bottomland by *nuttallii* as another example of a western California (e.g., *Lophortyx californica*, see Grinnell and Miller, 1944), or a montane (*Picoides villosus*, personal observ.) species extending onto the desert in this area, except that the older specimens suggest that *scalaris* was at one time more prevalent than *nuttallii*. Mailliard and Grinnell (1905) collected one specimen of *nuttallii*, in addition to three of *scalaris* and one hybrid at Victorville in 1904. They clearly regarded *scalaris* as the commoner species there, and indeed considered the single example of *nuttallii* to represent a visitor from the mountains to the south. There is a possibility

that their field observations were biased by the proportion of specimens they collected. Also, all the older *scalaris* specimens from Victorville are fall and early winter birds, and these could represent wandering, post-breeding individuals. The fact remains however, that they obtained three *scalaris* and only one *nuttallii*, although *nuttallii* is prevalent there today, and one would find it difficult or impossible to find a single Ladder-back. Thus, evidence suggests a replacement of *scalaris* by *nuttallii* along the upper Mohave River. This replacement seems attributable to successful competition by *nuttallii*. Another possible factor is the deterioration of the desert vegetation surrounding the river, which has posed a barrier to the immigration of Ladder-backed Woodpeckers from the desert farther east.

THE BAJA CALIFORNIA SITUATION

The distribution of Nuttall's and Ladder-backed woodpeckers in Baja California has been discussed earlier (see fig. 4). Briefly, *P. nuttallii* is sympatric with *P. scalaris eremicus* at scattered favorable sites within a small region of northwestern Baja California from about Ensenada south to San Quintin inland from the coast and west of the mountains. Three hybrids, and 17 of the 36 possible hybrids, backcross products and probable and possible introgressant individuals come from localities within the area of sympatry in Baja California. Of the latter group four are introgressant *nuttallii* and 13 are introgressant *scalaris*, the reverse of the situation in California. Six sites merit detailed discussion. Representing these sites, all of which are described and two of which are illustrated by Short and Crossin (1967), are three of the Baja California hybrids and six of the 17 introgressants.

STUDY SITE, 31 MILES EAST OF ENSENADA

This area is figured and its ecology is discussed by Short and Crossin (1967, fig. 2, p. 283; see also fig. 17 herein). Briefly, the upper reaches of a small stream are bordered by small groves of cottonwoods and willows, surrounded by desert, but adjacent to upland chaparral and connecting upstream with live oaks and sycamores. Separated from this riparian growth by a tree-

less gap of 2 to 3 miles is an isolated large grove of cottonwoods and willows completely surrounded by desert (for several miles) at 25½ miles east of Ensenada (fig. 18). Birds from this isolated grove area are included in the present discussion. Altogether, Crossin and I obtained 15 specimens: three of *nuttallii*, one introgressant *nuttallii*, three introgressant *scalaris* and five *scalaris* specimens from the major riparian woodland and one introgressant *scalaris* and two *scalaris* at the isolated grove of trees downstream. The specimens of *scalaris* definitely represent the race *eremicus* and this is the northernmost record of that subspecies during the breeding season. Although I took no hybrids at these localities, the introgressant birds and interactions between the species there suggest that hybridization occasionally occurs. Interactions among the birds at these localities, and their territorial borders are discussed below.

It is impossible to establish how recent the xeric conditions are in this region. I believe that there has been at least some recent enhancement of aridity, which has allowed *scalaris* to extend its range into the area. The formerly more extensive riparian habitat of *nuttallii* has been constricted generally, and restricted eastward toward the base of the mountains, according to this view. Under such circumstances *nuttallii* has been subjected to severe competition from

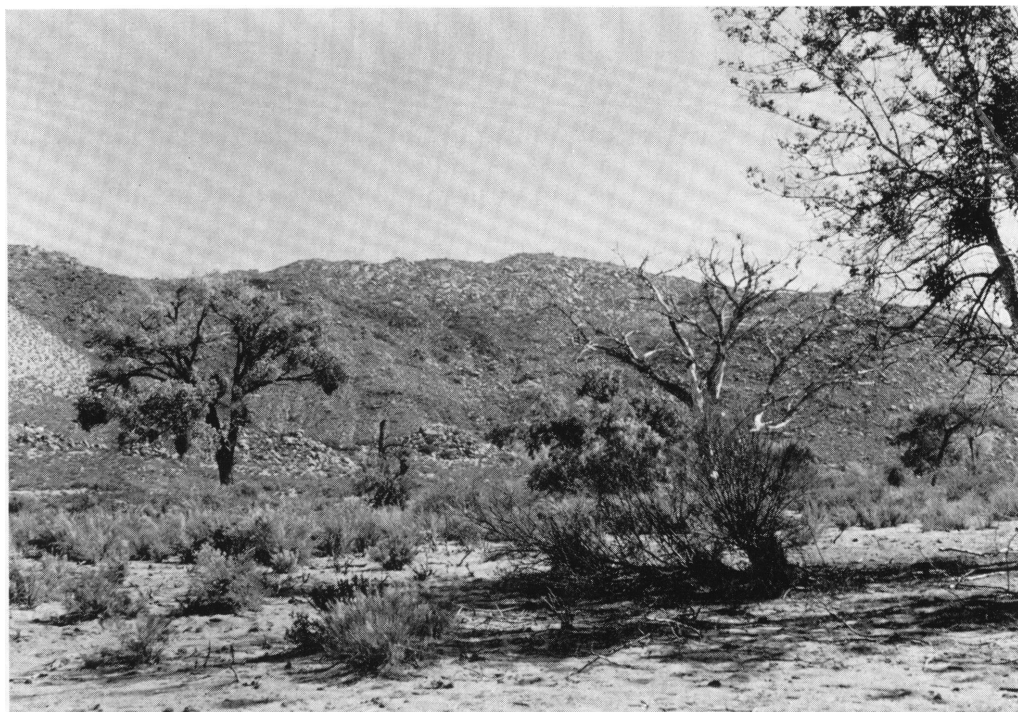


FIG. 17. Study area 31 miles east of Ensenada, Baja California. Open area back from stream showing two large cottonwoods (center left with foliage and dead tree center right) in which extended encounters took place between male Nuttall's and Ladder-backed woodpeckers.

scalaris, and reduction in its numbers may have favored an increase in hybridization.

RANCHO ESCONDIDO

This locality, situated 23 miles southeast of Ensenada, is discussed by Short and Crossin (1967, p. 287). A large grove of cottonwoods and willows with no understory, used as a woodlot, comprises virtually the only arboreal cover. There are some small trees leading up and down the Arroyo San Carlos from the main wooded area, but the woodpeckers were found only in the latter. The surrounding arid countryside is ecotonal in its vegetation, containing chaparral and desert plants. The area appears to have suffered severely from overgrazing and cultivation, and I strongly suspect that luxuriant and extensive arboreal vegetation once occurred along the arroyo.

One apparent pair of woodpeckers occupied the woodlot, and no other birds were found upstream, downstream, or in the surrounding country. The male (A.M.N.H. No. 791485) of

the apparent pair, a hybrid, was collected on April 15, 1967, as it excavated a cavity 13 meters up in a cottonwood tree. It gave the sharp "peek" call of *scalaris*. The testes of this bird were very large (10 by 6 mm.) and it had a well-developed brood patch. Its apparent mate (A.M.N.H. No. 791501) was taken feeding nearby at the edge of the woodlot. This female, possibly an introgressant *scalaris*, called "peek" (as *scalaris*) and had a large ovary and ova (ovary damaged, but ova to 5 mm.), and a fully formed brood patch.

Perhaps an isolated population of *nuttallii* once inhabited this area, became reduced in numbers, and an occasional bird interbred with a wandering individual of *scalaris*. Or occasional individuals of both species may reach the area and hybridize in the absence of conspecific mates.

RANCHO SANTA CLARA

This ranch is in the upper Arroyo Uruapan, 26 miles southeast of Ensenada, and 7 road miles south of Rancho Escondido (see Short



FIG. 18. Small, isolated willow-cottonwood grove, south end of Ojos Negros Valley, northern Baja California. Habitat of at least three, probably four Ladder-backed Woodpeckers. About 5 to 6 miles downstream from study area 31 miles east of Ensenada, this grove is surrounded by overgrazed desert grassland (foreground) and desert (hills to left of picture).

and Crossin, 1967, p. 287, and fig. 1). Here we found relatively good grassland in the valley with scattered willows and cottonwoods along the stream. The surrounding country is open and xeric, but with occasional low chaparral, and some well-scattered live oaks and scrub-oaks on the lower slopes just above the valley. Trees are too scattered and small to support woodpeckers farther east, but a broken line of small and moderate-sized trees leads westward down the ravine. At the west end of the ravine, 5 or 6 miles west and 1500 feet in elevation below Rancho Santa Clara only Nuttall's Woodpeckers were encountered in live oaks, sycamores, cottonwoods, and willows.

About the scattered trees just west of Rancho Santa Clara, we obtained from adjacent territories a pair each of *nuttallii* and *scalaris*. On April 18, 1967, the female Nuttall's Woodpecker was about to lay eggs (ova to 15 mm.), and the Ladder-back female had laid eggs (in a cavity in a willow tree). No hybrids were observed, and the birds collected proved essentially pheno-

typically pure (the male *scalaris* has a few features tending slightly toward *nuttallii*). Individuals of both species were seen in oaks, willows, and cottonwoods. This is another case in which limited numbers of both species occupy together a rather limited habitat. A rather similar situation was noted (Short and Banks, 1965, p. 48) farther south at Rancho Rosarito, where a pair of each species was obtained, although other individuals of *scalaris* were observed and the riparian habitat is more extensive.

SAN JOSE

This locality, the site of the Meling Ranch, is illustrated and discussed by Short and Crossin (1967, pp. 285-286). The figures show the rather barren hills containing a mixture of desert and low chaparral vegetation surrounding fine riparian woodland. Although the woodland is in good condition, increasing aridity has reduced considerably the extent of the woodland and of the wet (swampy) area at the ranch itself (Short and

Crossin, *ibid.*). The riparian woodland, which provides the only habitat for woodpeckers in this region, extends for about 8 miles along the Arroyo San Jose and the Arroyo San Telmo. This habitat is sufficiently wide for two pairs of woodpeckers to have territories across it within 1 mile of the ranch, but beyond that to either side it becomes a thin, often broken line of trees immediately adjacent to the stream. The woodland is isolated, for trees disappear for at least 2 miles beyond them to the north, and for 2 miles beyond them (nearly to Las Cabras) along the Arroyo San Telmo. Pairs of *Picoides* were recorded and their distribution was mapped, indicating that approximately 35 pairs comprised the total population of this woodland (20 pairs were located within $1\frac{1}{2}$ miles of the ranch; the remainder were scattered along the stream farther from the ranch).

In this area we collected 18 adults, of which 17 were *nutallii* and one (female A.M.N.H. No. 791444) was a probable introgressant *nutallii*. One of the specimens of *nutallii* does not represent the riparian population, but was taken 5 miles northwest of San Jose in a small grove of willows and live oaks beside a small stream. This bird (female A.M.N.H. No. 791447) was mated with an oddly plumaged, possibly hybrid male which we were unable to obtain. Three additional adults, all *nutallii*, were collected at San Jose by Crossin in 1968. Older collections include 12 specimens from San Jose, nine *nutallii*, a probable introgressant *nutallii*, and one *scalaris*. The probable introgressant bird is a male (A.M.N.H. No. 363667) taken in June, 1923. The specimen of *scalaris* is a female (M.V.Z. No. 46241; label data, "San Jose, Lat. 31° , 2500'") collected there on October 23, 1925.

Altogether 29 *nutallii*, two probable introgressant *nutallii*, and one older specimen of *scalaris* comprise the sample from San Jose. The nature of these specimens suggests somewhat less influence of *scalaris* on the essentially *nutallii* population around San Jose today than in the past. The 1925 *scalaris* specimen may have been a fall wanderer. Nevertheless, both probable introgressant *nutallii* exhibit strong *scalaris* tendencies, a possible hybrid was seen nearby, and *scalaris* occurs both downstream (Las Cabras) and upstream (Concepcion) from San Jose, all of which suggest that occasional interbreeding may occur at San Jose.

Las Cabras is a small ranch in the Sonoran

Desert along the Arroyo San Telmo just a few miles beyond the end of the riparian woodland extending downstream from San Jose. The ranch is barren, with a few scraggly small trees that are probably a remnant of a larger grove. No woodpeckers were found in this poor habitat, but $1\frac{1}{2}$ miles to the west we took a nesting pair of birds in agaves and cacti (see Short and Crossin, 1967, figs. 1 and 6). The male (A.M.N.H. No. 791496) of this pair was a probable introgressant *scalaris*, the female was *scalaris*, and several other individuals observed in the desert were apparently *scalaris* (only *scalaris* has been taken downstream from Las Cabras near San Telmo). Older specimens from Las Cabras include two males and a female taken June 6 and 7, 1923. One of the males (M.N.H.S.D. No. 8739) is *nutallii* and the others are *scalaris*. This indicates that *nutallii* once was found downstream as far as Las Cabras, that *scalaris* occurred with it there, and that the situation was favorable for *scalaris* to be found, at least sporadically, upstream in the riparian timber. Contact between these species is more tenuous in this region today than it was in the past.

VALLADARES

The next major arroyo south of the Arroyo San José-Arroyo San Telmo is that of a small tributary of the Río Santo Domingo. In this arroyo, several ridges and a small plateau to the south of San Jose, there is a small ranch that comprises the hamlet Valladares. The locality is described by Short and Crossin (1967, p. 287). At a slightly higher elevation than San Jose, the riparian trees include a few poor specimens of Jeffrey pine (*Pinus jeffreyi*) and some scattered live oaks. In contrast to the lush riparian woods of San Jose, the thin stand at Valladares contains trees in bad condition, many of them partly dead, cut or broken, innumerable stubs, and much dead wood (fig. 19). A very thin line of trees, often scattered, extends up and down the stream for at least 2 miles. The surrounding hills appear overgrazed and barren, and bear scattered mixed chaparral, cacti, and other desert plants.

All eight of the specimens collected in April, 1967, are Nuttall's Woodpeckers. Specimens taken from there in the past, however, include one hybrid and one introgressant *scalaris*, as well as two *nutallii*. The last two specimens were



FIG. 19. Xeric aspect of riparian woodland along stream near Valladares, Baja California, habitat of Nuttall's Woodpeckers, but where a hybrid between *nutallii* and *scalaris* was collected in 1893.

taken in the 1920s. The hybrid (female C.M. No. 20027) was collected in 1893, and the introgressant *scalaris* (female C.M. No. 20026) was taken in 1889. These specimens indicate that there was greater influence of *scalaris* in the area in the past than there is at present.

CONCEPCION

A small ranch, part of the Meling Ranch, marks this old collecting locality, described by Short and Crossin (1967, p. 287; also map, fig. 1). It is situated at the western base of the main mass of the Sierra San Pedro Mártir, and at the western end of an upland plateau covered with tall chaparral and groves of oaks. A small stream has cut a ravine through which it drops rapidly southwest to the Arroyo San José. The very rocky slopes of this ravine, and a few exposed southward-facing slopes south of the ranch bear xeric vegetation which contrasts sharply with the prevalent chaparral. The desert aspect of these slopes was unexpected at this elevation (4700 feet). Thus, the habitat is predominantly chaparral with oaks and other large trees, although some xeric vegetation occurs.

We observed four apparent Nuttall's Woodpeckers and a single apparent Ladder-backed Woodpecker along the stream on April 26, 1967. A male of a mated pair of apparent Nuttall's Woodpeckers was collected (A.M.N.H. No. 791474) and proved to be a possibly introgressant *nutallii*. This pair was in evidence about the ranch building. In willows a mile downstream we collected a female that proved to be *nutallii*. Its mate was not observed. About one-quarter of a mile south (downstream) of the ranch we observed the apparent Ladder-backed Woodpecker, a female, foraging in two live oaks, and in a willow. This bird called like *scalaris*. After we collected the bird (A.M.N.H. No. 791503), which proved to be a probable introgressant *scalaris*, a woodpecker that had been feeding only one tree away commenced calling (like *nutallii*) and was collected (A.M.N.H. No. 791475). It proved to be a phenotypically pure male individual of *nutallii*. No other birds were observed nearby, the nearest being the pair to the north near the ranch, and the lone female three-quarters of a mile to the south. Thus it is possible, even likely, that the male Nuttall's and intro-

gressant female *scalaris* comprised a mated pair. The male had enlarged testes (9.5 by 7 mm.) and the female an enlarged ovary (11 by 7 mm., ova to 2 mm.), and both had a brood patch.

Older specimens from Concepcion include but two specimens, one of *scalaris* and the other a hybrid male (M.V.Z. No. 46918). These birds indicate that *scalaris* is not casual at this high elevation, but regularly occurs there. It is difficult to understand why no specimens of *nuttallii* were obtained earlier, although the hybrid indicates the presence of *nuttallii* with *scalaris*. Thus, the situation at Concepcion seems to have been relatively stable for a long time.

DISCUSSION

A total of 74 birds, taken recently by me and my associates, and 81 birds taken in the past represents specimens from the area of northern Baja California from the latitude of Ensenada south to the latitude of San Quintin. Most of the areas visited recently are discussed above. One area not discussed above, and represented by 19 older specimens, is the Valle de la Trinidad. There the Sonoran Desert spills over the mountains through San Matias Pass and into the flat Trinidad Valley. The edges of the valley are marked by wooded streams issuing from the mountains. *Picoides nuttallii* occupies such woods in proximity to the desert-inhabiting *scalaris*. Five specimens from this area represent *nuttallii*, 12 *scalaris*, and two are introgressant *scalaris*.

The following totals are from the entire region of overlap in northern Baja California:

FORM	OLDER SPECIMENS FROM LOCALITIES OF RECENT		
	SPECIMENS	SPECIMENS	SPECIMENS
<i>nuttallii</i>	28	47	11
introgressant <i>nuttallii</i>	1	3	1
hybrids	2	1	2
introgressant <i>scalaris</i>	5	8	1
<i>scalaris</i>	45	15	2

Most of the hybrid and introgressant birds come from few localities. Many of the *nuttallii* and *scalaris* specimens come from areas where one or the other is prevalent. As I concentrated my efforts on those regions where the two species

were apt to meet, the recent figures are especially biased, and the conclusion cannot be made that hybrids occur more frequently today than they did in the past. Rather, we have noted for certain localities a distinct tendency for the elimination or reduction of one or the other species, and a reduction in the number of hybrid and introgressant individuals. The figures show that roughly 10 to 20 per cent of the birds may be expected to represent hybrids or introgressant individuals at localities where both occur or closely approach each other. The actual per cent is probably greater because introgression affects more birds than those included as "hybrids" and "introgressants," as discussed above.

I have attempted to show the relation between various habitats and the external morphology of specimens taken at the localities in Baja California where I have encountered these woodpeckers (table 23). The specimens form the main basis for the table, but of course we saw individuals other than those that we managed to collect. The birds observed near El Socorro and San Telmo were undoubtedly *scalaris*, as determined by their appearance in the field; these localities are in the Sonoran Desert, and the woodpeckers were observed in desert vegetation. The table shows rather clearly that *nuttallii* favors riparian woodland associated with oaks and chaparral, whereas *scalaris* occurs in desert habitats. None of the essentially desert localities had significant riparian vegetation, but it is known that *scalaris* occurs, often commonly, in riparian woods situated in the desert (e.g., the Colorado River bottomland). More important, the table indicates that both species tend to occur together, there to hybridize occasionally, in riparian woodland with immediately accessible chaparral and oaks, as well as desert vegetation. The data suggest (and I believe that further data will demonstrate) that where *scalaris* and *nuttallii* occur together, the dominant phenotypes are those of *scalaris* when desert vegetation predominates about a riparian woodland, and those of *nuttallii* when oaks are frequent, and chaparral is the dominant vegetation surrounding the riparian woodland. However, *nuttallii* may be able successfully to occupy extensive riparian woodland regardless of the surrounding country (as at San Jose and Valladares). The Ladder-backed Woodpecker appears to require a diversity of vegetation, such as that provided by mixed mesquites and desert scrub. It seems un-

TABLE 23

DISTRIBUTION OF WOODPECKERS AND HABITATS AT 17 LOCALITIES IN NORTHERN BAJA CALIFORNIA^a

Locality	Habitat						
	Cultivated Land	Chaparral	Oaks	Riparian Woods	Mesquites	Shrub Desert	Open Desert
<i>nuttallii</i> ONLY							
18 mi. S. Ensenada (1)	X	—	X	X	—	—	—
Arroyo Santo Tomas (6)	—	X	X	X	—	—	—
Arroyo Uruapan (2)	X	—	X	X	—	—	—
22 mi. S.S.E. Tecate (1)	—	X	(X)	X	(X)	—	—
BOTH SPECIES, HYBRIDS, INTROGRESSANTS							
San Jose (21)	X	(X)	X	X	—	(X)	—
31 mi. E. Ensenada (12)	—	(X)	(X)	X	X	X	X
Rancho Rosarito (4)	X	—	—	X	X	X	X
Valladares (8)	—	(X)	(X)	X	—	—	X
Rancho Santa Clara (4)	—	(X)	X	X	—	(X)	—
Concepcion (4)	—	X	X	X	—	X	(X)
Rancho Escondido (2)	X	(X)	—	X	—	X	—
Las Cabras (2)	X	—	—	—	—	X	X
11 mi. S.S.E. Santo Tomas (1)	—	—	—	X	—	X	—
25½ mi. E. Ensenada (3)	—	—	—	X	X	X	X
<i>scalaris</i> ONLY							
El Palmarito (3)	—	—	—	(X)	X	X	X
4 mi. E. El Socorro (0)	—	—	—	—	X	X	X
San Telmo, coast (0)	—	—	—	—	—	X	—

^aThe central group of localities is arranged from those at which birds tended toward *nuttallii* in morphology, to those at which *scalaris* traits predominate. Numbers in parentheses denote specimens taken by Short and his associates since 1964. Habitats marked with parentheses occur only sparingly.

able to utilize oaks effectively, at least in the presence of *nuttallii* (which is an oak woodland bird in central California). Nuttall's Woodpeckers forage in low chaparral and scattered oaks when they are available, but they are able to exist entirely in riparian woods if the latter are sufficiently extensive.

Thus, in the area of sympatry *scalaris* appears to predominate in desert habitats and in riparian woodlands, especially those of small extent, which have some desert vegetation (including mesquites) surrounding them. On the other hand, conditions favoring *nuttallii* are extensive riparian woodlands, and riparian woodlands of any size if the surrounding area is dominated by chaparral vegetation. Of course certain small patches of suitable habitat, such as that at Rancho Escondido, may be populated sporadic-

ally and randomly by individuals of either or both species. Both species are apt to occur together where the riparian woodland is moderate or small, and the surrounding country has a mixture of chaparral and desert vegetation. Man undoubtedly has disturbed the region, and today the original conditions probably obtain at few localities that I visited, namely at 31 miles east of Ensenada, and at Rancho Santa Clara. Perhaps the most unusual site of occurrence of both species is at Rancho Rosarito (see Short and Banks, 1965), where both species occur in a narrow but long (1 mile) riparian woodland entirely surrounded by desert. Unfortunately, insufficient information is available concerning the precise nature of recent environmental changes at localities represented by older specimens.

HYBRIDS AMONG OTHER NORTH AMERICAN SPECIES OF *PICOIDES*

OTHER THAN the three hybrids of *P. pubescens* and *P. nuttallii*, and at least eight hybrids of *P. nuttallii* and *P. scalaris* discussed above, only one other hybrid is known among the North American species of *Picoides*. This is a hybrid of *P. scalaris* and *P. villosus* (M.V.Z. No. 129727) collected in the Sierra del Carmen, Coahuila, Mexico (Miller, 1955). This female, taken above the altitudinal range of *scalaris* and within the range of *villosus* at 7000 feet, closely resembles hybrids of *P. pubescens* and *P. nuttallii*, and to a lesser degree, both *P. nuttallii* and *P. borealis*. Miller suggested that the hybrid resulted from a restricted choice of mates (occurrence of an out-of-range individual of *scalaris* within the range of *villosus*, and thus forced to mate with a bird of the latter species at the onset of the breeding season).

I have noted elsewhere (Short, 1969) that a lone hybrid between two species is not particularly indicative of the degree of relationship of the species involved, but may be useful in the study of the evolution of the group to which the species belong. This seems true of the *villosus-scalaris* hybrid, which indicates the rather close relationship obtaining among North American species of *Picoides*. Within such a group, given the relatively close relationship among component species, hybrids should be expected especially among allopatric species, or essentially allopatric species, or at the extremes of ranges of one or another species where restricted mate choice may play a role. The several hybrids between the semispecies *P. scalaris* and *P. nuttallii* illustrate the former expectation, and the three *pubescens* and *nuttallii* hybrids and lone *villosus* and *scalaris* hybrid the latter. The greater number of *scalaris* and *nuttallii*, and *nuttallii* and *pubescens* hybrids suggests a close relationship among these three species, and this is supported by evidence derived from their distribution and differences in habitat preference (see also the behavior section). The lone hybrid of *villosus* and *scalaris* indicates that these species are rather

closely related, but so are other species in the group. Indeed, hybridization appears most likely to occur among species (such as *scalaris* and *villosus*) which are barely sympatric. Other such hybrids that I predict will eventually be found are between: *Picoides scalaris* and *P. pubescens* (contact in Texas, southwestern Kansas); *P. scalaris* and *P. borealis* (if they should meet in Texas); *P. lignarius* and *P. mixtus* (if they should meet in Bolivia or Argentina); *P. pubescens* and *P. borealis*; *P. villosus* and *P. stricklandi*; and *P. stricklandi* and *P. scalaris*. I do not rule out the very rare occurrence of hybrids between sympatric species, such as *P. villosus* and *P. albolavatus*; *P. villosus* and *P. arcticus* or *P. tridactylus*, *P. arcticus* and *P. tridactylus*, and possibly even *P. villosus* and *P. pubescens*, but I believe the previously mentioned hybrids are more likely to occur, or will prove to occur more frequently than the possible sympatric species hybrids just listed.

Resemblances of the hybrid of *P. villosus* and *P. scalaris* with hybrids of *P. pubescens* and *P. nuttallii* are of interest in considering relationships among the New World species of *Picoides*. *Picoides pubescens*, patterned like *villosus*, has hybridized with *nuttallii*, a very close relative of *scalaris*. The resemblance of the *villosus* and *scalaris* hybrid to the *pubescens* and *nuttallii* hybrids hence is not surprising. *Picoides borealis* and *P. nuttallii* are derivatives directly descended from the ancestral stock of *scalaris*, and they possess plumage modifications (more white tail, reduced nuchal patch, white nasal tufts, less barred upper parts, more black plumage) that parallel some features of *villosus* (see discussion below). Hence it is not unexpected that the hybrid of *villosus* and *scalaris*, being intermediate in morphology between those two species, should resemble *nuttallii* and *borealis*. This hybrid attests to the evolution of various states of plumage characters such as white-backed versus barred-backed condition, but it does not indicate which state is derived and which is ancestral.

FORAGING ACTIVITIES

I FOUND ANALYZING the foraging sites of the various woodpeckers to be extremely difficult because of various biasing factors. There is no question that an observer influences the movements and foraging of Nuttall's, Downy, Hairy, and Ladder-backed woodpeckers. Individuals of the first three species frequently move upward in a tree, toward the center of a dense tree, or to the other side of the tree, when they meet an observer. "Displacement" tapping was frequently noted when I approached a woodpecker. This tapping is rapid and frequent, and the agitated actions and calls of the bird, its failure to secure food, and the unlikely nature of the sites utilized, all suggest that its tapping is not involved in foraging. Ladder-backed Woodpeckers in Joshua trees move frequently and for greater distances when an observer comes close, in contrast to their actions when an observer is farther away (and therefore cannot discern the bird's actions!). It is my experience that Downy and Nuttall's woodpeckers also move more frequently from tree to tree when an observer is close to them. The approach of an observer often seems to evoke calls from the moderately alarmed birds; these calls may in turn trigger an interaction between members of a pair, or territorial rivals, thus terminating foraging activity. Indeed, various social activities during the breeding season may drastically affect the data accumulated because the observer tends to be attracted to vocal, conspicuous individual woodpeckers. Interactions necessary for territorial establishment and courtship indeed may largely determine foraging sites, the time spent foraging, and even foraging mode (as, for example, the case of a male hearing the distant drumming of other woodpeckers and reacting by selecting foraging sites within easy access of a drumming site of its own). Of course, the variation in vegetation from locality to locality strongly affects the data obtained for foraging sites, rendering meaningful comparisons difficult to establish.

Another simple factor influencing the data obtained for the mode of foraging is the relative conspicuousness of the different foraging modes (see Short, 1970a). One is attracted to loud and persistent excavating or tapping of woodpeckers, and hence to the species and individuals of a

species which are loudest and most persistent in these activities. This factor most strongly influences observations obtained in surveys, that is, when the observer passes back and forth through a woodland attempting to record observations on several or many birds. The remedy for this problem is to study individual birds continuously for long periods of time. Unfortunately, because of the limited time available, most of my observations were of the former type.

Finally, I must stress the need for observation at all times of the year. My studies suggest that woodpeckers breed when food is most readily available, and that several species may forage similarly and on the same foods when these foods are in plentiful supply. I suspect that the critical period when interspecific (and intraspecific sexual) competition is greatest is that following nesting and the break-up of family parties. This is when intraspecific and interspecific foraging differences are apt to be most strongly pronounced. At this time numerous young of the year must forage in competition with conspecific, territorially established adults, and with adults and young of the year of the other sympatric, related species. In the region in which my studies were conducted, this time of the year (summer, early fall) coincides with a rather dry period, which places further stress on these woodpeckers. My own investigations were conducted primarily in the breeding season, with only limited late fall observations. Studies of these species (and indeed of all North American species of *Picoides*) during the immediate post-breeding period and early fall would be rewarding.

Despite the various difficulties and biasing factors, certain data that I acquired are suggestive of the sites and modes of foraging of these woodpeckers, at least during the seasons and at the localities where they were observed.

NUTTALL'S WOODPECKER

At the Hastings Reservation in Carmel Valley, central California, the Nuttall's Woodpecker forages mainly in oaks (live oak, *Quercus agrifolia*; blue oak, *Q. douglasii*; and valley oak, *Q. lobata*). Figures from Alden H. Miller's field

notes (data being prepared for publication by Miller and Bock) indicate a preference for oaks throughout the year. The use of other trees, mainly sycamores (*Platanus* sp.) and willows (*Salix* sp.), varied from a high of about 43 per cent of the sites in the late summer and fall to about 25 per cent of the sites in winter, spring, and early summer.

Foraging sites of Nuttall's Woodpeckers in southern California are more variable, depending somewhat on the locality. In areas where live oaks occur these seem to be preferred, at least during November and February to March. Other low trees such as scrub oaks and *Caenothus* are also used frequently. It appears that, in the rather open situations of southern California, the choice of foraging sites may be influenced by predation selection. Foraging birds utilizing sites in or near live oaks, scrub oaks, and dense chaparral plants, such as *Ceanothus* are readily able to evade predators. More exposed sites, such as isolated, large trees (*Platanus*, *Populus*), and scattered smaller but not dense deciduous trees, may be avoided or used to a lesser extent when they are bare of leaves. Riparian situations in which young tree growth is prevalent are especially favored; dense dwarf willow (*Salix*) thickets are utilized and the birds forage down to the ground. Nuttall's Woodpeckers were commonest at localities where there occurred dwarf willow thickets and dense groves of young cottonwoods and willows.

Golden oaks (*Quercus chrysolepis*) serve as centers of activity of Nuttall's Woodpeckers around the north side of the San Bernardino Mountains. This occurs in areas (such as at Rattlesnake Spring) which are largely pinyon-Joshua tree woodland. A male Nuttall's Woodpecker mainly foraged in Joshua trees and in pinyons (during four hours of observation), returning occasionally and briefly to one of three golden oaks in the Rattlesnake Spring area on November 7. Another male foraged for several hours entirely in pinyons on slopes east of Cactus Flat in the northeastern San Bernardino Mountains on November 14.

During March, 1967, I recorded the foraging sites of Nuttall's Woodpeckers east of Onyx, Kern County, California, as listed in the next column.

Of those trees, only cottonwoods, willows, and dwarf willows occurred within the territory of

	MALES	FEMALES
Cottonwood	155	202
Willow	37	27
Dwarf Willow	22	23
Oak	15	28
Sycamore	6	12
Ash	1	11
Other	16	1
<i>N</i>	252	304

every pair of Nuttall's Woodpeckers. A major portion of the foraging in cottonwoods involved bud-foraging, and this undoubtedly accounts for the inordinate utilization of cottonwoods compared with that of the almost equally common willows. I have inadequate comparative data for the same area from November, 1966, but I believe that dwarf willows and willows are utilized much more at that season than in March. The above data indicate no marked difference in the type of tree used for foraging by the sexes. The preference of both sexes for willows and cottonwoods is not surprising as these trees comprise more than 90 per cent of the available arboreal vegetation in this riparian locality; hence the decided contrast with Miller's (see above) data from a northern California oak woodland.

Data from observations elsewhere are too meager, or too subject to biasing factors to permit comparison with the Onyx birds. In an area of oak woodland (Santo Tomas Valley) in Baja California during April, Nuttall's Woodpeckers were observed foraging, displaying, and calling entirely in oaks; however, few other trees occur there, notably a few willows and some eucalyptus. The restricted number of arboreal plants at the riparian localities visited in Baja California obviously enables a high predictability in ascertaining the trees utilized for foraging, mainly cottonwoods and willows. At one of the more botanically diverse study areas, 31 miles east of Ensenada, Nuttall's Woodpeckers were encountered almost as frequently as were Ladder-backed Woodpeckers in mesquite (*Prosopis*) trees bordering the taller riparian trees.

Nuttall's Woodpeckers collected while (or shortly after) foraging numbered 56. The birds were taken in February, March, and April in various parts of southwestern California and Baja California. The trees utilized by these birds for foraging are listed on the next page:

	MALES	FEMALES
Cottonwood	17	15
Willow	7	8
Dwarf willow	1	1
Oak	3	2
Ash	0	0
Sycamore	2	0
Ground	0	0
<i>N</i>	30	26

Like the other data, these observations suggest that there is no difference between the sexes in the kind of tree preferred for foraging.

The actual sites of foraging varied from an occasional hopping about and feeding on the ground, to foraging on the main trunk and branches, feeding at the tips of tiny branchlets, and even aerial foraging (see below regarding foraging modes). I found it convenient to categorize feeding sites chiefly by the diameter of the branch or trunk. In the Kern River area east of Onyx the following data were secured during March:

FORAGING SITE	MALES	FEMALES
Trunks, branches more than 2 inches	177	44
Per cent	61	13
Branchlets 2 inches or less	113	301
Per cent	39	87
<i>N</i>	290	345

Instances included were of 2 minutes' duration and were noted only at the initial contact with an individual woodpecker (repetitive foraging sites, after the initial one, were excluded). During this period there was a strong tendency for the birds to forage in cottonwood buds, presumably for insects. This tendency probably exaggerates the amount of branchlet foraging for both sexes. Particularly noteworthy is the observation that birds of either sex encountered foraging on the trunk of a tree frequently would move up the tree rather rapidly and commence foraging among the buds. Thus, despite the rather striking difference in preferred foraging sites between the sexes, males can readily utilize the same sites as the females.

My observations of foraging mode corroborate much of what Miller and his students (in Miller's field notes) found among Nuttall's Woodpeckers, chiefly in the Hastings Reservation near Monterey, central California. Indeed a few details from a draft manuscript of the Miller and Bock

paper in preparation presents well the foraging modes:

The Nuttall's Woodpecker "engages in . . . typical woodpecking routine less of the time (than *pubescens* or *villosus*) and in a fashion that leads one to think that it is less strongly motivated or equipped to do vigorous pounding." (Miller hypothesizes that the reason for this is partly structural, and partly due to a lesser demand for a vertical pose on trunks because of the diverse and often horizontal branches of oaks and chaparral where the woodpecker feeds.)

The Nuttall's has a less bounding upward hop in trees, it does more creeping, moving diagonally and seldom straight up or out for any distance. It looks hunchbacked, shorter-necked, and it swings its head back less often for hammer blows. Its bill is "pointed up at 45 degrees to the trunk so that it probes, flecks off bark, scans and pries laterally much more than it taps or drills perpendicularly." It can and does hammer, but its tail when so doing is more often lightly appressed, or free from contact with the surface. In digging, the bird seldom taps loudly for more than a minute, and the noise produced is less than that by *villosus*. Deep penetration of the bark is infrequent. "On small 1-3 inch branches or trunks where so much work is done, apparently shallow or quick penetration is achieved in 3 or 4 blows on most occasions." It is more versatile. (Comparisons are with *pubescens* and *villosus*, and the notes above are quoted or paraphrased; some are those of J. T. Marshall, others are Miller's.)

Among the modes mentioned by Miller are trunk and limb probing and drilling, foliage and twig scanning, and special methods including berry or fruit snatching, sapsucking and fly-catching. Miller and Bock summarized the obtaining of food by *nuttallii* as follows:

- 1) It seldom moves more than 1 foot without sidling laterally or to the other side of the trunk or branch.
- 2) It frequently hops to adjoining surfaces.
- 3) It often hops weakly with hunched posture and the bill held tangentially or to the side.
- 4) Bark scaling and slant probing are more common than right angle tapping.
- 5) It frequently hops freely into small twigs using the tail little or not at all, and it creeps through the foliage on twigs no more than one-eighth inch thick, fluttering and balancing with its wings.
- 6) It scans surrounding leaves and twigs, peering as a warbler or titmouse does.
- 7) On small limbs

it hops at a right angle to a small branch and often perches crosswise to such a branch. 8) It occasionally pursues insects. 9) Fruits are gathered from clusters, often by hanging upside down with or without the tail spread.

I observed all of the methods noted by Miller and Bock except sapsucking. Without question the Nuttall's Woodpecker is mainly a bark surface gleaner, securing its food at the surface or immediately adjacent to the surface. The tapping (for definitions of foraging modes used herein see Short, 1970a) done by this species is often related to its surface gleaning, used to break off a piece of bark to lay open a crevice rather than to dig below the surface. Tapping often is not loud because the blows frequently are directed laterally or as a hard probing movement, and not a determined tapping. Such tapping does not require tail-propping and a "normal" woodpecker stance like that used for sustained excavating.

Probing is extremely frequent, the woodpeckers putting their bill into every type of crevice. Occasionally the bill is used as a pry to break off a flake of bark. Bill flicking is also very common, especially in the foliage. The bill is swept from side to side, rapidly, presumably to allow scanning under and between leaves. A male *nuttallii* in Banning Canyon (north of Banning, San Bernardino County, California) on February 9 was extremely active in four, well-spaced, bare sycamore trees. The male moved spirally up the trunks, hopping a distance of one foot or so with no feeding, then it paused to pick items from the surface and to probe the bill in a deft sideways movement. At the top of one tree, as the bird foraged in the twigs it flew out three times in pursuit of undetermined insects. As it moved about rapidly, it flew on four occasions to hanging sycamore fruits, there to flutter awkwardly, hummingbird-like, for an instant, presumably seeking insects. The four sycamores were examined by this bird, and food sought for about 15 minutes before it went back into an oak tree. Perhaps such active movements relate to the exposed position of the birds in these open trees. One probing and tapping female was observed to gape once after delivering a peck at a piece of bark—the bark was pushed aside by the gaping.

Although excavating (sustained bursts of tapping, exposing the subsurface) was noted only rarely, it is possible that it occurs more fre-

quently at other seasons. If not, then the excavation of nesting and roosting cavities would seem to comprise the major amount of excavating undertaken by this species.

Foraging in cottonwood buds was observed frequently, and is of special interest because individuals of four species of *Picoides* were seen foraging at the clusters of these buds. Bud-foraging by *nuttallii* is accomplished slowly, by the birds crooking their neck, searching into the buds, moving slightly, scanning, then poking and prying with the bill. Light taps occasionally were delivered. The birds often pulled off pieces of the buds. One female fed for a half hour in a $4 \times 4 \times 8$ -foot volume of budding cottonwood foliage, giving some indication of the deliberateness of this foraging activity.

Bill flicking, scanning, and probing often are not perceived at a distance. It was particularly difficult to quantify these modes of feeding. Tapping varies from direct (involving the head drawn back to deliver the blow) to lateral and from a tap-probe to a strong peck. I found it impossible to detect the nuances of the movements and actions of foraging precisely enough to warrant quantifying my observations. The rapid movements of the birds, their frequent disappearance in the foliage, and my attempts to record their foraging sites all contributed to frustrate my efforts to note exactly the modes utilized. This is best accomplished by the extensive analysis of movies of foraging birds, which I did not have time to undertake.

I observed no sexual difference in foraging mode other than that correlated with differences in foraging sites. That is, females hung and probed from a hanging position more frequently than did males, but they feed more frequently in tiny branchlets where they are forced to hang, use their wings, and tap less frequently. Data from foraging in comparable situations indicate that similar modes of foraging are employed in similar circumstances, although males excavate more than do females regardless of the sites of foraging (18 instances of excavating by foraging males, only one instance, by a female).

Thus, foraging modes may be listed as follows, in descending order of the frequency of their employment: surface gleaning (includes scanning, bill flicking, and picking up food); probing and prying; tapping; and excavating. Fly-catching, food gleaning by hovering, gaping, and sapsucking are infrequently used additional

modes of foraging in Nuttall's Woodpeckers. None of these modes is unique to this species (see below); indeed, they are identical to the modes used by the Ladder-backed Woodpecker.

An analysis of stomach contents was not undertaken principally because field work indicated that food items taken by Nuttall's and by Ladder-backed woodpeckers are similar where they are sympatric, at least in the localities and at the seasons in which they were studied. Remains of dark insects, probably mainly beetles (adult beetles in several instances) were found in eight stomachs. Nine stomachs contained large white or yellow coleopterous larvae appearing identical to those found in cottonwood foraging *scalaris* individuals (see below). Insect eggs (species undetermined) were found in one stomach, and a lepidopterous larva was noted in another. Obvious plant remains were found in only one stomach (containing mainly insects); the material was yellow and grainy, and appeared like the yellowish bloom on the buds of the cottonwoods in which the bird had been feeding. I have already mentioned the yellow cast on the nasal tufts of some spring Nuttall's Woodpeckers, probably due to the same material. Beal (1911) reported the food of *nuttallii* to consist mainly of animal matter, including 28 per cent beetles (cerambycids, elaterids, and others), 14.7 per cent Hemiptera, 14.2 per cent lepidopterous larvae, 8 per cent ants, and the remainder other animal and vegetable matter (12.10 per cent). Of these foods only the beetles perhaps are obtained by sub-surface boring (excavating); however, as Miller's field notes suggested, part (or even most) of these may be obtained by surface probing or prying, or by tapping (barely penetrating the surface). Thus, about 85 per cent or more of the food of *nuttallii* may be taken on the surface or on the wing. These data are meager, and are drawn from all times of the year as well as from diverse localities. Detailed information regarding food items taken within a small area throughout the year would be welcome, and would enable a more meaningful comparison of different species of woodpeckers, as well as shedding more light on the sexual dimorphism in feeding habits within species.

LADDER-BACKED WOODPECKER

The available information concerning the

foraging behavior of *P. scalaris* is considerably less than for *P. nuttallii*, and the data are in many ways not comparable. For instance, few *scalaris* were studied in California, and these occurred in desert vegetation, not in riparian woods frequented by *nuttallii*.

The study of one pair of *scalaris* in Joshua tree desert east of Onyx in the Kernville region yielded much information concerning foraging sites and modes of this species. I followed this pair for 16 hours on March 13 and March 15 (I also observed them on six other days in November and in March, but for short periods), and had one or both birds in sight for all but one hour of this time. The birds foraged over an area of about 17 acres, roughly 400 yards long by 200 yards wide. Within this area the pair foraged moving clockwise in a narrowing circle during each day. The male and female maintained vocal contact with Peek Calls uttered occasionally throughout the day. Both birds were in my view for about half of the 16 hours of observation, but even when relatively close together their foraging was such that they were usually out of sight of each other. Their desert habitat consisted of: a good stand of Joshua trees (mainly 8 to 18 feet in height); much open space between the trees; scattered cholla cacti (three or four species of cylindropuntias) occurring individually or in moderately dense clusters up to 100 feet across; and scattered small bushes of various species. The entire area was grazed by cattle.

The male of the pair foraged and perched only in Joshua trees during my observations. The female foraged 80 per cent of the time in chollas and small bushes, and only 20 per cent of the time in Joshua trees. The male's foraging was accomplished mainly (75 per cent) on the trunk and branches of Joshua trees, and only 25 per cent on old seed clusters and new blossoms (the trees were flowering in mid-March). The female foraged almost entirely on new blossoms when utilizing Joshua trees. Only 3 per cent of the female's foraging was on the trunk and limbs of Joshua trees. I have excluded from these values a small amount of "foraging" on Joshua tree trunks and branches by the female when it was alarmed. The female invariably flew to a Joshua tree when startled by me or by a passing truck. There it picked and probed abnormally rapidly, and it called frequently. Usually it flew to a cholla when its alarm lessened.

Once the female flew to a bent and broken Joshua tree limb to drink water standing there; I later saw the male drink at this site. On one occasion the female foraged for four minutes in a scarred and decayed area on a Joshua tree; then the male flew in and supplanted the female, which flew to a nearby cholla cactus and commenced foraging. Thus, a clear difference in foraging sites existed between the members of this pair. It would be interesting to study pairs living where there are riparian trees as well as Joshua trees.

One female was observed in November foraging in cholla cacti and Joshua trees, and then in willows and cottonwoods at Bloomfield Ranch east of Onyx. A female in Joshua Tree National Monument foraged in old seed clusters of Joshua trees, and in junipers growing there, while its mate fed only in Joshua trees during part of a day in February. In the Anza-Borrego Desert of eastern San Diego County, where there are no Joshua trees, males of *scalaris* foraged on cacti (chollas, prickly pears) and on mesquites, especially on their trunks. Females foraged in cacti, and in mesquites; in the latter they were seen more frequently in the branches and twigs than were males. It is well to note that, in contrast to *nuttallii*, females of *scalaris* are considerably lighter in weight than males, and perhaps they are better able to utilize smaller branchlets for their foraging.

In Baja California we observed *scalaris* foraging on many different plants, including cholla cacti, prickly pear cacti, mesquite trees, agave stalks, cottonwoods, dwarf willows, and willows. With the variation in feeding sites and rather few individuals observed, it was impossible to show a sexual difference in foraging sites (although 23 of 34 trunk-foraging birds were males, suggesting a difference). Ladder-backed Woodpeckers appear to forage more rapidly, and they often fly farther from site to site than do Nuttall's Woodpeckers. It is obvious that cacti, agaves, acacias, and mesquites provide major foraging sites for *scalaris* in the desert portions of Baja California. Where such plants occur near riparian woods, they are utilized along with the larger trees. In the ecotonal area between chaparral and desert in northern Baja California, *scalaris* even may forage in scrub oaks or live oaks (three instances), suggesting that *scalaris* might be capable of inhabiting chaparral and oak woods if *nuttallii* were absent from them.

The modes of foraging employed by *scalaris* are identical to those of *nuttallii* in so far as they could be ascertained. Males and females probe, pick, bill flick, pry, tap, and occasionally excavate. No flycatching was observed, and foraging on the ground was seen only once, briefly, in a bird feeding among fallen cactus stalks. Persistent, loud excavating was noted seven times in males, and no females were observed to excavate. Bark-foraging individuals frequently lifted their tails clear of the bark, even when they tapped.

Females feeding in Joshua tree flower clusters probed and pried, clinging, often laterally to the cluster. Males foraging at such sites tended to tap more frequently than females. Males at old seed pods of Joshua trees tapped laterally and directly, breaking apart the pods. Both sexes fed among cottonwood buds, hanging from the tips of branches, and, more commonly reaching out from one branch to the buds. Feeding was mostly by probing and prying, following scanning of the buds. The birds appeared even more versatile in their actions while foraging than are Nuttall's Woodpeckers, with much turning, twisting, lateral and tangential movements, fluttering, and other movements. While moving up a tree, the hops of *scalaris* appear longer, the head is held out farther, and there is a less hunched appearance than in *nuttallii*.

Little is known of the food of *scalaris*. Beal (1911, p. 63) reported 92.07 per cent of the food in 14 *scalaris* stomachs from Texas to be animal matter, and the remainder vegetable matter. The bulk of the food was composed of wood-boring beetle larvae, caterpillars, and ants, in that order of occurrence. My own observations of food in the stomachs of *scalaris* specimens from Baja California indicate that beetle larvae and adult beetles, hemipterans, and lepidopterous larvae comprise, in that order of occurrence, the bulk of the food. Large whitish larvae up to 1 inch long made up a portion of food items in the stomachs of birds from 31 miles east of Ensenada, and these larvae appeared identical to those in the stomachs of specimens of *nuttallii* taken at that locality. I observed one male probing and tapping in crevices of a cottonwood, pulling out large larvae, and rapping them sideways on the tree several times before eating them.

It seems clear that in the riparian habitats where *scalaris* and *nuttallii* are sympatric in Baja

California the foods of these species are largely similar in the breeding season.

HYBRID AND INTROGRESSANT WOODPECKERS

As might be expected, the foraging sites and modes of hybrids and possible hybrids and introgressant individuals do not differ from those of the parental species. Foraging introgressant *nuttallii* individuals were collected in willows (two), a cottonwood and on the ground (one each). Hybrids were collected while foraging in an ash, and in a cottonwood. Three of four foraging introgressant *scalaris* individuals were taken in cottonwoods and the fourth was in a live oak.

Modes of foraging observed were those typical of the parental species. Stomach contents of six hybrids and introgressants included the large white coleopterous larvae found in the stomachs of both parental species, and adult black beetles, finely ground dark insects (beetles?), and insect eggs.

DOWNY WOODPECKER

Few Downy Woodpeckers were observed in the region of southern California approximating the area of contact between Nuttall's and Ladder-backed woodpeckers. As noted above, they occur near Kernville with Hairy and Nuttall's woodpeckers and there they must meet sporadically with Ladder-backed Woodpeckers. The considerable racial variation, the extensive geographic range, and the varying number of species of *Picoides* with which it is sympatric in different parts of its range make it reasonable to assume that there will be considerable variation in the foraging habits of the Downy Woodpecker. Hence I restrict myself to a brief discussion of the meager data gathered from the southern California population (*Picoides pubescens turati*).

In the Kernville area Downy Woodpeckers were noted feeding mainly in the smaller branches, on twigs and in the buds of cottonwoods, willows, and dwarf willows. Only one bird, a female, was observed to forage on the trunk of a large tree, a cottonwood about 16 inches in diameter. Other birds landed on trunks, and occasionally picked or probed a few times, but then they moved rapidly into the branchlets and twigs. A male foraged for 20 minutes on November 15, tapping very fre-

quently in small bushes (from the ground up to the tops) and the tops of willows. It seemed to be boring just below the surface (no sustained excavating to greater depths). On March 7, males of *nuttallii* and *pubescens*, and a female of *villosus* foraged in cottonwood buds within about 18 feet of one another; the *pubescens* male was nearest (5 feet) the *villosus* female. The Downy foraged very much like *nuttallii*, but was more agile (hanging more, often upside down) and less versatile in its modes of foraging (more direct tapping, less probing, prying and sideways flicking of the bill).

There was no indication of a foraging difference between the sexes of *pubescens* (although too few birds were observed to allow me to state that it does not exist) in southern California. The stomach contents of a Downy Woodpecker collected near Onyx, Kern County in March, 1967, contained remains of several pale insect larvae that appeared identical to those in the stomachs of sympatric specimens of *P. nuttallii*. The replacement of the Downy Woodpecker by the Nuttall's Woodpecker in the riparian woods of southern California suggests that Nuttall's Woodpeckers in the latter region may utilize many of the same foods as do Downy Woodpeckers farther north.

HAIRY WOODPECKER

This brief discussion treats only the southern California and Baja California populations (*P. villosus scrippsae*) of the widespread and very variable Hairy Woodpecker. Foraging sites of this species are diverse, as are its habitats. Foraging birds were noted in pinyons and Joshua trees in the San Bernardino Mountains, and individuals of this species may subsist in winter almost entirely by foraging on these trees. The trunk and branches, and twigs are utilized. In riparian woods Hairy Woodpeckers utilize virtually all trees and bushes, exploring fallen logs, and even hopping about in leaf debris near logs. Although I could spare little time to observe this species, I noted particularly the birds foraging on the trunks of larger (diameter 6 inches or more) trees, and 29 of 31 birds so noted were males. Some females were observed to forage in larger branches, but only two foraged actively on large tree trunks. Most females were observed foraging on small branches. Of 17 observations of Hairy Woodpeckers foraging in the buds of cotton-

woods, 12 were females. These data suggest a sexual difference in foraging sites similar to that described for this species in the northeast by Kilham (1965).

Foraging modes of the sexes seemed alike at each kind of foraging site. Although Hairy Woodpeckers probe, pry, and scan frequently, they tap and excavate more than do the other species that I observed. This tendency was noted for all foraging sites. At the buds of cottonwoods, for instance, Hairy Woodpeckers hammer and tear apart the buds much more than do the Nuttall's, Ladder-backed, and Downy woodpeckers that utilize the same sites. Perhaps partly as a consequence of these methods, and partly because of their greater weight than the other species mentioned, the Hairy Woodpecker uses larger branches and branchlets for perches from which to reach the buds. Hence, some buds

are inaccessible to this species, but accessible to the species that are able to cling to, and hang from, the tips of smaller branchlets and from the bud clusters themselves.

The foraging of a male Hairy Woodpecker in Joshua trees in the north fringe of the San Bernardino Mountains (on February 22) suggests the versatility of this woodpecker. Foraging was accomplished in old fruiting clusters and on the branches and trunk as well. Methods employed were similar to those of the Ladder-backed Woodpecker (probing, tapping, prying), except for a greater amount of tapping on the trunks and branches, and the more vigorous tapping apart of seed capsules by the Hairy Woodpecker.

Data on foods utilized were insufficient to enable a comparison of diets of the Hairy with other woodpeckers in the region where my studies were conducted.

SOCIAL BEHAVIOR

MY PURPOSE in this section is to describe various patterns of behavior of the woodpeckers discussed above, especially their behavior as it may relate to their systematics. The bases for the discussion are observations and, to a lesser extent, movies and tape recordings of Nuttall's and Ladder-backed woodpeckers obtained in California and Baja California (chiefly in November, 1966, and February to May, 1967). Although I do not pretend to have analyzed the behavior of other species of *Picoides*, I have observed, and to a minor extent, studied the behavior of the following additional species of *Picoides*: *P. pubescens*, *P. villosus*, *P. albolarvatus* (casually in the spring 1967), *P. borealis* (casually, May 1969), *P. stricklandi* (spring, 1963; April, 1969), *P. lignarius* (November, 1967), *P. mixtus* (fall, 1967; September, 1968), *P. major* (casually, summer 1966) and *P. minor* (casually, summer 1966). I also have observed the behavior of various other woodpeckers on four continents over the past 15 years. Nevertheless, the behavior of woodpeckers is sufficiently complex and studies so few and incomplete as to warrant the statement that the behavioral (including vocal) repertoire of no species can be considered completely known. My own investigations of the behavior of *P. scalaris* and *P. nuttallii* are incomplete, and I have seen actions and recorded calls that cannot be interpreted without the benefit of further studies. I have endeavored to limit my remarks to the more frequently observed actions, and frequently heard vocalizations, which tend to have counterparts observed (and heard) in other, related species. I allude to movements and vocalizations other than those discussed below only when I have suggestive evidence that upon further study they may assume importance with respect to systematics, in order to encourage such studies.

I believe that an objective observer, who is not a trained ethologist but knows animals, can contribute to our knowledge of animal behavior. Statements about function are valuable without treatment of their underlying neurophysiological causation when based upon observational data, and when they enable the prediction of behavior patterns (see Klopman, 1968, p. 288). I define agonistic behavior functionally; that is, all behavior associated with supplanting, attacking,

threatening, appeasing, and fleeing. Despite the warning of Brown and Hunsperger (1963), I am compelled to use the term "tendency" to mean simply an observationally based likelihood (to attack, threaten, appease or submit, or flee) and not a specific motivation or drive. This is meaning (1) of Brown (1964, p. 54), defined by him as likelihood or probability. I do not mean to imply that other behavioral tendencies (e.g., reproductive behavior) may not occur simultaneously with tendencies associated with agonistic behavior. The basic displays discussed herein in the context of agonistic behavior resemble those known to occur (Short, notes) in young woodpeckers not in reproductive condition, and hence they are considered to be part of the agonistic behavioral repertoire whether or not they sometimes serve other functions. For various reasons, which I shall not discuss fully in the present report woodpeckers are highly aggressive birds. Their aggressiveness is often sexually based, and it occurs (along with territoriality) to a greater or lesser extent throughout the year. Hence it is not surprising that it is difficult to detect non-agonistic displays, or even components of displays that seem to relate to tendencies other than those included in agonistic behavior.

There have been several important descriptive reports of the behavior of New World species of *Picoides* (notably the various papers of L. Kilham; and L. deK. Lawrence, 1967). However, the context and interpretation of agonistic behavior herein differs from theirs, and hence the terminology of postures, displays, and vocalizations is somewhat different. Much of the terminology is taken directly or modified from that used by Blume in his excellent studies of European woodpeckers (*Picoides major*, Blume, 1958; *Picus viridis*, Blume, 1955, 1957; and *Dryocopus martius*, Blume, 1956).

VISUAL SIGNALS

An array of postures and movements are utilized as displays, or comprise the elements of elaborate displays in these woodpeckers. These displays and movements primarily involve the position of the bill and head (probably also the head pattern), the crown-nuchal feathers which

may be raised to form a crest, and movements and probably the patterns of the wings, and of the tail (see figs. 20–22). Various vocalizations may accompany, precede, or follow these displays (see figs. 23–25). Most of the data concerning these displays were gathered from Nuttall's Woodpeckers in the West Fork Kern River Valley near Onyx, California, and from Nuttall's and Ladder-backed woodpeckers at the study area 31 miles east of Ensenada, Baja California. At these sites the woodpecker populations were rather dense, affording the opportunity to observe many interactions.

More than 1500 separate encounters were observed involving two or three displaying individuals. Most of these encounters were between Nuttall's Woodpeckers, but about 100 involved interspecific interaction between individuals of a pair of Nuttall's and a pair of Ladder-backed woodpeckers. Fifty or so episodes were noted involving the male and female of a pair of Ladder-backed Woodpeckers. Episodes including recurrent encounters were frequent. In one case conflicts occurred between two female Nuttall's Woodpeckers during most of each day on five days over a two-week period of time in March. Conflicts between a pair of Nuttall's and a pair of Ladder-backed woodpeckers (chiefly the males) took place recurrently during four days of observation over a nine-day period in April. Although the number of observations is great, most encounters were not seen in their entirety. The rapid movement and displays of the birds and frequent chases through the trees prevented me from following many interactions to their conclusion. In many cases the foliage obscured one bird of a displaying duo, or parts of both birds. These factors made it difficult to obtain movies and to make observations. Fortunately I was able to obtain movies of encounters involving several different pairs of Nuttall's Woodpeckers, including one trio of birds, and of encounters between adjacent territorial Nuttall's and Ladder-backed woodpeckers. Nevertheless, I doubt that all the nuances of posturing and display, as well as all vocalizations were noted for even a single full episode of encounters.

BILL POSITIONING POSTURES

A common agonistic posture involves Bill Directing. This is a threatening posture which at

its greatest intensity has the bill pointing at the antagonist, held at the horizontal, and with the head stretched forward and body and tail in line with the head and bill (as in final position of fig. 20F). Progressively less threatening conditions involve raising the bill upward at an angle, rarely reaching the vertical position (90 degree angle, Bill Raised Posture, fig. 21C), or sideward away from an antagonist (Head Turned, fig. 21G). In a simple shift from the Bill Directing to the Bill Raised Posture the head and bill are raised, often imperceptibly, but sometimes rapidly from the horizontal, raising the bill away from the antagonist. Ritualization of the movement from Bill Directing to Bill Raised postures probably resulted in the Head Bobbing Display (see below). In a simple shift from Bill Directing to a Head Turned Posture (fig. 22G, two instances), the head is rapidly turned to one side, presenting the cheek (and face pattern) to an antagonist, and turning the bill away. Just as the Head Bobbing Display seems to be a ritualized movement from Bill Directing to the Bill Raised Posture, Head Swinging (see below) appears to be a ritualized display including stylized, repetitive movements between a Bill Directing Posture and a Head Turned Posture. The signal characters involved in all of these postures, and movements would appear to be 1) the bill position; 2) the color and pattern of the face, throat, and perhaps the nasal tufts; and 3) the crest of males (see below).

Many instances of the various postures associated with bill position were observed in both Nuttall's and Ladder-backed woodpeckers. Full Bill Directing itself was observed infrequently (about 21 times in *nuttallii*, eight in *scalaris*), and always when two birds were in conflict at close quarters (within 4 feet, except that when one bird flies, its antagonist may Bill Direct prior to pursuing it). This posture invariably preceded movement of the aggressor toward its antagonist. At such times it is associated most frequently with Wing Flicking (see fig. 20F and H, and fig. 21E) among the other displays. In long-lasting encounters and those recurring between almost equally aggressive birds, both individuals usually maintain some form of Bill Raised Posture (at an angle from about 30 to 65 degrees; see fig. 22B), especially when faced with a display. Literally hundreds of Bill Raised Postures were observed, and this posture is typical of both species. The Head Turned Posture is

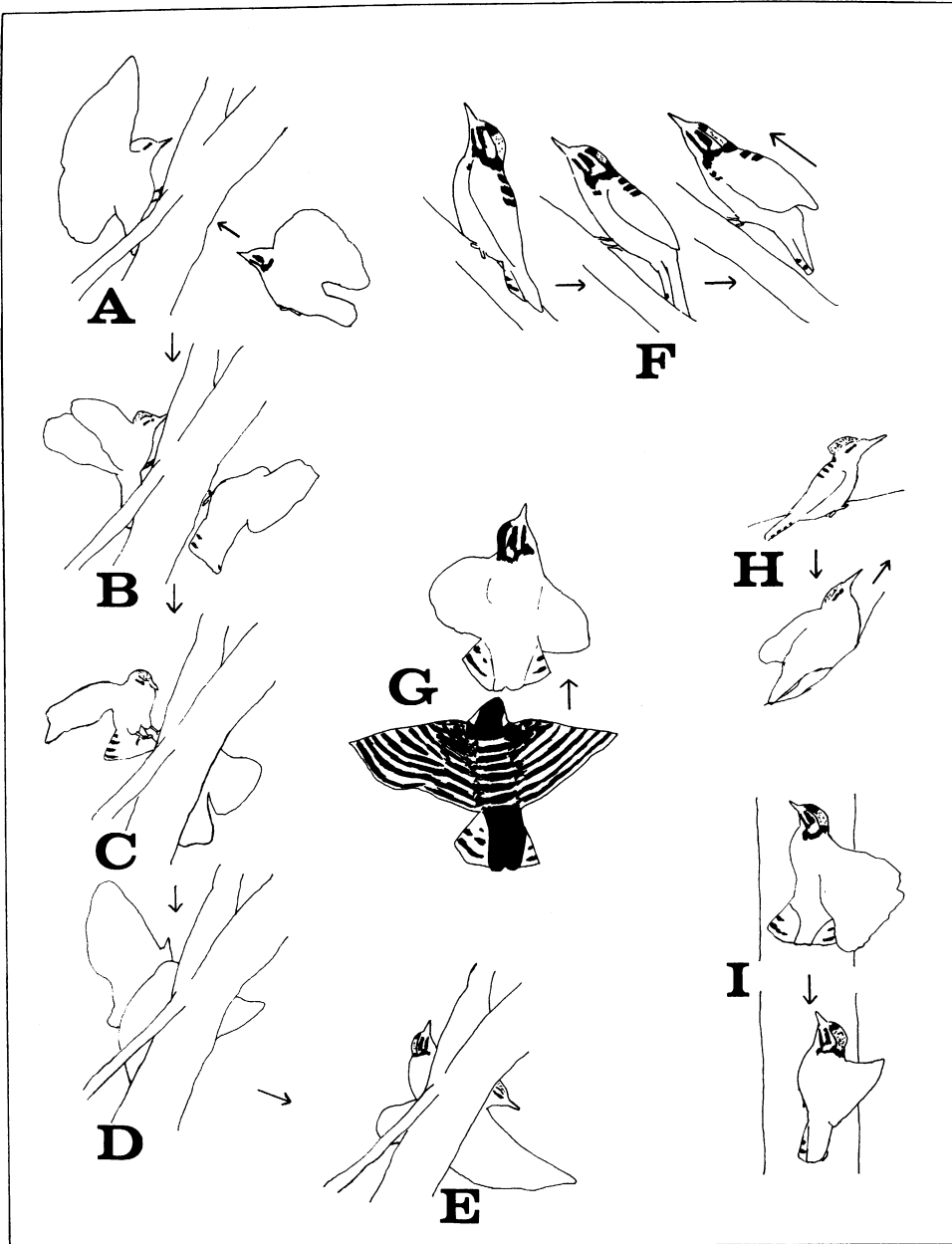


FIG. 20. Some displays of *P. nuttallii* and *P. scalaris*. A-E. Sequence showing supplanting attack on *scalaris* by *nuttallii*: latter comes in from right in Flutter Aerial Display (with Bill Directing, A), goes around tree Wing Spreading (B-D) and supplants *scalaris*, assuming Head Raised Posture (E); *scalaris* meets attack with Wing Spreading (A-B), Head Raised Posture (B), slight Crest Raising (B), but is supplanted (C-D) and flies to right (E). F. Male *nuttallii* moving to attack *scalaris* (above and to left), going from Head Raised, Tail Spread displays (left), to advance with Bill Directing (right; tail closed). G. Female *nuttallii*, partly flying (Flutter Display) partly Wing Spreading; note tail spread more to left, away from opponent (a male *nuttallii*). H. Male *scalaris* moves to attack male *nuttallii*; Bill Directing, Wing Flicking (tail closed). I. Displays of male *nuttallii* during unsuccessful supplanting attack by male *scalaris*: (upper) Wing Spreading, Tail Spreading, Bill Directing as *scalaris* advances; then (lower) Wing Flicking and Bill Directing (tail closed) as *scalaris* withdraws. Tracings from 16 mm. movies. Birds (not all same scale) are about 17.5 cm. in length; *nuttallii* is shown blacker faced than *scalaris* and males have red (shown stippled) on crown.

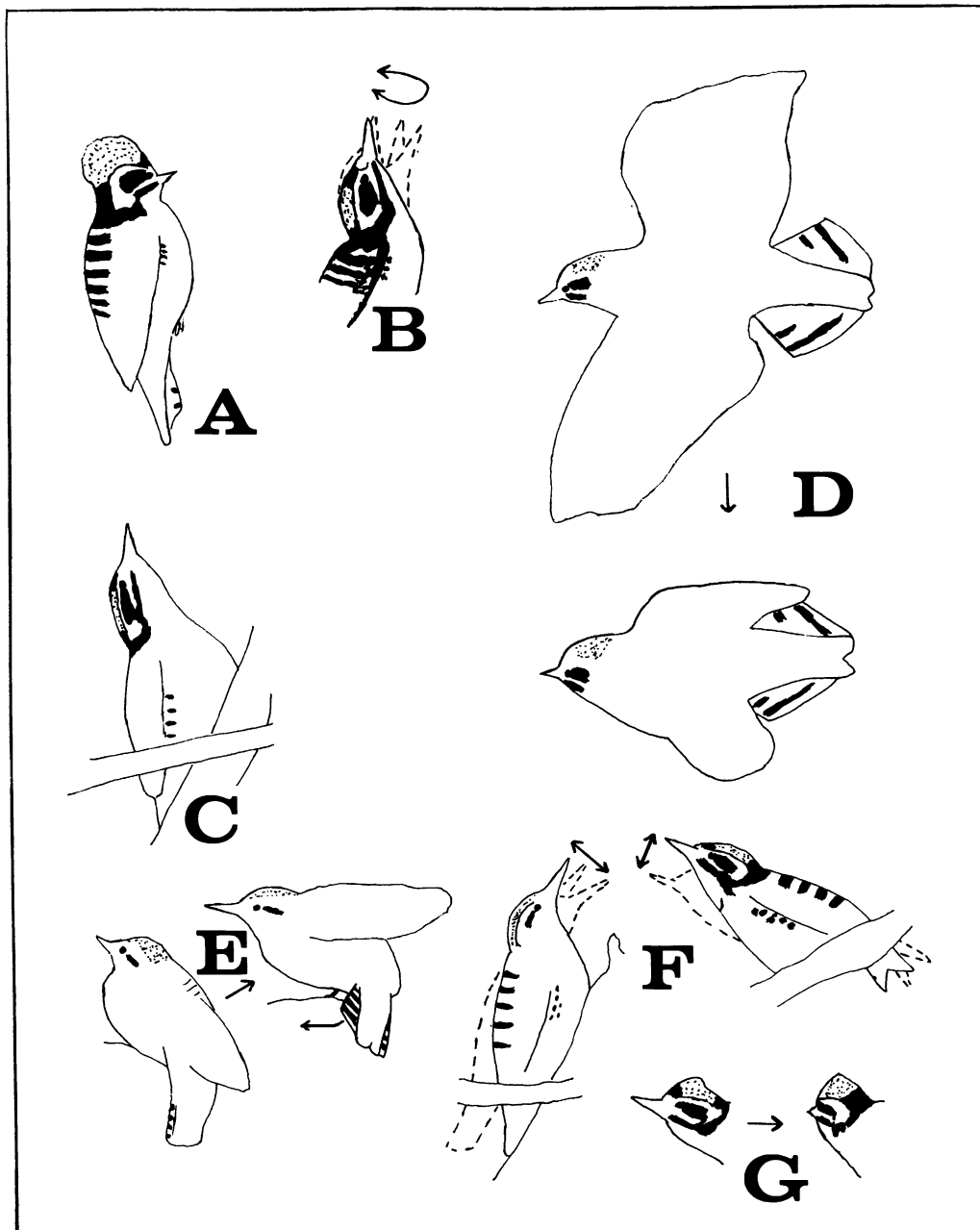


FIG. 21. Some displays of male *P. nuttallii* (A–D, G), *P. scalaris* (E), and both together (F). A. Crest Raising in presence of two displaying females of *nuttallii*. B. Head Swinging at high angle, at *scalaris* (positioned above it). C. Extreme Head Raised Posture in encounter with *scalaris*, as third bird flies by. D. Tail Spreading at end of Flutter Flight Display, directed against *scalaris*. E. Tail Spread and turned at *nuttallii*, with Wing Flicking and Bill Directing, from Head Raised Posture. F. Head Bobbing of *nuttallii* on right, followed in 0.25 second by Head Bobbing of *scalaris* at left (birds 30 cm. apart). G. Head Turning with Crest Raising, directed at *scalaris* to left. Tracings, not all at same scale, from 16 mm. movies. Birds are about 17.5 cm. in length, *nuttallii* with blacker face, less red (shown with stippling) crown.

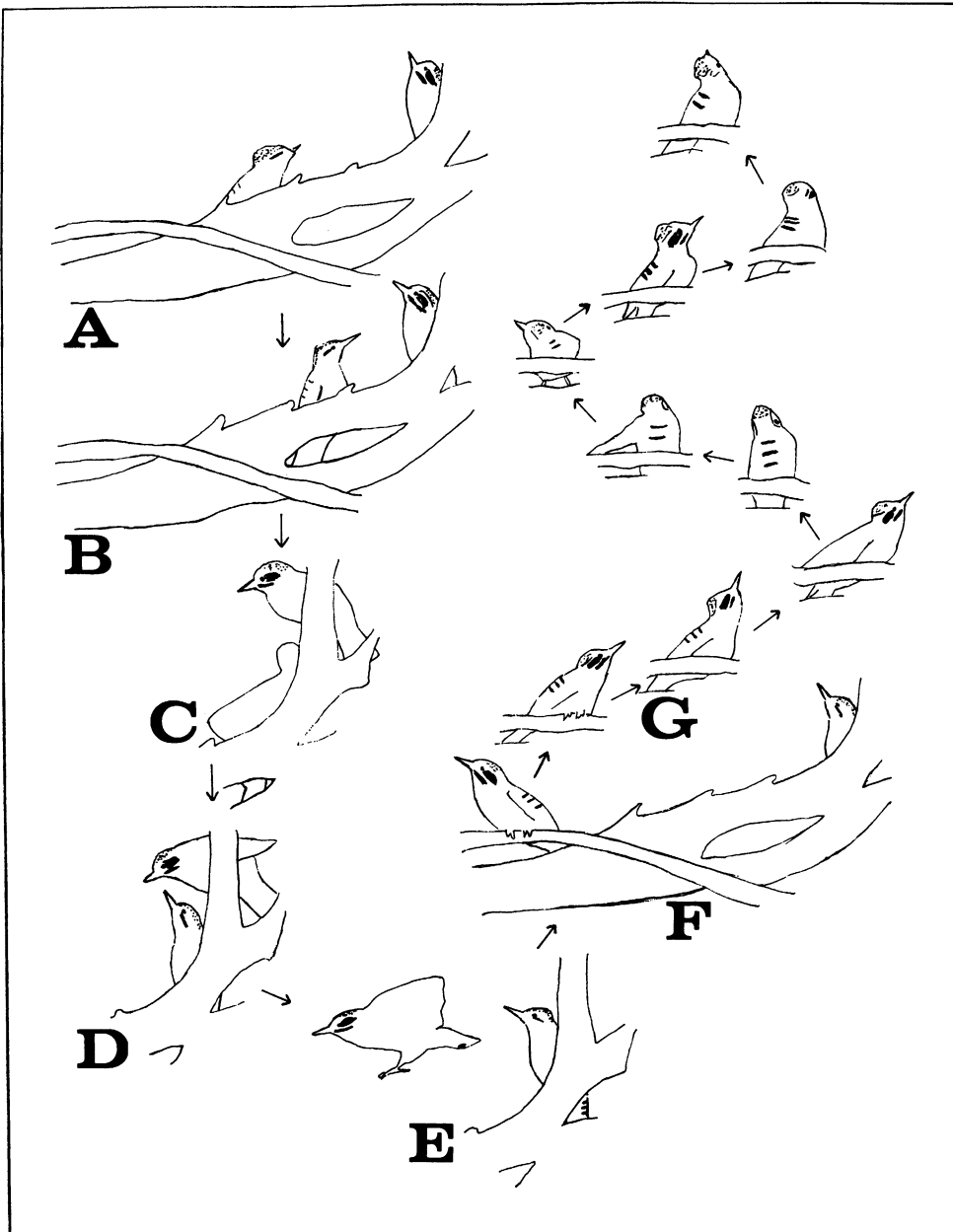


FIG. 22. Sequence of displays during 8 seconds of an encounter between males of *P. nuttallii* and *P. scalaris*. A, B. Approach of *scalaris* from left Bill Directing and Crest Raising. C, D. From below, *scalaris*, Wing Flicking, attacks *nuttallii*. E. Supplanted by Bill Directing *scalaris*, *nuttallii* flies left, landing, F, close by. G. There continues a sequence of *nuttallii* displays: Bill Directing, Head Raising, Wing Flicking, turning body away, Wing Flicking (wing away from *scalaris*), Head Raised and Crest Raising, and finally (top) Head Turning. Throughout G, *scalaris* remains in place, Head Raised, but lowering its bill (Bill Directing) when *nuttallii* Head Turns. Tracings from 16 mm. movies. Birds are about 17.5 cm. in length, *nuttallii* with blacker face, less red (shown with stippling) crown.

assumed in response to Head Swinging, Wing Spreading, Tail Spreading, and Crest Raising displays. It is not held for long because the posturing bird again turns its head toward its antagonist (usually in the form of a Bill Raised Posture) after the latter terminates the display that evoked the Head Turned Posture. Seven definite Head Turned Postures were given by individuals of *scalaris*, whereas 22 such instances involved *nuttallii*.

Bill Directing and Head Raised Postures were observed in *P. villosus* and *P. pubescens*. Kilham's (1962, p. 127) "frozen pose" of *pubescens*, an extreme form of the Head Raised Posture, was noted in response to danger, such as a hawk passing over. This same Head Raised Posture was described for *P. tridactylus* by Ruge (1968, fig. 8). The importance of bill positioning postures has been stressed for many birds by various authors, and it is obvious that such "weapon presenting" and "weapon withdrawal" movements and postures are effective in communicating tendencies to attack and to flee, respectively.

CREST RAISING

Erection of the red posterior crown feathers was observed frequently in male-male encounters, and in males of *nuttallii* present during disputes between two females. Female Nuttall's Woodpeckers also employ Crest Raising, but much less commonly—it was never conspicuous in the field, but instances were detected through analysis of movies. Movies and observations suggest that male Nuttall's Woodpeckers usually erect the crest more or less fully or not at all. Full raising of the crest was not seen in the Ladder-backed Woodpecker. Of course, woodpeckers of the genus *Picoides* do not have a crest as such, but the red feathers of the hind crown and nape of males are rather long, and when erected, they give the appearance of a short crest.

Crest raising is difficult to discern during encounters, because of the birds' movements. Movies verify that the "noticeable" red hind-crown feathers that are observed actually are erected and are not simply conspicuous because of their bright color. During the few well-observed and photographed encounters between two female Nuttall's Woodpeckers in the presence of a male, the latter maintained an erected crest (fig. 21A) except in the few instances when it displayed actively (Bill Direct-

ing, Wing Flicking, Tail Spreading) to one of the females. The female to which it displayed, interestingly enough, was one of the females seen to Crest Raise. Crest Raising seems more prevalent in the Nuttall's Woodpecker than in the Ladder-back. It is also known in the Downy Woodpecker, the Hairy Woodpecker (personal observ.), and the Northern Three-toed Woodpecker (*P. tridactylus*; Ruge, 1968).

HEAD BOBBING

Head Bobbing is a ritualized movement using the Head Raised and Bill Directing postures. It involves an up-down (or down-up) movement from the Head Raised Posture, which emphasizes a fleeing (escape) tendency in raising the bill away from an antagonist, to the threatening Bill Directing Posture with the bill thrust toward the opponent (fig. 21F). Variables include: 1) the vertical plane of the movement, that is, whether the movement is carried out in a line toward the antagonist (more threatening) or in a vertical plane that is directed to the left or right of the direction of the antagonist (the farther off this direction, the less threatening is the display); 2) the starting and stopping points—the Bobbing may be directed forward, say within 45 degrees of horizontal (hence the forward thrust of the bill is emphasized, and the display is more threatening), it may be directed upward, only within 45 degrees of vertical (hence emphasizing bill withdrawal and thus escape tendency), variously in between these, or fully from the horizontal (Bill Directing Posture) to the vertical (highest Head Raised Posture); and, 3) the speed of the Head Bobbing may be faster, or slower, and the forward or the upward portion of the bob may be emphasized by a slowdown in that region of the bob. Unlike the Head Bobbing of the Flicker (*Colaptes auratus*, Short, unpublished data), which employs this display in a more elaborate and continuous Head Bobbing-Head Swinging composite display, that of the Nuttall's, Ladder-backed and Hairy woodpeckers (probably the Downy also) is simpler and shorter. Rarely are more than two consecutive Head Bobs given by a displaying bird of any species of *Picoides*.

Only three full Head Bobbing Displays of the Ladder-back were observed. Their form seemed entirely like those of *nuttallii*. I saw about 30 Head Bobbing Displays of *nuttallii*, and five such

displays of *villosus*. Displaying birds usually called or performed other displays in conjunction with the Head Bobbing. A female of *scalaris* Head Bobbed once with upward emphasis while calling "peek" after landing close to its mate. A female Nuttall's Woodpecker rendered a slight, upward emphasized Head Bob as a female opponent flew directly over it calling queek in a Flutter Flight. In an encounter between a male and a female Hairy Woodpecker, the more aggressive male gave a double Full Head Bob, while calling week-a, week-a, and it followed this with Head Swinging. A female Nuttall's Woodpecker in conflict with a more aggressive female Ladder-back gave several upward inflected double Head Bobs, then a slight Head Swing, followed by a Head Raised Posture. Crest Raising may accompany Head Bobbing in males, and Tail Spreading and Wing Spreading have also been noted with, or just after Head Bobbing.

"Bill Waving" has frequently been noted (e.g., Kilham, 1966) in the Hairy Woodpecker and the Downy Woodpecker and in the Northern Three-toed Woodpecker, but this may refer to both Head Swinging and Head Bobbing displays, for descriptions in the literature are not clear as to the precise movement of the bill and head.

HEAD TURNING

Head Turning, as opposed to simple assumption of a Head Turned Posture (see above) is a deliberate movement, which may be repeated (fig. 21G), and which often accompanies an advance with Wing Spreading. I have seen the display only six times for certain, although it probably occurs more often. An advancing, Wing Spreading bird often moves so that its wings and movements obscure its head. Both Ladder-backed and Nuttall's woodpeckers use this display, which I have not seen in other species of *Picoides*.

This display, which may be mildly threatening but also shows an escape tendency (bill away from the opponent), seems to lend ambivalence to a Wing Spreading advance. The emphasis on the withdrawal of the bill in Head Turning seems to balance or lessen the threat posed by the bird's advance and Wing Spreading. Further observations and study of this display are needed, particularly of the relation between the bill position and the face pattern (the black malar stripe and eye stripe seem to accentuate the bill,

standing out against the contrasting white superciliary stripe, subocular stripe, and throat).

HEAD SWINGING

Head Swinging is a more ritualized, repetitive form of the Head Turning Display. The bill and head are moved from side to side, the essential element being the position of the bill. At the central bill position, pointing toward an antagonist, threat is emphasized, while movements to either side withdraw the bill, emphasizing a tendency to flee. The variables are: 1) the lateral distance of the swinging from a forward position; 2) the speed of swinging and relative speed (hence emphasis) of the forward and lateral components; and 3) the vertical position of the head (high or low). A strong threat involves emphasis on the forward aspect, that is, Head Swinging over a narrow arc directed forward and not far to either side, and with the head held low. More tendency to flee is evident in wide (lateral) Head Swinging with the head held high and the bill pointing upward (fig. 21B), or in wide Head Swinging with slow (hence emphasizing) movements laterally and a fast movement across the front. Slight, very aggressive (forward directed) Head Swinging is difficult to detect. It often precedes an actual attack, and it is associated with Bill Directing. Wide Head Swinging with emphasis on the lateral components and the head held high is much more conspicuous and most observations are of this form of the display. Such wide Head Swinging is seen in long-lasting episodes of encounters, where the opponents seem equally matched and strongly exhibit both attack and escape tendencies. The number of head swings per episode is usually one or two, and rarely up to four in Nuttall's and Ladder-backed woodpeckers, in contrast to the Flicker in which Head Swinging is more elaborate (hence more conspicuous) and involves up to 20 or more side-to-side movements (Short, unpublished ms.).

Head Swinging may follow or precede Head Bobbing, Bill Directing, Head Turning, and Wing Spreading, and it may be accompanied by Wicka Calls and Tail Spreading. Lateral Head Swinging with the head held high was observed occasionally in *nuttallii*, *scalaris*, *villosus*, and *pubescens* (for *villosus* and *pubescens* see also "bill waving" in Kilham, 1960, 1962; and "bill swinging" and "wobbling" in Lawrence, 1967),

whereas forward Head Swinging was noted only in the more thoroughly studied *nutallii*. A male Nuttall's Woodpecker and a male Hairy Woodpecker simultaneously employed the former type of Head Swinging in an agonistic encounter (see below). Likewise, a female Ladder-back and a female Nuttall's Woodpecker at the same time indulged in such Head Swinging during an encounter. Altogether some 30 Head Swinging Displays were observed closely, and of these 22 were in the Nuttall's Woodpecker.

WING FLICKING

Wing Flicking is a rapid out, then in, flick of the wings or of one wing. The wings are extended about one-third of the way out or less, in contrast to Wing Spreading. This display seems similar in appearance and function in *scalaris* (figs. 20H, and 21E) and *nutallii* (figs. 20F, and 22G). It is reported in *villosus* and *pubescens* (Lawrence, 1967), but I am not certain if that author distinguished Wing Flicking from Wing Spreading. About 20 incidents of Wing Flicking were noted, mainly in movies of the birds, for the movement is too rapid to be seen readily except under very favorable conditions. In all cases the display was observed in an aggressive bird, usually with some form of Bill Directing or with the bill between the Bill Directing and Head Raised Postures. Occasionally a forward directed Head Bob occurred after it. The antagonist usually remained quiet, frequently in a Head Raised Posture.

I judge this to be a threat display. Never was Wing Flicking noted prior to the fleeing of a woodpecker. Rather the Wing Flicking often preceded a supplanting attack (without the Flutter Display). It is a less ambivalent display than Wing Spreading, which often is associated with Head Turning, a display showing a tendency to flee.

WING SPREADING

The full extension of the wings, or rarely of one wing, is a characteristic display seen in more intense, long-lasting encounters, both in the Nuttall's and the Ladder-backed woodpeckers (see fig. 20A-C and I). This display is often associated with Head Turning (fig. 22C)—the wings are spread, one side toward the opponent, and as the wings are stretched fully the bird turns its head and bill away from the antagonist.

Wing Spreading often is directly related to the Flutter Aerial Display. The most ritualized form of Wing Spreading can indeed be considered intermediate between Wing Spreading and a Flutter Aerial Display. This form of Wing Spreading is characterized by: 1) fully spread wings; 2) a half-hopping, half-flying approach toward the antagonist along the bark; and, 3) a zigzag in the approach, actually a full head and body swing from side to side, coordinated with the spread wings (an example is shown in fig. 20 G). The latter zigzag component has aspects of Head Swinging and of Head Turning, both of which show strong tendency to flee. One instance of Wing Spreading by a male Ladder-backed Woodpecker was directed away from its opponent (a male Nuttall's Woodpecker), after the Ladder-back had been supplanted. This too suggests association with a tendency to flee.

Queek Calls frequently are associated with Wing Spreading Displays, and to a lesser extent Head Raising, Tail Spreading, and Head Bobbing are too. I was unable to detect interspecific differences in this display, which has been observed in the Hairy Woodpecker (Kilham, 1966) and especially the Downy Woodpecker (Kilham, 1962; Lawrence, 1967), as well as the Northern Three-toed Woodpecker (Ruge, 1968) and the Great Spotted Woodpecker (*P. major*; Blume, 1958, 1961).

FLUTTER AERIAL DISPLAY

The Flutter Aerial Display is essentially an aerial form of the Wing Spreading Display, employed in flying over an opponent, flying in to land near an opponent, or, occasionally in supplanting an opponent. Moth flight (Lawrence, 1967), floating flight, and flutter flight (Kilham, 1960, 1966) are some of the terms used to describe such flight displays in Downy and Hairy woodpeckers. Kilham (1962, 1966) also incorrectly termed these courtship flights. He has described a distinct "duet flight" of male and female Hairy Woodpeckers that seems to be involved in courtship (see below) and is unknown in Downy, Nuttall's, and Ladder-backed woodpeckers. The Flutter Aerial Display involves ritualized, halting wing movements, the wings being held momentarily in a spread (dihedral) or downward position (displaying the wings and their markings fully; fig. 21D). The display is usually accompanied by Queek Calls, as is the

comparable, so-called "courtship flight" (Kilham, 1962, p. 127) of the Downy Woodpecker. As far as could be determined by observations and limited movie analysis, the Flutter Aerial Display is similar in the Nuttall's and Ladder-backed woodpeckers (however, the accompanying Queek Calls differ, see below).

Observations of more than 120 Flutter Displays clearly indicate that it is primarily, if not entirely a threat display. In only 19 instances was this display used by a bird of one sex against an individual of the opposite sex. Even in these cases the aggressive function of the display was clear. The only possible connection with "courtship" appears to be its prevalence in more intense, sustained encounters—such encounters are sometimes intense because of the presence of a bird of one sex close to two aggressive birds of the opposite sex. The last two birds, highly aggressive, may chase each other about and employ Flutter Aerial Displays over each other and the third onlooking bird as well. Flutter Displays occur principally during and just prior to the breeding season. Nonetheless, it appears that the heightened aggressiveness of the birds at this time, and not pair formation activities themselves, is responsible for the prevalence of this display. Of course, it may be used as a threat display at the onset of pair formation (or even later after the pair bond is formed) between still aggressive birds that may mate later. In most of the situations in which I observed the display no member of the opposite sex was present, and in all cases the display was clearly agonistic. On rare occasions the fluttering bird attacked its antagonist, always of the same sex, and employed the wings in batting its antagonist as it fluttered toward it. In only one of four such instances did the displaying bird successfully supplant its antagonist. Although mainly functioning as a threat, ambivalence in the display is suggested by occasions when the displaying bird flies away from its antagonist as it displays, or when it flies past its antagonist displaying at a considerable distance away, instead of close to it. Of course, a tendency to flee is evident in the bird displaying, instead of flying directly at its opponent in a full attack.

Several instances involving birds of opposite sexes might be mentioned. In one case both male and female Nuttall's Woodpeckers gave a Flutter Display, the male as it came in to the female, and the female as it then left. In another instance

both male and female Nuttall's Woodpeckers gave Queek Calls, one (I was not sure which one, because of the distance) flew off queeking and in a Flutter Display, and the second flew off in the same manner after about 10 seconds, in the direction of the first bird.

Another incident began with the Queek Call of a perched male Nuttall's Woodpecker. A female responded by flying in giving the Flutter Aerial Display and queeking, landing a foot from the male, which had withdrawn partially—the male then attacked the female, employing Bill Directing as it moved toward her, and she immediately fled from the area. In no case did copulation occur during episodes in which there were Flutter Displays, and I saw no sign of "courtship" behavior.

Further study of the Flutter Aerial Display of the four species is needed to establish what, if any, differences exist among them in the form or function of this display. It is clear that it functions as an agonistic display in all four, and that it is sufficiently similar to be employed in comparable situations interspecifically, at least between *nuttallii* and *scalaris*, and between *nuttallii* and *villosus*.

TAIL SPREADING

The spreading of the rectrices is another display (fig. 20C, G, and I) common to the four species of *Picoides* under consideration. Encounters have been observed in which one bird held its tail spread throughout an episode, during which it gave various displays. The tail may also be directed at an antagonist by a lateral movement of the feathers and forward turning so that the undersurface of the spread tail is directed at the antagonist (fig. 21E). Also, during Wing Spreading and the body swinging sometimes accompanying it, the tail is often spread and the body movements allow maximum emphasis on the spread tail. However, the tail is not turned so often toward an antagonist as is the case in the Flicker.

Tail Spreading does not accompany overt attacks, but rather an attacking bird closes its tail if it previously has been spread (see fig. 20 F and I). A bird under attack usually has its tail spread more fully than that of its attacker. Thus, I feel that some tendency to flee is expressed in this display, and it is regarded therefore as predominantly a threat display, but not fully so.

Tail Spreading is similar in Nuttall's, Ladder-backed, Downy, and Hairy woodpeckers, as far as I could determine. Of course, the spreading tail emphasizes the white corners of the tail with their often species-specific patterns (heavily barred in *scalaris*, moderately barred in *nuttallii* and *pubescens*, unmarked in *villosus*, see fig. 1). It remains to be established whether these markings play a role in species recognition. If they are important in species recognition, it is probably during this display that they so function.

OVERT ATTACK

Overt Attack without flight involves a sleeked plumage, Bill Directing Posture, often Wing Flicking, and a steady advance toward an antagonist (fig. 20F and H). Of 34 such attacks that I observed closely, all were successful, leading to supplanting and in many cases pursuit of the fleeing antagonist. Attacks came most often after a series of display episodes by one bird, during which the other bird was quiescent, usually holding a Head Raised Posture. Other instances were elicited by Head Turning of an antagonist, and, especially by an antagonist that for any reason (sometimes accidentally, as when a bird moves down from an insecure perch, or slips when off balance) moved away from its opponent.

SUPPLANTING ATTACK

Supplanting Attacks may be Overt Attacks if accompanied or followed by displays, but at times there may be no prior displays. A common circumstance is as follows. One bird calls or drums. This attracts the attention of an antagonist, which flies in from some distance, causing the first bird to flee directly and the second bird to take its place. A Supplanting Attack during an encounter between evenly matched birds often results in a reciprocal Supplanting Attack by the bird originally compelled to flee. Figure 22 shows part of a such sequence (the supplanted Nuttall's Woodpecker successfully supplanted the Ladder-back after the illustrated sequence). Overt Attacks are more apt to terminate an encounter than are Supplanting Attacks. Supplanting during Overt Attacks is seemingly incidental, the aggressive attacker either continuing its pursuit of the fleeing bird, or moving away to commence other activities. Supplanting Attacks rather seem to have the supplanting itself as the

objective, for the supplanting bird usually pauses after its antagonist leaves. Supplanting Attacks, too, seem associated with simple assertion of dominance, as when a Hairy Woodpecker supplants a Nuttall's Woodpecker without other displays (see below).

If a bird flies in and supplants an antagonist, it may utilize a Flutter Aerial Display (fig. 20A), or if supplanting without flight a Wing Spreading Display may accompany or precede the attack (fig. 22C). Only twice have I seen a female supplant a male, both instances involving a Nuttall's Woodpecker female attacking another female with a male nearby. No interspecific differences were noted in either form of attack among the species observed.

FLEEING

Fleeing birds moved off directly (fig. 20E), either by flight, or by hopping (the latter especially when there was dense foliage nearby). The bill and head are turned away from the attacker, and indeed Head Turned and Head Raised postures (fig. 22A) often precede fleeing. Rarely did a fleeing bird call (Queek Call), give a Flutter Aerial Display, or a Wing Spreading Display as it fled. A supplanted bird often assumed (or reassumed) an aggressive role after it had been forced to flee, particularly in episodes involving extended encounters between more or less evenly matched antagonists. No differences in fleeing were noted among the species observed.

INSTRUMENTAL SIGNALS

Signals received by the auditory apparatus include vocalizations, and instrumental signals. Two types of instrumental signals were noted in Nuttall's and Ladder-backed woodpeckers.

RUSTLING

A sound delivered in flight, produced by the wing (feather) movements, was heard on many occasions. The muffled irregular rustling sound, which I have termed Rustling (called "Wing Ruffle" by Kilham, 1962, but "ruffle" seems inappropriate, because as a sound it means a low roll, like that of a drum) is louder than the slight sound produced in normal flight, but it is difficult to evaluate because it is not audible at great distances, and seems to vary in intensity. Thus, only in favorable circumstances (very loud

Rustling, or proximity of the observer to the flying woodpecker) can it be detected. It accompanied the Flutter Display on every occasion in which I was close to the displaying bird. In eight instances in the Nuttall's Woodpecker, and three cases in the Ladder-back, I heard rustling when an aggressive bird landed near an antagonist without an accompanying Flutter Display. Indeed, it may be used extensively by aggressive birds when landing near an opponent.

The sound is presumably produced by a special movement of the wings, or by manipulation of the feathers. Such a sound also may be produced as a consequence of flight maneuvers,

and not as a display. For example, a flying bird approaching an observer without seeing him, and intent upon landing on a nearby tree, may produce a rustling sound when it detects the observer and suddenly veers (usually upward and laterally) away to land elsewhere. Without movie analysis (I did not obtain movies at a speed sufficient to enable analysis of wing and flight feather movements of flying birds) it is impossible to rule out the possibility that these sudden rustlings were (threat?) displays, although I think not.

I believe that further studies will show Rustling to accompany Flutter Displays, and to pre-

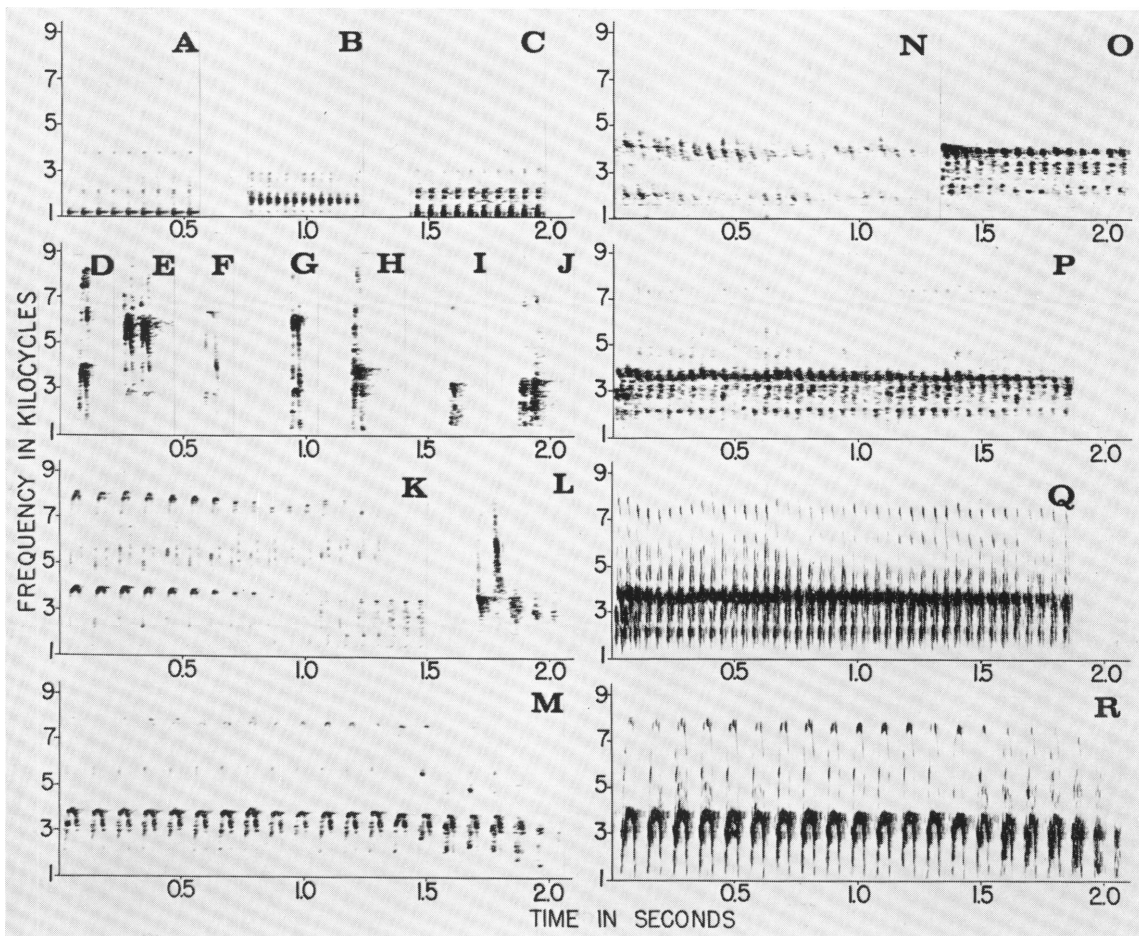


FIG. 23. Sound spectrograms of four species of *Picoides*. A-C. Drumming of *pubescens* (A), *scalaris* (B), *nuttallii* (C). D. Pit Call, *pubescens*. E. Pitit-like "distress" call, *pubescens*. F. Peek Call, *villosus*. G-H. Peek Calls, *scalaris* (H more common). I. Pit Call, *nuttallii*. J. Pitit Call, *nuttallii* (same bird as I). K. Rattle Call, *pubescens*. L. Short Rattle Call, *scalaris*. M. Rattle Call (incomplete), *scalaris*. N. Rattle Call, *villosus*. O. Brief Rattle Call, *nuttallii* (notice paired tendency of notes). P. Rattle Call, *nuttallii*. Q. As P, wide band. R. As M, wide band. All narrow band unless stated otherwise.

cede Wing Raising Displays just prior to the landing of an aggressive bird. Also, it is likely that Rustling at lower intensities will be found normally to accompany the landing of one of these woodpeckers whenever it perches near a second bird, even (presumably at low intensity) its mate.

Rustling was noted in males and females both in *scalaris* and in *nutallii*.

DRUMMING

Drumming is a familiar instrumental sound of most woodpeckers, except the majority of African woodpeckers, which appear not to drum. Most Nuttall's Woodpeckers were engaged in encounters at the time when they drummed. The birds were displaying and using various vocaliz-

ations during the late winter and spring; the drumming reported herein undoubtedly differs in frequency and intensity from that employed earlier in the year (i.e., early winter). I heard no drumming from either *nutallii* or *scalaris* in November. During February to April only 10 Ladder-back drumming episodes were heard (one recorded). Nuttall's Woodpeckers drummed more frequently, but the drumming often preceded or followed a Rattle or a Queek (see below) vocalization, and various displays. The available data hence do not permit a broad functional comparison of drumming in the two species, but only a simple, general comparison.

The number of individual taps in drumming bouts varies considerably depending on the circumstances and probably on the time of year. Miller's field notes from Hastings Reservation in

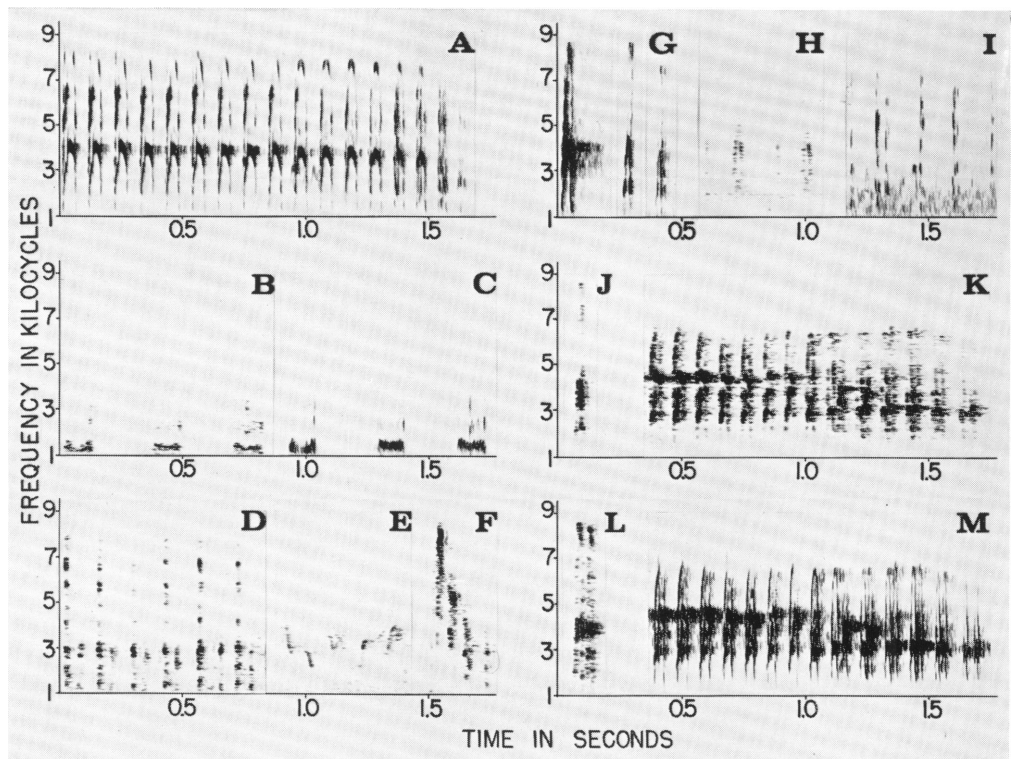


FIG. 24. Sound spectrograms of two species of *Picoides* and their hybrids. A. Rattle Call, variant *scalaris*, wide band. B. Part of Kwah Call, *scalaris*. C. As B, but wide band. D. Part of Wicka Call, *nutallii*. E. Faint Tewk Call, *nutallii*. F. Intermediate Short Rattle Call (see text). G. from left, Peek Call, *scalaris*; Peek Call of hybrid male; Pit Call, *nutallii* (all wide band). H. Part of low Wicka Call, *scalaris*. I. Part of more intense Wicka Call, *scalaris*. J. Peek Call of hybrid male (as in G, but narrow band); K. Last part of Rattle Call of hybrid. L. Peek-it Call of hybrid male. M. As K, but wide band (note pitit-like paired tendency of the last six elements). All narrow band unless stated otherwise.

California indicate seasonal variation in the number of drumming bouts (fig. 23C) of Nuttall's Woodpeckers. It is likely that the number of taps per drumming bout varies seasonally as well. In 58 instances of drumming by the Nuttall's Woodpecker during March and April, the number of taps per drum varied from 10 to 28 (average 21), and the bouts lasted from 0.70 to 1.45 seconds (average 1.06 seconds). The number of taps per second averaged 19.08. Both sexes drum, although males seem to drum more

often than do females. For comparison, data from 20 incidents of drumming by Downy Woodpeckers (fig. 23A) in Tenafly, New Jersey, during March and April averaged 13 taps per bout, 16.38 taps per second, and 0.9 second in time.

Ladder-backed Woodpeckers in the areas of study rarely drummed (fig. 23B). The few bouts noted suggest that drumming is more rapid (about 30 taps per second) and that the drumming bouts are shorter in duration. Al-

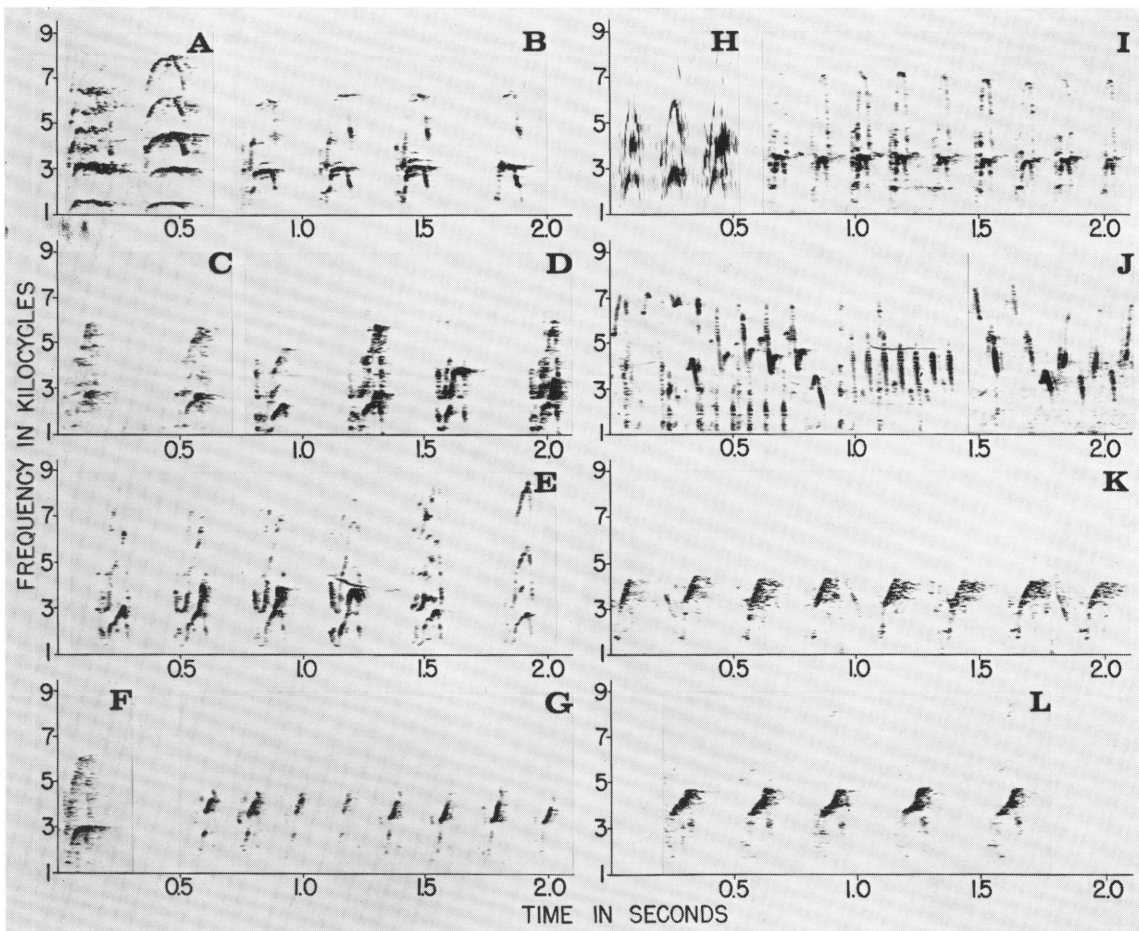


FIG. 25. Sound spectrograms of four species of *Picoides* and intermediates of *scalaris* and *nuttallii*. A. Queek-like notes, *pubescens*. B. Part of Type B Queek Call, *villosus*. C. Two-note Queek Call, *scalaris*. D. Part of Queek Call (Type A), *scalaris*. E. Part of Queek Call, *scalaris* (ignore horizontal element at 4 kc. of fourth note). F. Single Queek Call, *scalaris*. G. Part of Type A Queek Call, *nuttallii*. H. Part of mixed Queek Call, *nuttallii*, showing from the left an intermediate element, a Type B element, and a Type A element, all wide band. I. Part of Type B Queek Call, *nuttallii*. J. Mixed Wicka Calls and Tewk Calls (see fig. 24D, E, H, I) of male *scalaris* and male *nuttallii*, recorded during an encounter (ignore horizontal element at 5 kc. just after 1.0 second). K. Part of an intermediate Queek Call (*scalaris* and *nuttallii*; see text). L. Queek Call of hybrid male (*scalaris* × *nuttallii*; see text). All narrow band unless stated otherwise.

though potentially of significance, this possible difference in cadence and duration of drums is unlikely to play a role interspecifically, for observations indicate a ready reaction to inter-specific drumming among Nuttall's, Downy, and Hairy woodpeckers. However, the apparently infrequent use of drumming by *scalaris* may serve to reduce contact between individuals of that species and of *nuttallii*. Further studies of drumming, especially earlier in the year, are highly desirable for both Nuttall's and Ladder-backed woodpeckers.

Drumming in the Nuttall's Woodpecker (and in the Ladder-back, but too few instances were noted to be certain) seems not to be closely associated with fixed drumming sites. Rather the birds drummed in diverse sites as the occasions for drumming arose. This causes variation in loudness and resonance of drumming. Only two instances of repeated drumming bouts were noted at nest sites of the Nuttall's Woodpecker, although nest construction was going on during the period of study.

VOCALIZATIONS

CALL NOTES

Serving as location notes and low intensity alarm-threat notes are the Peek Call of *scalaris* (fig. 23G and H) and the Pit (fig. 23I) and Pitit (fig. 23J) calls of *nuttallii*. These have as their equivalents various peeklike calls in *villosus* (fig. 23F), *borealis*, *lignarius*, and *stricklandi*, Pit calls in *pubescens* (fig. 23D) and *mixtus*, and a Pitit call in *albobarvatus*. The Peek Call of the Ladder-back is louder, more variable, often higher in pitch, and longer than the simple Pit Call of the Nuttall's Woodpecker. Analysis of 38 Peek and 14 Pit calls showed no overlap in duration (*scalaris* range 0.04 to 0.06 second, averaging 0.49 second; and *nuttallii* from 0.020 to 0.038 second, with an average of 0.031 second). The Pitit Call has two notes, the notes being identical, or with the second note falling slightly in pitch, and it ranges from 0.08 to 0.09 second in duration. The included notes vary in duration from 0.020 to 0.038 second, and each is virtually like the single Pit Call (the pitit notes tend to be slightly higher in pitch). The interval between the two elements of the Pitit Call varies from 0.010 to 0.038 second.

Pitit Calls may be more complicated (as pit-it-it, see below) or more rapid (as prrit), and

they are often uttered in a sequence of separate calls. Their structural relationship to Pit Calls and to the Rattle (see below, and fig. 23 O and P) are clear, and it is likely that there is a functional sequence from pit to pitit to pit-it-it to the Rattle (rendered pititititititit). The equivalent sequence in *scalaris* is from low peek to high peek to the Short Rattle to the Rattle (see below for the last two vocalizations).

The Peek Call is readily distinguished from the Pit Call in the field, especially as the latter is often accompanied by a Pitit Call. The Pitit Call was much more frequently heard in the late winter and spring than was the Pit Call, whereas in November Nuttall's Woodpeckers uttered both about equally often. Thus, during the breeding season these calls afford a means of distinguishing the two species wherever they occur sympatrically, although it is a moot point whether the calls actually function in species recognition.

These calls seem to reflect an aroused, alert state of the calling woodpecker. There is a tendency of fear, and yet one of threat evident in a calling bird. The simple peek or pit calls are given by woodpeckers that are slightly alarmed by the approach of an intruder, or by any sudden noise or movement at a distance. The same notes are employed as location calls by members of a pair. Two pairs of Nuttall's Woodpeckers followed for long periods (up to 5 hours) in March called for short intervals every 15 to 30 minutes when the mated birds foraged out of sight of each other. Likewise members of a Ladder-backed pair called in 1- to 5-minute bursts every half-hour or so for the greater part of two days during which I followed them. The Ladder-backs foraged up to 100 meters (or even more) apart, and when one commenced calling it did so until a like response came from its mate, even moving about frequently apparently seeking to make vocal contact.

Pitit Calls and sharper Peek Calls seem to indicate moderate alarm or threat tendencies. Threat is evident in the frequency with which these calls give way to drumming (in *nuttallii*) and to Rattles (in both species). Both of these calls may evoke drumming or a Rattle not only from conspecific individuals, but also from other congeneric species. I noted one incident in which a Pitit Call from a Nuttall's evoked a Rattle from a Downy in an adjacent tree, and the latter's vocalization prompted a vigorous Peek Call

from a Hairy Woodpecker some distance away.

The Ladder-backed Woodpecker seems to call more persistently and regularly than does the Nuttall's. I have heard the latter call pit or pitit 15 times per minute (female in a dense tree with me close to it). Ladder-backs often call more frequently, and I have heard as many as 32 per minute from a female apparently alarmed by my presence and unable to locate its mate. It is worth noting that this female, after 5 minutes of calling finally gave a Rattle and flew toward me, before circling away. I believe this illustrates the threat element in alarm calls or actions that are prompted by someone or something which disrupts a bird's activity, but does not offer sufficient "danger" signals to frighten it.

The Peek Call of *villosus* (fig. 23F) and Pit Call (fig. 23D) of *pubescens* resemble the respective calls of *scalaris*, and *nutallii*. Analysis of a few Peek and Pit calls of *villosus* and *pubescens* recorded in New Jersey suggest that their calls are long, but overlap with those of *scalaris* and *nutallii*. Five Peek Calls of *villosus* range from 0.05 to 0.07 second (average 0.062 second) in duration, and 10 Pit Calls of *pubescens* range from 0.038 to 0.050 second (average 0.043 second). Thus, the calls of *pubescens* barely overlap those of *nutallii* and more broadly overlap those of *scalaris* in duration. The Hairy Woodpecker's call is loudest, followed by that of the Ladder-back, Nuttall's, and Downy. It is interesting that the peculiarly patterned White-headed Woodpecker apparently is the only other New World species of *Picoides* that has a Pitit Call like that of Nuttall's Woodpecker. The Pitit Call of the White-headed Woodpecker (*Picoides albolarvatus*) differs from that of the Nuttall's (with which it is

marginally sympatric in the San Jacinto Mountains) in being of longer duration, higher pitch, and more nearly a peek-it than a pitit. The analysis of recently recorded distress calls of Downy Woodpeckers in the hand by my student assistant Jerome Barry shows that one type is a 1- to 3-note call (pit to pititit) very like the Pitit Call of *nutallii* (fig. 23E). I have not heard this call in wild Downy Woodpeckers, however.

RATTLE AND SHORT RATTLE CALLS

The Rattle Call may be considered simply as a series of peek notes in *scalaris* (fig. 23M and R, and 24A), or pit notes in *nutallii* (fig. 23O-Q). This call is the equivalent of the calls designated variously as a Rattle or Whinny in the Hairy (fig. 23N) and Downy woodpeckers (fig. 23K). There are many variables involved in this vocalization, including: 1) the duration of the call; 2) the number of notes per unit of time; 3) the pitch of the fundamental; 4) the interval between notes; 5) the relative loudness of the different portions of the call; and 6) a pairing tendency of the component notes. I do not intend to discuss all variation I encountered, but rather to summarize it in comparing species of *Picoides*. Some characteristics of the Rattle Calls of four species are summarized in table 24. The calls included in that table were recorded only in March, April, and May. Those of *scalaris* and *nutallii* are from the areas of study in California and Baja California, and the relatively few calls of *pubescens* and *villosus* are from New Jersey. The last named are included for general comparison with *nutallii* and *scalaris*, although I expect considerable geographic variation will be

TABLE 24
ANALYSIS OF RATTLE CALL OF FOUR SPECIES OF *Picoides*^a

Species	N	No. of Notes	Notes per Second	Internote Time	Note Duration	Frequency Change	Duration Change
<i>nutallii</i>	12	14-45	19.27	0.050-0.070	0.030-0.040	—	0
<i>scalaris</i> , SR	3	4-7	12.9-15.2	0.070-0.090	0.045-0.050	— —	+
<i>scalaris</i> , R	20	12-25	9.79	0.085-0.125	0.045-0.070	—	—
<i>pubescens</i>	6	11-19	10.63	0.065-0.130	0.02-0.06	—	— —
<i>villosus</i>	4	14-23	17-19	0.060-0.070	0.03	—	0

^aN is Number of observations. Internote Time is time in seconds from beginning of one note to beginning of next note. Note Duration is in seconds of a single note. A change in frequency, or in duration from the beginning to the end of a call is indicated by + (increase) or — (decrease). The magnitude of the change is suggested by the number of plus or minus symbols. For *scalaris*, R is the Rattle Call and SR the Short Rattle Call.

shown ultimately within *pubescens* and *villosus*.

The Rattle Call of *nutallii* is generally shorter than that of *scalaris*, but the number of component notes per unit of time is twice as many. The individual notes of *nutallii* are shorter, and sound more "mechanical," producing a true rattling sound. The notes of *scalaris* are longer, with more distinct fundamental and harmonic tones. Also, the Rattle of *nutallii* tends to be given evenly throughout, with only a gradual, slight lowering of frequency and little or no change in interval between notes during the call. In contrast, the Rattle of *scalaris* shows lessening of the pitch and tempo of the notes toward the end, and there is a reduction in intensity as well. Comparison with the Downy and Hairy woodpeckers indicates that their Rattle calls differ from each other about as much as Rattle Calls of *scalaris* differ from those of *nutallii*. The Downy has a characteristic speedup in tempo and reduction of intensity toward the end of its Rattle, but otherwise it resembles *scalaris*. A limited analysis of the Rattle of *villosus* indicates that its call is intermediate between *scalaris* and *pubescens* on the one hand and *nutallii* on the other, but tending toward *nutallii*, especially in the frequency of delivery of its notes.

Not included in the analysis of the Rattle Calls of Nuttall's Woodpecker in table 24 are shorter calls that are identical with full Rattle Calls except for their shorter duration. This does not mean that the shorter calls necessarily are functionally equivalent to full Rattle Calls. The Ladder-backed Woodpecker has, however, a distinct Short Rattle Call (fig. 23L) of four to five notes which descend in pitch from about 0.3 to as much as 2.5 kilocycles. These notes are similar in structure to those of a Rattle Call, but they are delivered more rapidly (see table 24; the range of rates varies from 12.9 to 15.2 notes per second for the Short Rattle, compared with 8.7 to 10.8 per second in the Rattle). Thus in tempo the Short Rattle is intermediate between the Rattle Call of *scalaris* and of *nutallii*. A post-copulatory Short Rattle was given by one *scalaris* female—no Rattle Calls followed other copulations observed in that species. Hence there is a suggestion of a functional difference in these calls.

In approximately half of about 20 partial or complete Rattles of *P. nutallii* analyzed, I noted a tendency for some of the notes to be paired (see fig. 23O), either as pairs containing identical

notes, or pairs with virtually identical notes set apart from other pairs by a greater time interval than occurs between the two notes within the pair. Such a pairing tendency reflects the similarity of the Rattle Call with the double-noted Pitit Call, as well as with the Pit Call. A tendency toward pairing of the component notes of the Rattle Call was not observed in *scalaris*, *pubescens*, and *villosus* but was noted in one "hybrid" Rattle (see below).

Rattle Calls are associated in late winter and spring with drumming, and especially with Queek Calls. It is noteworthy that the Nuttall's Woodpecker gives its Rattle Call more rapidly, but seems to drum more slowly than the Ladder-back. Frequently Rattle Calls were invoked by drumming, and Nuttall's Woodpeckers engaged in long drumming sessions invariably interspersed Rattle Calls. Displaying males, during encounters, gave Rattle Calls, in many instances before a Queek Call, and particularly after an intimate session of displays when the antagonists had moved apart. An aggressive individual of *scalaris* or *nutallii*, which has supplanted an antagonist (of its own or the other species) may Rattle, and this call is answered (from a safe distance) by the just-departed antagonist. Rattle Calls seem to be threat displays of moderate intensity especially used during encounters and in proclaiming territories. Drumming is judged to be a less intense display, functioning similarly, which is more prevalent in territorial proclamation at a distance, and not so often used in actual encounters.

Neither Rattle Calls nor drumming nor Pit, Pitit, and Peek Calls are exclusively intraspecific signals. That is, a calling or drumming bird of one of the four species of *Picoides* may elicit a response from an individual of any of these species which happens to be close by. The greatest response usually is elicited in a conspecific individual, but interspecific encounters occasionally, and in certain cases frequently follow an initial interaction between individuals of different species. These interactions demonstrate the basic similarities of these signals among these species. Thus, despite easily detectable (to us, as well as to the birds) differences among these species in their drumming, and in their Rattle and Pit-Pitit-Peek calls, interspecific encounters occur frequently enough to preclude my assigning great significance to them in species recognition. Interspecific responses may involve

lowered thresholds in certain individuals because of their particular physiological state in times of stress (like the height of the breeding season). More observations are needed to establish the frequency and nature of these interspecific responses. Nevertheless, it is clear that, despite the occurrence of interspecific encounters that occasionally result from these instrumental and vocal displays, conspecific responses are in general more frequent and more intense than are interspecific responses. As these signals are by combinations of their traits species specific, they can play a role in limiting interspecific contacts. Further studies are required to elucidate this role.

QUEEK CALL

The Queek Call has been noted in *scalaris*, *nutallii*, *pubescens* (Kilham, 1962), and *villosus* (Kilham, 1966). This is a variable call, and may include at least two functional types of calls. It is usually rendered in series in *nutallii*, and usually in *villosus* and *pubescens*, whereas in *scalaris* single or double queek notes are often uttered.

Single (fig. 25F) or double Queek Calls (fig. 25C) of the Ladder-back are comprised of notes typically beginning at a low pitch with a drop, then a gradual rise in pitch most intense at about 2.8 kilocycles, followed either by an abrupt drop in pitch or by a continuation on the 2.8 kilocycle plateau gradually fading out. One peculiar single Queek Call made by a Ladder-back was 0.22 second in duration, and composed of an inverted U-shaped element with several strong harmonics closely resembling the Queek of *pubescens* (see below). Queek Calls in series contain essentially similar notes (fig. 25D and E), but these are at higher frequencies (most intense at 3.5 kilocycles) and they rise to a peak more abruptly. The notes of both calls have a less intense, inverted U-shaped element over the main component. Also, there are harmonic tones that tend to be stronger in the Long Queek Call than in the Short Queek Call. Short Queek Calls containing two notes are rendered more rapidly (average 3.54 notes per second) than are Long Queek Calls (3.28 notes per second). The spacing of notes in the Long Queek Calls of *scalaris* is variable even within a single call, and the duration of the call varies from 1.75 to longer than 3 seconds.

Nuttall's Woodpeckers rarely uttered a Short

Queek Call, and none was recorded. Their Long Queek Calls are of two types, Type A (fig. 25G) which is similar to the Long Queek Call of *scalaris*, and the somewhat different Type B Long Queek Call (fig. 25I), which resembles Queek Calls of *villosus* (fig. 25B) and *pubescens* (fig. 25A). Both of these calls are more regular (evenly spaced notes) and the delivery rate more rapid than in *scalaris*. Type A Long Queek Calls are like those of *scalaris*, but they are higher pitched (most intense at 3.5 to 4.5 kilocycles) and clearer, having weaker harmonics. They are not given as single or double notes as in *scalaris*. The duration of the call varies from 1 to longer than 3 seconds, and the average number of notes per second is 5.16 (N=10), compared with 3.28 for *scalaris*. The individual notes vary from 0.10 to 0.13 second in duration, and they are from 0.2 to 0.3 second apart.

The Type B Long Queek Call of *nutallii* contains notes in which the major element is in the shape of an inverted U, either longer in duration (0.09 second) and lower pitched (2.4 kilocycles) or shorter (0.06 second) and higher pitched (3.4 kilocycles). The former notes often come at the end of the call. Type B calls are rendered more rapidly than Type A calls, at 6.14 notes per second. It will be seen from the sonograms (fig. 25G and I) that a Type A note can be regarded as a Type B note with: 1) an added rapidly rising element; 2) a muted inverted U element; and, 3) stronger harmonic tones. In fact, some intermediate notes have been noted (see fig. 25H). Type A and Type B notes are often given in the same Long Queek Call, usually with notes of Type A preceding those of Type B. In one call of 3.15 seconds' duration three Type B notes preceded 13 Type A notes.

Queek Calls of *villosus* recorded in Baja California are all of Type B (fig. 25B), the individual notes being of longer duration (0.10 to 0.13 second) and rendered less rapidly (3.5 to 4.0 notes per second) than those of *nutallii*. The notes are given at varying intervals within a series, as in the case of *scalaris*. No single or double queeks were heard.

I have not recorded the Queek Call of the Downy Woodpecker in the wild, but "distress" calls of trapped individuals in the hand were recorded (fig. 25A) by Jerome Barry on Long Island. These distress calls are of two types, one of which contains inverted U-shaped elements given in series and sounding like queek notes.

These are variable, some being flat-topped rather than curved, and of longer duration than other notes in the same series. Generally the individual notes are 0.18 to 0.28 second long for the flat-topped, and 0.13 second for the round-topped elements. The latter resemble the queek notes of *villosus*, but the harmonic tones are louder and the fundamental is at a lower frequency.

Queek Calls function as threat displays often in combination with visual displays. They may be regarded as a more aggressive replacement of the Rattle Call. Queek Calls are given by aggressive birds in encounters, and they are associated with Overt Attacks, with Fluttering Displays, with a Bill Directing Posture and other threatening actions. In the spring an intruder may elicit a single queek note in *scalaris*. In such queeking birds other threat signs are evident, whereas birds which call peek or rattle instead show signs of alarm (e.g., they move rapidly about, and flee more readily).

The differences in the nature of Queek Calls in *scalaris* and *nutallii* are significant, but studies are needed to establish whether the long versions differ functionally. My studies took place at the height of breeding activities when individuals, particularly unmated birds, may have had lowered thresholds of reaction to calls and displays. The use of Queek Calls in the context of similar displays in interacting individuals of *scalaris* and *nutallii* suggests that they are interspecifically "recognizable" under certain circumstances. Long-lasting encounters between individuals of *nutallii* and of *villosus* at San Jose, Baja California are of interest in this connection. The intensity of the encounters, with many Queek Calls, suggests that lowered threshold responses may result in learned reactions to displays of a related species. At any rate, the differences in types of Queek Calls (A and B in *nutallii*, A only in *scalaris*), in the rate of delivery of component notes, and in the relative use of Short Queek Calls between *scalaris* and *nutallii* appear of the same magnitude as those between Queek Calls of *nutallii* and of *villosus*.

WICKA, TEWK, AND OTHER CALLS

Several distinct calls uttered during encounters in species of *Picoides* are so muted that one is fortunate to be sufficiently close to the birds to hear them at all. Often the calls are rendered by

two displaying birds. This fact, plus the distance of the observer from the displaying bird, and the softness of the vocalizations, make it difficult to analyze them. Different calls may be uttered simultaneously by the displaying birds so that details of the softer calls cannot be studied. Figure 25J shows a sequence of several kinds of calls uttered simultaneously during an encounter between a male Ladder-back and a male Nuttall's Woodpecker, and illustrates the variation and switching of types of notes during displays.

One such soft call is the Wicka Call of *scalaris* (fig. 24H and I) and *nutallii* (fig. 24D) composed of a series of from three to 10 or more double notes. Each note contains a preliminary sharp element with components at diverse frequencies, followed by an inverted V-shaped element with a strong first harmonic tone. In *scalaris* the first element of 0.005 second's duration is followed in 0.11 to 0.12 second by a 0.04-second inverted V element. Notes are uttered at a rate of 3.5 to 4.5 notes per second, with 0.12 to 0.14 second between notes. In *nutallii* the first element is louder and longer (0.03 second in duration), and is followed by an indistinct inverted V-shaped element that is at a lower pitch than that of *scalaris*. These elements are closer together (0.035 to 0.04 second apart) in *nutallii* than they are in *scalaris* and they are delivered at a more rapid rate (5.7 to 8.9 notes per second).

These data are fragmentary, based only on about six partial calls of *scalaris* and 10 of *nutallii* that were adequately recorded. The inverted V element of the Wicka Call could be a form of the inverted U element of Queek Calls. In any event, the Wicka Call is used in aggressive encounters especially when the antagonists seem equally matched and are displaying close together (the louder Queek Call is not used often during agonistic display bouts when the opponents are very near each other). Both antagonists frequently call simultaneously. The Wicka Call resembles in quality the Wickup Call of the Flicker, which is louder and definitely a vocalization associated with threat displays. Similar calls have been noted for the Hairy Woodpecker (Kilham, 1966) and Downy Woodpecker (Short, personal observ.).

Another vocalization, even less audible than the Wicka Call is the Tewk Call of *scalaris* and *nutallii* (it is also known in the Downy and Hairy woodpeckers, and called "teuk" or "intimate

notes" by Kilham, 1966). Very few Tewk Calls have been recorded (see fig. 24E, for *nuttallii*) although I have heard them (barely) frequently. In most cases they are interspersed with Wicka Calls, and sound like "tew-tew-tew" or "tewk-tewk-tewk." In rare cases they are a louder "ee-chew, ee-chew, ee-chew." Usually no more than five or six such notes are given at once, and often only three are heard. The call is variable, and is more or less continuous (the individual notes are separate, but sometimes they run together), sometimes regular but often irregular, and sharply rising and falling. The pitch varies from 1 to as great as 8 kilocycles. The elements in their sharp, inverted V-shape resemble the "-ka" element of the Wicka Call and the elements of the Queek Call.

The Tewk Call is especially heard in displaying birds that are very close to each other. Studies are needed to determine how the call varies structurally and functionally within and between species of *Picoides*. Although heard from members of a pair when they are close together, it is often uttered in encounters between intensely displaying, threatening birds of the same sex. In fact, the loudest of these calls heard in the field was during the prolonged encounters between a male Ladder-back and a male Nuttall's Woodpecker with no female close by. I therefore do not doubt that this call serves as a threat, or possibly an appeasement (hence its employment in members of a pair?). Lawrence (1967) considered the Tewk Call ("eyew-jew-jew") of the Hairy Woodpecker as contact notes indicative of pairing. However, I have heard these notes from a male Hairy Woodpecker in a conflict with a male Nuttall's Woodpecker. The prevalence of this call between members of a pair probably indicates appeasement, or a fleeing tendency as great or greater than the tendency to attack. Perhaps there are several forms of the same call. At any rate, despite the general similarity of this call among the four species, it is likely that its context, and the relationship of the Tewk Call to the Queek and Wicka calls vary interspecifically. Studies of unisexual and bisexual encounters in each of the species would elucidate the function of these calls, particularly in relation to agonistic and pair-formation behavior.

A soft call I heard several times between the male and female of a pair of Ladder-backed Woodpeckers is the Kwah Call (fig. 24B, C).

This is a series of notes given by one or both individuals over 2 or 3 seconds, at a rate of three to three-and-one-quarter notes per second. Each note is 0.11 to 0.13 second in duration, at a frequency of about 1.4 kilocycles, with very weak harmonic tones. The clear notes are slightly U-shaped. Their shape, duration, and low pitch make them distinct among vocalizations of these woodpeckers.

Further observations are needed before significance is attached to the rendering of the call during an encounter between the sexes. The Kwah Call may be a "contact call" between paired birds, found only in *scalaris*, but this remains to be established. The other species may have similar, uncommonly used calls, and for that matter all these woodpeckers may have other, as yet undescribed calls.

INTRASPECIFIC ENCOUNTERS ENCOUNTERS IN NUTTALL'S WOODPECKERS

It is surprising that so few encounters are observed in which one has some confidence that all salient displays and interactions have been noted. Even when moving pictures are used to document encounters, the birds are not always in view, and only a partial record of the events is available. Nevertheless I was fortunate to observe all or part of more than 1300 encounters during March and April, 1967. Many of these have been mentioned or described in part in the above discussion of the individual displays.

UNISEXUAL ENCOUNTERS

Most unisexual encounters were brief. Included among these are the short, common Rattle responses to a distant drumming, or vice versa, or the occasional Queek Call elicited by an unseen bird drumming or rattling. During March, episodes involving Queek Calls, Rattle Calls, Head Raised and Bill Directing postures, and Wing Spreading were common and often lasted only a few seconds. A burst of queeks from a perched bird in many cases elicited a Flutter Display by an incoming bird, calling queek, and perhaps flying by, thus terminating the "encounter." A flying bird in a Flutter Display and calling queek usually elicited long Queek Calls from birds other than the individual at which the display was directed. Also, chases were interrupted by Queek Calls from birds adjacent to

the path taken by the pursuing birds. Wicka Calls became more common during the month, and occasionally Tewk Calls were heard. Two females crouched low, Bill Directing, then called wicka as they gave Head Swinging Displays; then one suddenly turned and drummed.

The following is an account of an episode involving two females and a male in mid-March.

A male is on a stub. About 5 feet below is a female (female 2), probably not the male's mate. The male raises his Crest, wing spreads laterally, the right wing held toward female. Female 1 flies in using Flutter Display, calling queek. Female 2 reacts to displays of female 1 and male by flying out a few feet, and dropping down several feet on the trunk. Female 1 supplants female 2, landing where the latter had been, holding Wings Spread. As female 1 lands, displaying, the male rapidly retreats around the trunk. Female 1 faces in direction of the male (not female 2) Wing Spreading, moves toward where male was, thus supplanting male. Female 1 then moves up the trunk, Wing Spreading, Tail Spread, Head Swinging on "tiptoes," her whole body moving from side to side (fig. 20G). As female 1 moves up (thus away from female 2), female 2 advances up trunk with her body held far out from the tree, Wing Spreading and Bill Directing at female 1. As female 2 reaches level where male had been supplanted, she veers around the trunk after the male, Wing Spreading but now with Head Raised. Female 1, now on top of the stub, has wings and tail spread, facing down. Male comes around trunk, going up, Tail Spread, Bill Directing, supplanting female 1. Female 2 follows male around ("supplanting" it), then halts. The male above, with Tail Spread, Bill Directs down at female 2, turns tail so that it is spread, but with the lower surface "aimed" at female 2. Female 2, with spread tail, Head Turns about one side. At this point both females flew, female 2 chasing female 1 through the foliage. I could not be sure which bird was calling, but Wicka and Queek calls were heard during the display.

Another episode involving the same individuals follows. Female 1 is perched on the stub of a cottonwood tree. Female 2 flies in from above, queeking and in Flutter Aerial Display. Female 2 turns toward female 1, flying at the latter in full display. Female 1 flies out about 20 feet, but turns about and chases female 2 around two trees. Female 2 then flies to the cottonwood stub.

Female 1 and the male fly in from the left—female 2 reacts with Bill Pointing and Spread Tail as the two come in, then abruptly turns and flees around the stub as female 1 supplants her, landing with wings and tail spread. The male alights on the other side of the stub. Female 1 follows female 2, Bill Directing as the male comes in view with Crest Raised and Tail Spread and turned toward females. The females then fly off in a chase.

A third episode involving the same birds differs in the participation of the male: Female 1 on the stub drums. Female 2 flies in using the Flutter Display and queeking and lands 2 feet away and drums. Both females Queek Call with tails spread. The male lands above the two females. Female 2 Wing Spreads almost flying (Flutter Display), turning from side to side up the trunk at female 1. As female 2 nears the male and female 1 she advances, Bill Directing and Wing Flicking, then chases female 1. One of the females, probably female 1, returns and drums. The male supplants female 1, which flies after female 2, flying overhead in Flutter Display, queeking. The male queeks as the females chase. The females circle overhead. The male drums, crest raised (fig. 21A), which evokes a more vigorous chase and louder queeking from females. The females then fly off.

In the last encounter, and to some degree in the others, the presence and actions of the male seemed to enhance the intensity of the conflict. Occasionally the male acted aggressively against female 2. I judge that the male was paired with female 1, and that unmated female 2 was vigorously seeking to secure the male by driving female 1 off. Encounters between these females took place during a period of nearly two weeks in March. On March 17, I collected all three birds as they displayed. The male had enlarged testes (7 by 5 mm.) and a slightly developed brood patch; it weighed 39.5 grams. The female that was perched near the male (female 1?) weighed 34.5 grams; it had a slight brood patch, and an enlarged ovary (9.5 by 7 mm., ova to 2 mm.). The other female (female 2?) remained on the stub and was collected immediately after the male and other female were collected. This second female weighed 37.9 grams, and had a slight brood patch and an enlarged ovary (9 by 6 mm., ova to 2 mm.). The persistent, aggressive attempts of female 2 to drive away female 1 may have resulted from the former having lost her

mate. At any rate, if the heavier female was female 2, its slightly larger size and similar physiological state (as evidenced by the size of the ovary) in relation to female 1 may account for its persistence and for the two females being about equally matched. Such triangles have been noted in the Downy Woodpecker (Lawrence, 1967). Kilham (1969) described an instance involving two male and one female Hairy Woodpeckers, in which the intruding male successfully drove off the territorial male thereby gaining the latter's presumed mate.

ENCOUNTERS BETWEEN MALES AND FEMALES

Encounters observed between males and females were generally similar to unisexual encounters, except that Tewk Calls were more common. Of course, there is a difference in crown-nuchal color between the sexes, and Crest Raising was observed mainly in males during encounters between sexes. The crest of males was erected more fully during male-male encounters than during male-female encounters. Also, lone males present during female-female encounters raised their crests more often than they did during male-female encounters.

A few male-female encounters are described below. These encounters tend to be briefer than unisexual ones between territorial males or between territorial females. Whether the birds were already paired is not known. Studies of pair formation as it relates to territoriality are needed to interpret fully such encounters.

One encounter in Nuttall's Woodpeckers included a perched, queeking female whose call elicited drumming from a nearby male, which then flew over the female in Flutter Flight Display, also calling queek. Continuing the queek call, the female flew in Flutter Display to another tree in the direction in which the male had flown. The male returned and a chase began with the female flying normally and the male in Flutter Display. The birds circled around an area of 150 yards in diameter as one of them, probably the male, called queek.

The following is a common episode. After some Queek Calls and Flutter Displays, a male is alone. A female flies to the male in Flutter Flight calling queek. After she lands, the male supplants the female, which flies off.

A pair of Nuttall's Woodpeckers closely

perched engaged in a Head Swinging bout while both birds called wicka. Then both flew off.

Most episodes between sexes involve chases, and only brief bouts of displaying when the birds are close together. There is much supplanting, mainly of the female by the male. The dearth of pair-formation displays and the preponderance of aggressive behavior that marks the pair-formation period suggests that the female attracts the male by: persistent aggressive behavior; lack of emphasis on threat and strong emphasis on submissive behavior, as indicated especially by repeated supplantings by the male; and, lack of a male's red crown and the associated Crest-Raising Display, which probably inhibits intense threat and attack behavior by the male. The brevity of the individual encounters and the continued movement in flight of the birds greatly hinder precise observations of their actions.

ENCOUNTERS IN LADDER-BACKED WOODPECKERS

About 50 encounters were observed in Ladder-backed Woodpeckers, and all of these involved individuals of presumed pairs. The few encounters that were observed closely were brief and lacked the intensity of the unisexual encounters of *nuttallii*. They consisted of, at most, a slight Head Swinging accompanied by a Wicka Call after which the birds resumed foraging or other activities. A number of supplanting attacks highlighted these encounters, which seemed identical with those in the Nuttall's Woodpecker.

One Flutter Displaying female called queek then wicka as it flew over a male, which responded with a Tewk Call. Low Wicka Calls often were the only indication of an interaction between two birds perched or foraging close together. Low Crest Raising of the male, and a tendency to supplant the female when a pair happened to be in proximity also marked the occurrence of otherwise inconspicuous interactions. I have noted that members of a pair ordinarily forage apart, calling frequently to maintain contact. At irregular intervals the tempo of the calling increased, and one bird (usually the female) flew to the vicinity of the other. At this point there was usually an interaction, often at a distance—perhaps a Rattle by each bird. If they came within 2 or 3 meters of

each other low Wicka Calls were uttered, with a slight Head Swinging.

Once the female of a pair, away from its mate, commenced calling peek when two distant peek notes were heard. The female looked about, became quiescent for 2 minutes, then began to call and move about excitedly. Reaching the tip of a Joshua tree branch, the female gave loud Peek Calls accompanied by Head Bobbing movements. She continued calling rapidly, uttering 32 peek notes in 1 minute, then gave a Rattle Call. The distant male failed to respond. The female became silent for several minutes, called again, and at hearing a distant peek, moved to the tip of a branch. The female flew to the west and was joined by or joined the male there, for I found both together 3 minutes later.

Males supplanted females regularly, mainly when females were in Joshua trees (male's foraging sites). The female usually moved rapidly, showing fear (Wing Flicking, turning body away, crouching) whenever the male faced her. It is possible that the sexual size difference in *scalaris* renders males dominant over females more in that species than is true of *nutallii*.

When a pair fed close together, then separated, the female initiated the separation, just as she seemed to initiate contact after birds were apart for some time. Usually the departing female flew (sometimes in a Flutter Display) over or near the perched male, uttering low Wicka or Tewk calls. The male responded when the female called, usually with a very low Tewk Call, and sometimes with slight Head Swinging.

INTERSPECIFIC ENCOUNTERS

ENCOUNTERS BETWEEN NUTTALL'S AND LADDER-BACKED WOODPECKERS

Most of the observed interspecific encounters involved adjacent pairs of Nuttall's and Ladder-backed woodpeckers in the study area east of Ensenada, Baja California, during April. Separate episodes lasted as long as 2 hours, although most of the 18 observed episodes lasted about one-half hour. The males of the two pairs were the main antagonists, although one or another of the females was nearby during parts of some episodes. Only twice did the females engage in unisexual encounters in the absence of the males. A few brief interactions were noted between Nuttall's and Ladder-backed woodpeckers near Onyx, California, in November.

Chases involving females of *nutallii* and of *scalaris* were observed east of Ensenada on April 5. Several display bouts were observed in part. In one episode both females were close together, and I saw Head Bobbing and Head Swinging, their bills between Bill Directing and Bill Raised postures (the bill of *nutallii* was held higher); Wing Spreading and Tail Spreading followed with Wicka Calls from both birds. Then came a drumming bout. Another episode featured an attack by the Nuttall's Woodpecker female on the *scalaris* female in the presence of a displaying male Nuttall's Woodpecker. As the latter bird perched 50 cm. away, it turned its head, displaying its face toward the females and at the same time raising its crest fully. Movies showed no other displays of the male. The female Ladder-back Head Turned, the Nuttall's female Bill Directed at the other female, and after a few flicks of the wing, the Nuttall's female flew at the Ladder-back female and supplanted her. Thus, the male seemed to incite an attack by the female Nuttall's Woodpecker. On another occasion, a male Nuttall's Woodpecker, apparently alone, attacked and supplanted a female Ladder-backed Woodpecker, which flew off after giving a Queek Call.

The presence of a female near displaying males of the two species seemed also to elicit more vigorous displays. A female Nuttall's Woodpecker perched close to males of the two species that had been quiescent until the arrival of the female. The male *scalaris* suddenly gave a Rattle then a Peek Call, followed by repeated Peek Calls. The male *nutallii* advanced, Bill Directing; both males gave Wicka Calls and the Ladder-back also swung its head, then the male Nuttall's Woodpecker supplanted the Ladder-back. During these activities, the female *nutallii* remained silent and did not render postures or displays so far as I could determine. In another instance a female Ladder-back approached the same two males as they perched quietly between display bouts. The male *scalaris* suddenly moved toward the male Nuttall's Woodpecker, which flew a few feet away, but did not quite supplant the latter. Instead, before reaching the position the Nuttall's male had occupied, the male Ladder-back abruptly turned, flew to the Ladder-back female, and copulated briefly. Thus, if only one female is at hand, its mate appears to become more aggressive, taking the offensive in the encounter.

Any action, such as a shift in the displays being used, brought quick reactions from the interacting male Ladder-backed and Nuttall's woodpeckers. At the end of one encounter, the Ladder-back, perched below the Nuttall's Woodpecker, Wing Raised upwards; the Nuttall's Woodpecker, perched crosswise on a branch above, Tail Spread and Wing Raised. Both birds simultaneously flew, the Nuttall's Woodpecker down and to the right, with the Ladder-back in pursuit. After flying only a few centimeters (halfway to the Nuttall's Woodpeckers' perch, hence not quite supplanting the latter), the Ladder-back suddenly reversed direction and flew to the left. The Nuttall's Woodpecker continued flying to the right for about 0.2 second (covering $1\frac{1}{2}$ meters, approximately 23 kilometers per hour) after the Ladder-back had switched directions, and then the Nuttall's Woodpecker reversed its direction and chased the Ladder-back to the left. Assuming that the encounter kept both birds attending each other even when in flight, the 0.2 second would seem to be the time required to perceive an action, and to translate this perception into a reaction. I have noted that reactions, when they occur during encounters in perched woodpeckers, seem to develop within 0.1 to 0.2 of a second after the display eliciting the reaction.

Another encounter commenced with the same males about 15 cm. apart, the Nuttall's Woodpecker on the left with Head Raised and Wing Flicking, and the Ladder-back on the right with Crest Raised, almost a Bill Directing Posture (head with a one-quarter turn away from *scalaris*) and no Wing Flicking or Tail Spreading. As the Ladder-back held its position, the Nuttall's male Bill Directed, then abruptly raised its head so that its bill pointed upward and slightly to the rear (beyond vertical, at an angle of about 100 degrees). At the same time the latter bird held its wings spread slightly. The Nuttall's male then moved about 7 cm. toward the Ladder-back, Wing Spreading, holding the bill partly raised, Tail Spreading, and erecting its crest slightly. The Ladder-back retained its position but lowered its crest somewhat. The Nuttall's Woodpecker then performed the following actions in order: a) Head Turning to left (away from *scalaris*) with simultaneous spreading of the left wing, which was held up for 0.10 second; b) Head Turned farther left, left Wing Spread, Crest Raised slightly and Tail

Spread and directed toward *scalaris*; c) Head Raised, facing halfway toward *scalaris*, wings in at sides of body, tail remaining spread and turned toward *scalaris*; d) with Head Raised, Wing Flicking of left wing, Crest Raised markedly, Tail Spread more fully; e) Wing Spreading, both wings, head bowed low and strongly away from *scalaris*; f) Wing Flicking; g) Wing Flicking; h) turned toward *scalaris*, Head Raised (50-degree angle), Crest Raised slightly, tail and wings not spread; and i) Wing Flicking, Head Raised. Throughout these events the Ladder-back remained motionless except for a slight raising of the head. The Ladder-back then flew past the Nuttall's Woodpecker in Flutter Flight Display, landing behind it. The Ladder-back then Wing Flicked its right wing, then Spread both wings, Bill Directing at the Nuttall's Woodpecker. The Ladder-back gradually spread its tail to the full extent during Wing Spreading. It then advanced toward the Nuttall's Woodpecker, Wing Spreading. The Nuttall's Woodpecker perched upright, bill held high (75 to 80-degree angle). The Ladder-back advanced gradually raising its crest higher, Bill Directing (even while Wing Spreading), Wing Spreading twice, and Tail Spreading only during the Wing Spreading Displays. As it drew close to the Nuttall's Woodpecker, the Ladder-back closed its tail, fully erected its crest, Wing Flicked (instead of Wing Spreading) and lunged. The Nuttall's Woodpecker lowered its head, spread its tail slightly, then flew a short distance to the left as the Ladder-back supplanted it. The Nuttall's Woodpecker seemed to give a Flutter or two in flight before landing 15 cm. away. The time lapse from the initial advance of the Ladder-back to the supplanting was 2 seconds. Both birds had now exactly reversed their positions.

The encounter continued, with the Ladder-back assuming a partial Head Raised Posture, and with its tail half-spread. The Nuttall's Woodpecker at first faced away from the Ladder-back and in this position Wing Spread once; it then turned toward the Ladder-back (which raised its bill slightly) and assumed a Head Raised Posture. The Nuttall's Woodpecker then advanced toward the Ladder-back, raising its head and bill higher and, as it approached, the Ladder-back also raised its head somewhat. The Nuttall's Woodpecker gave a Head Bob, then a full Bill Raised Posture. It

flicked its wings, partly spreading its tail as it Wing Flicked, and turned its head abruptly to the side as it finished Wing Flicking. Facing laterally it spread its wings, the right wing (toward *scalaris*) being spread higher, and simultaneously turned its head farther left, away from *scalaris*. After Wing Spreading it gradually (0.5 second) turned its head toward the Ladder-back, holding closed its wings (and tail), while markedly raising its bill as it turned. Then it lowered its bill (Bill Directing) and half-erected its crest. There followed a Head Swinging Display by the Nuttall's Woodpecker (the bill was held high during the swinging), with Crest Raised—as the bill of the Nuttall's Woodpecker moved laterally, the Ladder-back perceptibly lowered its bill almost to the horizontal, then raised it again as the Nuttall's Woodpecker swung its bill toward the Ladder-back. The Nuttall's Woodpecker gave one other full Head Swinging Display. Its bill was clearly raised higher in the center of the swing (toward the Ladder-back) than at the lateral extremes (away from the Ladder-back). As I moved to rewind my camera, both birds suddenly flew away. The entire encounter just described took place within a minute and a half. Most of the action occurred within about 25 seconds. Unfortunately I did not have my tape recorder during the encounter, so I have no record of the vocalizations uttered by the birds except that both gave Queek Calls.

In another similar encounter, the attacking male Ladder-back flew at the male Nuttall's Woodpecker in Flutter Flight, turned as it reached the Nuttall's and battered with its wings. The Nuttall's Woodpecker met the attack with Wing Spreading, batting at the Ladder-back in a flurry of wing smashing. The Ladder-back was unable to supplant the male Nuttall's, and finally flew, landing 15 to 20 cm. away. The male Nuttall's later supplanted the Ladder-back in a similar wing-batting bout, in which both birds' crests were erected, and the Ladder-back had its tail spread.

Parts of other encounters between these birds involving supplanting attacks and various displays are shown in figures 20 (A to E) and 22. Figures 20 and 21 also depict other displays filmed during their encounters.

Encounters between these males often lasted as long as one hour, with frequent supplantings, chases, and display sessions in different trees. Although I devoted one full day to observations

of these birds alone, observations over 10 days suggest that these males engaged in encounters for half or more of each day. Both males supplanted about equally, often reversing supplantings. Most encounters involved frequent movement of both birds, flights from one bush or tree to another or climbing and flight from branch to branch. The playback of vocalizations (mainly Wicka and Tewk calls) of the displaying males usually triggered a flurry of displays and calls.

I was able to collect both of these males, and their respective mates on April 18. The two pairs had nests in willow stubs within 90 meters of one another along the stream in the study area. Three other pairs nested nearby: a pair of *scalaris* to their east (away from the stream); a pair of *scalaris* along the stream north of the *nuttallii* pair under consideration; and a *nuttallii* pair still farther north along the stream. None of these other pairs had nests so close to that of the *nuttallii* pair as did the *scalaris* pair involved in the extended encounters that I observed. The male of the *nuttallii* pair weighed 38.9 grams and had a brood patch and testes measuring 4.5 by 2.5 mm. The Ladder-back male with which it engaged in encounters weighed 40.3 grams, and had testes measuring 11 by 7 mm. and a brood patch. The female of the *nuttallii* pair weighed 35.0 grams, and had a brood patch, an ovary measuring 6 by 5 mm., and ova to 1.5 mm. The female of the *scalaris* pair, a probable introgressant or hybrid (A.M.N.H. No. 791499; see discussion above), weighed 38.4 grams and it had an ovary measuring 10 mm. in diameter, ova to 3 mm., and a brood patch. Thus the individuals involved in the displays described above were nearly of the same size. The *scalaris* pair tended to be slightly larger (bills longer too, by 4.7 mm. in the males, and by 1 mm. in females), and perhaps slightly more advanced in their breeding condition.

Except for the difference in plumage between the two species, possibly important in displays, and in their vocalizations, described above, I could detect no definite differences between *nuttallii* and *scalaris* in their displays. The intensity and prolonged nature of the encounters between the Ladder-back male and the Nuttall's male described above lead me to suggest that some inappropriate elements of posture or displays, or of vocalizations may be involved. It is true that the habitat favorable for these woodpeckers at 31 miles east of Ensenada appeared

saturated, and many intraspecific conflicts were noted. However, none recurred to the same extent as the interspecific conflicts between the two above-mentioned males. The only similarly prolonged situation of this type occurred in California between the two female Nuttall's Woodpeckers apparently vying for the same conspecific male.

Some observations do suggest possible differences in displays between the two species. For instance, I did not see Ladder-backs erecting their crests as fully as male Nuttall's Woodpeckers commonly did. Perhaps the more extended red area of the crown in males of *scalaris* reduces the need for pronounced erection of the crest in that species.

Generally, however, displays of the two species were comparable, not only in form, but in their relation to one another. In both species Wing Flicking and Bill Directing tend to precede an overt attack. Both react to Wing Spreading or Bill Directing by withdrawal of the head and bill, either by Head Raising or Head Turning. In both species the head is turned away from an opponent when giving a Wing Spreading Display. Tail Spreading seems associated with Wing Spreading in both species. Also, the tail tends to be spread more fully in a retreating bird or in an individual showing a tendency to flee; it is not spread in birds about to attack.

ENCOUNTERS WITH OTHER SPECIES

Interactions with other species of *Picoides*, namely the Downy Woodpecker (*P. pubescens*) and the Hairy Woodpecker (*P. villosus*), were observed in the Kernville region of California, and at San Jose, Baja California. Alden Miller's extensive field notes (unpublished, on file at Hastings Reservation) on the Nuttall's Woodpecker at Hastings Reservation in California contain information about interaction between that species and *pubescens* (11 incidents) and between *nuttallii* and *villosus* (seven incidents). Among the incidents involving *pubescens* and *nuttallii*, reported by Miller, a Nuttall's Woodpecker twice "displaced" a Downy, another Nuttall's was displaced by a Downy, and another Downy attacked a Nuttall's Woodpecker on a stub three times within 5 seconds. Among the incidents noted between *villosus* and *nuttallii* is at least one case of an individual of the latter species attacking a Hairy Woodpecker.

An example from my notes shows rather clearly that interspecific interactions among closely related species of *Picoides* can be expected to occur frequently. A perched Nuttall's Woodpecker called pi-dit, and a female *pubescens* flew in, landing about 3 meters away. A male *pubescens* then came in, landing in the same tree. Both Downies uttered Rattle Calls, facing toward the Nuttall's Woodpecker. The latter flew off, but at the same time, apparently in response to the Rattle Calls, a Hairy Woodpecker called peek from a nearby tree. Thus it seems that individuals of the various species are aware of the actions of individuals of related species, and that they may react to them.

On March 6 a female Nuttall's Woodpecker was observed uttering a long Queek Call, repeated several times as it chased a female Downy. As the birds flew over, a Queek Call was elicited from a perched Nuttall's Woodpecker. On March 7 a male Nuttall's Woodpecker, a male Downy, and a female Hairy were feeding in a cottonwood tree. The Downy flew, calling pit. The Nuttall's Woodpecker immediately gave a Rattle Call, then flew off in the direction taken by the Downy, calling queek. On March 8 a male *nuttallii* fed in the top branches of a cottonwood, and, below it on the trunk, a male *pubescens* foraged. Off to one side of the tree a female *pubescens* foraged in the branches. A female *nuttallii* was in a nearby tree. The male Nuttall's Woodpecker called pitit, and flew at the female Downy, supplanting it. The female Downy flew to the top of a branch, where it was joined by the conspecific male. The female Nuttall's Woodpecker then flew in, calling pit, attacked the female Downy and supplanted it—the Downy flew to another branch. The male Downy then flew away. The female Nuttall's called pit, and a Hairy Woodpecker flew over the tree, called queek, and gave a Rattle Call as it proceeded on its way. The male *nuttallii* flew to a perch close to the female Downy, but rather than supplanting it, the Nuttall's Woodpecker flew away.

In three additional brief interactions between Nuttall's and Downy woodpeckers, a female of the former species supplanted a female of the latter once, and a male of the former supplanted a female of the latter twice. All of the interactions between these two species occurred within a two-week period in March near Kernville, California.

Incidents involving Nuttall's and Hairy woodpeckers were more commonly observed, for there was more opportunity to see these two species together. On March 7 a female *nuttallii* feeding in the buds of a cottonwood tree gave a Rattle Call then called pit or pitit seven times. A male Hairy Woodpecker two trees away then drummed. The female Nuttall's Woodpecker reacted by flying to the trunk of the tree, drumming, then flying to the tree beside the Hairy Woodpecker, where she drummed again. The Hairy drummed louder than before. The drumming continued, each bird apparently replying to the other three times. Then after more drumming followed by three queek notes the female Nuttall's Woodpecker flew out of sight to the north. From the distance I heard her drum twice before she stopped; the Hairy Woodpecker responded each time. On the same day a displaying pair of Hairy Woodpeckers gave seven or eight Queek Calls, then a Wicka Call—an adjacent pair of Nuttall's Woodpeckers instantly responded to the Wicka Call with an intense (ka-weep, ka-weep) burst of Queek Calls.

On March 9 females of both species were observed in a cottonwood, the Nuttall's Woodpecker on a trunk and the Hairy feeding in the buds. The Nuttall's called pitit, and the Hairy flew to an adjacent tree. The Nuttall's followed the Hairy to that tree, where they were joined by a male Nuttall's Woodpecker. The female Hairy faced the incoming male *nuttallii*, called peek, and advanced toward the latter bird. She then flew to an adjacent tree, leaving the two Nuttall's Woodpeckers in the tree. The female Nuttall's Woodpecker began preening, and, suddenly surprised by the landing nearby of a White-breasted Nuthatch (*Sitta carolinensis*), gave a Queek Call. At this the female Hairy returned, supplanted the female Nuttall's Woodpecker, and, following the latter, supplanted her again. Both Nuttall's Woodpeckers then flew away.

On March 10 a male Hairy Woodpecker drummed in response to a Queek Call from a nearby female Nuttall's Woodpecker. On the same day a long drumming bout occurred between a female *nuttallii* and a male *villosus* perched 50 meters apart. Both drummed more than 20 times in 10 minutes; first one then the other drummed.

An episode between a pair of Nuttall's Woodpeckers and a pair of Hairy Woodpeckers took place at San Jose, during April 20–22. In this

area, densely populated by Nuttall's Woodpeckers, the lone pair of Hairy Woodpeckers appeared to be establishing a territory (below their normal altitudinal range in Baja California; see Short and Crossin, 1967). Encounters were observed at all times when I was in that area (about 2 hours on April 20, 3 hours on April 21, and 2 hours on April 22). The encounters involved the pairs sex for sex, the females displaying with the same intensity and attacking each other with the same frequency as did the males. The Nuttall's Woodpeckers persistently flew near the Hairy Woodpeckers, calling and displaying, commencing encounters that usually led to their being attacked and chased by the Hairy Woodpeckers. Less chasing was noted in the females. The latter uttered Queek Calls whenever there were male-male encounters, and their calls seemed to "excite" the males. Displays culminating in attacks were evoked from a Hairy Woodpecker by a Nuttall's Woodpecker (of the same sex) either landing beside a foraging Hairy Woodpecker or giving a Rattle Call or drumming near a Hairy Woodpecker. The Hairy Woodpecker responded by flying near the Nuttall's Woodpecker, Bill Directing, Head Bobbing, Wing Flicking, and attacking and pursuing the Nuttall's Woodpecker. Queek Calls were especially prevalent during the displays (Wicka Calls may not have been heard, if uttered, because much of the fast-moving actions occurred high in the trees, which were quite tall at the site). Both species used Flutter Flight Displays, but these were especially conspicuous in Nuttall's Woodpeckers as they were chased. Wing Spreading was noticed too in the Nuttall's Woodpeckers when they perched after being chased. Rattle Calls were frequent during the chases, especially when the birds were out of sight of one another.

In one intense encounter between these males, both Wing Spread, Bill Directed, and both were seen Head Swinging as they called (*villosus*, week-weeek-weeek; *nuttallii*, wick-awick-awick-a. The Hairy Woodpecker chased the Nuttall's Woodpecker, both in Flutter Flight, and finally landed a tree short of that in which the Nuttall's Woodpecker had taken refuge. The latter bird then gave a Rattle Call, and flew to the trunk of the tree occupied by the Hairy Woodpecker—it landed, Wing Spreading, about 14 cm. from the latter. The Hairy Woodpecker immediately gave a Bill Directing Display, then a Head

Bobbing Display, and then flew directly at the Nuttall's male, which left abruptly. It appeared that the Hairy Woodpecker pair had recently entered the area, and were attempting to establish a territory incorporating part of the territory already occupied by the Nuttall's pair. The latter responded by repeated displays and calls. Although emphasizing "fear" aspects in their displays during encounters with the much larger Hairy Woodpeckers, the Nuttall's Woodpeckers' persistent efforts ultimately may have disrupted the Hairy Woodpeckers, causing the latter to shift their territory away from that of the former pair. My attempts to secure these birds were frustrated on April 22, when I obtained the female Nuttall's Woodpecker. Four days later the male of the Hairy Woodpecker pair was collected. The latter weighed 64.4 grams, and had large testes; the female Nuttall's Woodpecker weighed 38.1 grams, and was about to lay eggs (ova to 7 mm.).

No instances were noted involving the full supplanting of a Hairy Woodpecker by a Nuttall's Woodpecker, although many encounters were initiated by individuals of the latter.

In several cases Hairy or Downy Woodpeckers were seen near Nuttall's Woodpeckers with no interaction observed. Interactions between Hairy and Downy woodpeckers were not observed, although the birds were seen together in the same tree several times in California. On March 10 a female Nuttall's Woodpecker passed beside a male Red-naped Sapsucker (*Sphyrapicus nuchalis*) in a cottonwood, and no interaction ensued. The only interspecific agonistic encounter involving *scalaris*, other than the *scalaris-nuttallii* interactions, was an incident in which a Loggerhead Shrike (*Lanius ludovicianus*) flew to the tip of a Joshua tree branch occupied by a male Ladder-back, and supplanted the Ladder-back. Opportunities for contact between *scalaris* and other species of *Picoides* are few in the areas in which I studied; they are mainly limited to chance meetings of *scalaris* and *villosus* in winter when *villosus* individuals wander to lower elevations. These species breed within a few miles of each other near Onyx, and around Victorville.

INTERSPECIFIC TERRITORIALITY

Territories of the Hairy, Downy, and Nuttall's woodpeckers generally overlap where these

species are sympatric. The Downy and Hairy certainly overlap territorially in the East, although their habitat preferences differ somewhat and they do not always occur together. Behavioral interactions have been observed among the three species. It seems likely that under certain circumstances, such as their occurrence together in less favorable habitats, their interactions may affect the size and spatial distribution of their territories.

Hairy Woodpeckers require much larger territories than do the other two species, and hence their populations are less dense than those of *pubescens* and *nuttallii*. The Hairy Woodpecker is considerably larger in size, with a longer, more massive bill than that in *pubescens* and *nuttallii*, and it also ranges into more diverse habitats. In favorable habitats competition between *villosus* and the other two species may be minimal. However, in more uniform habitats, especially those suitable for the Downy or Nuttall's Woodpecker, competition may be more severe. The riparian woodland at San Jose, Baja California, is an example of such a uniform habitat favorable for *nuttallii* and supporting a dense population of that species in an area outside the normal range of *villosus*. The occurrence there of an isolated pair of *villosus* led to strong, repetitive interactions between the *villosus* pair and the *nuttallii* pair described above. Although the factors responsible for the strong interactions are unknown in this case, it is likely that the relatively uniform habitat and dense population of *nuttallii* would bring individuals of the two species into frequent contact while foraging, perhaps favoring interspecific territoriality. The Hairy Woodpecker, being larger, has an advantage in interspecific encounters with Nuttall's Woodpeckers. Despite this advantage, a Hairy Woodpecker pair on their greater territory may be so frequently engaged in interactions with the more abundant Nuttall's Woodpeckers as to hamper their efforts to nest.

The Downy and Nuttall's woodpeckers are more restricted in their habitat preferences than is *villosus*. Because of the strong preference of the Downy for riparian woodland, competition with the Nuttall's Woodpecker is likely wherever the latter inhabits the same woodland. The Downy favors riparian woodland in California, and pairs maintain small territories. Its size and bill structure are similar to those of *nuttallii*, and in contrast to the much larger, bigger-billed *villosus*;

in fact, *pubescens* and *nutallii* overlap in bill length. Furthermore, the abundance of *pubescens* sharply diminishes precisely in the area of California where *nutallii* comes to occupy riparian woodland, as well as oak woods and chaparral. Available data are insufficient to indicate whether interspecific territoriality occasionally obtains between these species. At Kernville, where both are sympatric with *villosus*, I saw some interactions between Downy and Nuttall's woodpeckers (described above), but no prolonged confrontations were noted. Also, individuals of the two species were occasionally seen near each other with no interactions. I judge that, as with *villosus* and *nutallii*, *pubescens* and *nutallii* normally occupy overlapping territories where they occur together (which may of course be only where the habitat is sufficiently diverse to permit their sympatry). Further studies of these two species in sympatry are needed, particularly in view of their close relationship.

In the riparian woodlands of western Nebraska, somewhat restricted in extent like those of the Kernville and Victorville regions, *pubescens* is numerous and *villosus* about as common as it is in California (no other species of this genus normally occur in western Nebraska). Nuttall's Woodpeckers are more common in the California areas cited than are Downy Woodpeckers in the valleys of the Great Plains, however. More abundant than all species of *Picoides* combined in localities in the regions just mentioned is the combined *scalaris* and *nutallii* population in the isolated riparian woodlands of northern Baja California, where they maintain small territories intraspecifically and interspecifically.

We have seen that no overlap occurs between *scalaris* and *nutallii* within California. Hence there is no interspecific territoriality. Indeed, contact between these species is sporadic, and occasional individuals of *scalaris* wandering into riparian habitats occupied by *nutallii* may secure mates of the latter species. It is well to recall the extended bout between two female Nuttall's Woodpeckers vying for a male near Onyx in March when nest building was about to commence. Excess birds such as one of those females might accept a mate of the other species.

In Baja California the distribution of pairs, responses to calls and displays, and actual interspecific conflicts indicate that *scalaris* and *nutallii* maintain territories against one another just as they do conspecifically. Presumably their

sympatry here is due to some difference between populations of *scalaris* in California and those in Baja California (probably separated by a geographical gap; *nutallii* appears to have an essentially continuous range into Baja California from California, although very small gaps may occur). At any rate the agonistic behavior of these species is similar and enables (perhaps with difficulty, as suggested by extended conflicts between adjacent pairs of the two species) establishment of territories at least marginally sufficient for the maintenance of their populations.

Interspecific hybridization between these two woodpeckers, although frequent, is not complete. The two species are closely related, and the fact that they maintain interspecific territories in the same habitat in Baja California (and not in California) suggests that selection against hybridization, favoring the reinforcement of isolating mechanisms, may be countered by selection favoring retention of similar agonistic displays for use in interspecific territoriality. Orians and Willson (1964, p. 738) suggested that "the nature of the environment may limit the types of efficient foraging patterns, thus reducing the possibilities for sufficient divergence to permit overlap in territories." One of the situations those authors mention that may restrict ecological divergence is a simple structure of the vegetation in an area. This indeed seems to hold with respect to the riparian woodlands in Baja California. Not only do the two woodpeckers maintain interspecific territories, but, indeed, they seem to occur *together* only when there is diversity of vegetation (table 23). Where the vegetation types are more limited and tend to be xeric, *scalaris* occurs alone; conversely, when the limited vegetation types tend toward chaparral (especially in the presence of oaks), *nutallii* seems to occur alone. Tiny isolated patches may be populated by one or both species (and hybrids may result). Where the vegetation is more diverse, hybridization may be facilitated by the frequent interspecific encounters resulting from interspecific territoriality.

I have noted above the particularly aggressive nature of woodpecker social behavior. It is difficult to establish even the presence of tendencies other than agonistic tendencies in the displays of these birds. It is apparent that *scalaris* and *nutallii* are very closely related, and that they are in secondary contact. Morphological traits, displays, and vocalizations of each species

that differ due to genetic events during their former separation and divergence, and which might be seized upon by selection acting to enhance reproductive isolation, are exposed to the other species during interspecific territorial encounters. Experience and habituation may tend to minimize any reinforcement of isolating mechanisms affecting these types of characters. For instance, there is a tendency for different tail barring in the two species—this difference (perhaps reinforced) could play a role in species recognition during pairing. However, frequent encounters between the species involve Tail Spreading Displays, so that each species might be habituated to the tail pattern of both species. This presumably would reduce its potential effectiveness in pairing. Regardless of what characters might be involved in the partial reproductive isolation of the two species, the familiarity gained through interspecific encounters is likely to pose a problem for the reinforcement of isolating mechanisms.

Johnson (1963, p. 195) has stated that "It is

conceivable that competition might favor the retention of similar territorial defense mechanisms, particularly if the closely related species had not developed different ecologic niches while in isolation." It is noteworthy that the various species of *Picoides* generally have retained similar "territorial defense mechanisms." There are of course differences, as has been noted above, but these differences do not preclude the occurrence of encounters between them, and even of apparent interspecific territoriality between *villosus* and *nuttallii*. Perhaps the similarity in agonistic behavior among these species is related to selection favoring interspecific territoriality under suboptimal habitat conditions. Interspecific territoriality may result in "simpler" habitats as an indirect, rather than a direct consequence of foraging patterns (see Orians and Willson, 1964, p. 738) that is, by individuals of the different but related species coming into contact so frequently as to "trigger" establishment of interspecific territories.

HYBRID OR INTERMEDIATE DISPLAYS AND VOCALIZATIONS

The behavior of hybrids was not studied because most hybrids were not identified as such until they were collected. The displays of both *scalaris* and *nuttallii* are sufficiently similar or identical so that "intermediate" displays were not noted. Further studies of the behavior of both species will permit the determination of their full behavior repertoires, and permit investigation of the displays of hybrids. However, I did record vocalizations of birds thought to be hybrids or introgressant individuals, and some of these vocalizations proved to be intermediate between those of *scalaris* and *nuttallii*.

CALL NOTES

Peculiar calls were recorded from a male that was not collected, but was regarded in the field as a possible hybrid. I recorded this male's vocalizations on April 22, 1967, in a small grove of live oaks in a ravine 5 miles northwest of San Jose, Baja California. The grove was isolated in low chaparral; no other large trees were nearby. Other woodpeckers were not seen in the area. When I returned on April 26, a pit-calling female

Nuttall's Woodpecker (A.M.N.H. No. 791447) in breeding condition was collected, but we could not locate the male.

Calls of the male were of two types, a peculiar Peek Call rendered peet (fig. 24G, J), and a Pitit Call sounding rather more like peek-eeek (fig. 24L). Five of the peet calls proved to be higher in pitch (average 4.02 kilocycles, one at 4.3 kilocycles) than any Pit Call of *nuttallii*. In duration these calls bridged the gap between *nuttallii* and *scalaris*, from 0.032 to 0.040 second (average 0.0355 second). Thus, these odd peet calls are intermediate in their characteristics.

The four recorded peek-eeek calls of this strange male proved to be beyond the range of variation of the *nuttallii* Pitit Call, and strongly tending toward *scalaris* in the characteristics of their component elements. The peek-eeek calls ranged from 0.09 to 0.10 second in duration, hence they are longer than Pitit Calls of *nuttallii*. In pitch they ranged from 3.5 to 4.1 kilocycles, two of the four calls exceeding in pitch all recorded calls of *nuttallii*. The double note aspect of the call is not known in *scalaris*. Thus the fact that the call is double noted, but has *scalaris*

traits renders it intermediate between calls (Peek of *scalaris*, Pitit of *nutallii*) of the two species.

These are the only apparently "hybrid" call notes that I was able to record. Of the three hybrids, which I managed to collect (none with vocalization recorded), one (male A.M.N.H. No. 791508) called pit like *nutallii*, a second (male A.M.N.H. No. 791485) called peet ("hybrid" call?), and a third was silent. The majority of the eight probable or possible introgressant *scalaris* individuals, and the six such individuals of *nutallii* that were obtained by me and my assistant gave call notes or Rattle Calls. Only a few of these were noted, but all were like, or within the limits of the variation of calls of the respective species (that is, introgressant *scalaris* sounded like *scalaris*, and vice versa), with the exception of a probable introgressant *scalaris* male (A.M.N.H. No. 791495) which gave a pik call (*nutallii*; see below under Rattle Call). It is of course possible that some of the intraspecific variation in calls described earlier is due to introgression. In any event, hybrids may have intermediate calls or calls tending toward one or the other species. Introgressant birds, or hybrids tending morphologically toward one or the other species, tend to have calls similar to those of the species they most resemble morphologically.

RATTLE CALLS

An unusual female woodpecker generally tending morphologically toward *scalaris* was observed, and its Short Rattle Call was recorded on April 6 along the stream in the study area 31 miles east of Ensenada, Baja California. This female, which very likely was the probable introgressant *scalaris* (A.M.N.H. No. 791499) mated to a male *scalaris* (A.M.N.H. No. 791490), gave a Short Rattle during an encounter between nearby males of *scalaris* and *nutallii*. Only one such situation involving the two species was encountered, and it is likely that this female was the mate of the displaying *scalaris* male.

The Short Rattle of the unusual female contains four notes (fig. 24F), and is generally like the Short Rattle of *scalaris*. However, it exceeds the variation found in the few recorded Short Rattles of *scalaris*, and tends toward *nutallii* in several characteristics. The duration of the call, 0.24 second, is less than that of the Short

Rattles of *scalaris*. The notes sharply descend in pitch from 7.5 to 5.0 to 4.0 to 2.7 kilocycles, the total descent of 4.8 kilocycles far exceeding that found (0.3 to 2.5 kilocycles) in *scalaris*. These peculiarities do not appear to be tendencies toward *nutallii*. The rate of delivery, 16.7 notes per second, is greater than the maximum (15.2 notes per second) found in *scalaris*, and represents a tendency toward the rapid delivery of *nutallii*. The time between notes increases during the call from 0.055 to 0.06 to 0.09 second. The first two of these are typical of *nutallii*, and the last (0.09 second) is within the range of *scalaris*. Finally, the duration of each note is, respectively, 0.02, 0.03, 0.03 and 0.025 second, all within the range of *nutallii* and well below the lower limit (0.045 second) of the range of *scalaris*. Further studies of the variation in Rattle Calls may show that this peculiar call is a variant of one or another species, but at our present state of knowledge it must be considered tentatively as intermediate between *scalaris* and *nutallii*. The likelihood that the female producing the call was the introgressant female taken later (April 18) reinforces such consideration.

On April 4 along the same stream but farther north I observed an encounter between two Nuttall's-like female woodpeckers. One of these was peculiarly marked, tending toward *scalaris* in face pattern, but resembling *nutallii* in its tail pattern. Two Rattle Calls of this female were recorded. It is conceivable that this bird was one of the introgressant *scalaris* females later collected along the stream, although none of these has a strongly *nutallii*-like tail. At any rate, these calls appear to be intermediate (fig. 24K, M). The female producing the calls was definitely not the same female that gave the intermediate Short Rattle Call described above.

The Rattle Calls of the unusual female are peculiar in several respects. A major feature is the mixture of single and double notes. I have mentioned (above) a pairing tendency in the Rattle Calls of Nuttall's Woodpeckers. Such a tendency, suggestive of the Pitit Call (see above for the relation between Pitit, Pit, and Rattle calls) of *nutallii* is not evident in the Rattle Calls of *scalaris*. Individual notes of the Rattle Calls were of the rapid rise-sharp fall type described above for *scalaris*. The tempo of the calls, considering the double-notes as single elements of them, clearly is like *scalaris* with a rate of 10.4 and 10.7 notes per second. Individually, how-

ever, both the single notes and the two elements of each double note are shorter in duration (0.030 to 0.042 second for single notes, 0.015 to 0.030 second for elements of double notes) than notes of *scalaris*, thus tending toward those of *nutallii*. Hence the tempo of the call is *scalaris*-like, but the component elements structurally are intermediate between those of *scalaris* and those of *nutallii*. Over-all the call resembles that of *scalaris* more than that of *nutallii*, but it has definite tendencies toward the latter—exactly what one might expect of the Rattle Call of an introgressant *scalaris*. In any event it exceeds the variation noted in Rattle Calls of *scalaris*, and it must be considered intermediate.

Rattle Calls were not recorded from hybrids or other introgressant or possibly introgressant birds. The male hybrid (A.M.N.H. No. 791485) from Rancho Escondido gave a Rattle that seemed to resemble that of *scalaris*, as well as a Peek Call, but these conceivably may have been somewhat intermediate. The probable introgressant *scalaris* male (A.M.N.H. No. 791495) from southeast of Santo Tomas called pik and gave a “*nutallii*-sounding rattle” (from field notes of R. S. Crossin), showing that birds morphologically tending toward one species can utter a Rattle Call that sounds like that of the other species. Of course these calls may have been more or less intermediate.

QUEEK CALLS

The variation in the Queek Call, even within a single type (A or B), is considerable and it is hence difficult to determine “intermediacy.” Perhaps the best means of separating the Queek Calls of *scalaris* and of *nutallii* is by their rate, which did not exceed 3.42 notes per second in *scalaris*, and was not less than 5.50 notes per second (Type A Queek Call) or 4.30 notes per second (Type B Queek Call) in *nutallii*. A second point is that Type B calls are found only in *nutallii*. Type A calls of *scalaris* tend to be lower pitched and to have stronger harmonics than do those of *nutallii*.

Two puzzling Type A Queek Calls were recorded that seem outside the considerable range of variation of either *scalaris* or *nutallii*. One of these was uttered on April 22 by the same probable hybrid male which gave the intermediate call notes described above. The call (fig. 25L) is a series of five notes delivered

in 1.5 seconds, at a rate of 3.33 notes per second (tempo *scalaris*-like). The harmonics are very weak as in *nutallii*, less intense than those of any *scalaris* Queek Call that I recorded. The intense portion of the individual notes rises gradually from 3.5 to 4.0 kilocycles, then rapidly to 4.5 kilocycles. All *scalaris* notes reaching 4.5 kilocycles in pitch (the highest pitch for *scalaris*, attained by notes in only two Queek Calls) do so abruptly from about 3.0 kilocycles, and they are intense notes with strong harmonics. The notes of the probable hybrid are long, 0.12 to 0.14 second in duration, and they tend to “plateau” after reaching their peak frequency, both conditions being *scalaris*-like. In total the call is thus closest to that of *scalaris*, but with a few *nutallii* features. The intermediacy of this bird’s call notes, its intermediate plumage, its occurrence in *nutallii* habitat close to a population (San Jose) in which only *nutallii* is found today (although with indications of past hybridization with *scalaris*), and its more *scalaris*-like Queek Call suggests that the bird was a hybrid.

The other odd Queek Call (fig. 25K) was recorded on April 18 at Rancho Santa Clara, Baja California. It was produced by the male Nuttall’s Woodpecker (A.M.N.H. No. 791478) of a pair of that species (female A.M.N.H. No. 791454) occupying a territory adjacent to a pair of Ladder-backed Woodpeckers (male A.M.N.H. No. 791492; female A.M.N.H. No. 791500). The male Nuttall’s Woodpecker specimen is phenotypically pure *nutallii*. Its Queek Call contained nine notes delivered in 2.4 seconds, a rate of 3.75 notes per second. Although closest to *scalaris* in tempo, this rate exceeds that of all Queek Calls of *scalaris*, and it does not closely approach *nutallii*. The intense portion of each note is a segment rapidly rising from about 3 to 4 kilocycles. The over-all configuration of each note is like typical Type A notes, except that they tend to “plateau” at their peak pitch. They are 0.14 to 0.18 second in duration, long even for *scalaris*. Thus their appearance is that of a basic *nutallii* note drawn out like notes of *scalaris*. The highest pitch is high for *scalaris*. The harmonics are very weak, as in many calls of *nutallii*, and unlike *scalaris* (unfortunately, some background sounds occur at similar frequencies in the sonogram of this call). Thus, this Queek Call is intermediate between those of the two species. Such intermediacy of the call in a bird phenotypically

like *nuttallii* suggests either that the bird is an introgressant individual which happens to show no external morphological indications of *scalaris*, or that the nature of Queek Calls (and others?) may be influenced by Queek Calls of surrounding birds of the same species and of closely related species. A moot point of course is whether the call is innate, and if not, then to what degree it is modifiable and under what circumstances. Such information is lacking for the vocalizations of most avian species, including all woodpeckers.

BREEDING ACTIVITIES

PAIR FORMATION

The prevalence of agonistic behavior in the social behavior of woodpeckers makes difficult the detection of reproductive elements of behavior. This problem was complicated by the fact that pair formation largely had been completed prior to my field studies. One of the very few displays or actions known to be definitely associated with pair formation in North American species of *Picoides* is the duet flight of Hairy Woodpeckers (Kilham, 1960). Another such display may be Crest Raising, which seems especially prevalent in males. Indeed, the sexual difference in coloration of the nape and crown in species of *Picoides* shown effectively during Crest Raising may be fundamental in determining the nature of an encounter between the sexes.

Pair formation may be accomplished largely through: 1) the attraction of females to males and their persistent approaches to males at the appropriate time; 2) their more submissive and less aggressive behavior, which would tend to reduce the aggressiveness of the males; and, 3) the absence of male colors on the female's crown which would lessen the male's aggressiveness and favor close contact with less intense agonistic behavior. According to this interpretation (see also Blume, 1955), persistent, low-intensity display bouts on a territory established by the male would, through repeated contacts, initiate pair formation. A further stimulant toward pair formation might be the strongly aggressive behavior of either male or female toward an intruder of the same sex in the presence of the prospective mate. If, for example, a male on territory is present during an intense encounter between a female with which the male has had

agonistic encounters, and another female, the male may raise its crest and otherwise (vocally) incite the female to greater efforts. Should that female be successful in her encounter, pair formation with the male might be facilitated.

Lawrence's (1967) observations of Downy Woodpeckers are important in connection with pair formation, and with the potential for hybridization as well. A mated female which Lawrence had been studying seemed to solicit (perching crosswise on a branch, crouching; see below) copulation with an unmated male that was not its mate. The male approached the female and mounted her for 10 seconds. After copulation the female followed that male, flying excitedly back and forth, erecting her crown feathers and pecking (displacing?). Later, that male paired with another female, while the female which had copulated with it nested with her own mate. Of course, she might have been fertilized by the other male (indeed hybridization could occur in this manner). The readiness with which these unmated birds copulated suggests that pair formation does not involve a complex series of displays. Of course one or both birds in this case may have had a lowered threshold for pre-copulatory behavior due to circumstances of which we are unaware. Nevertheless, such copulations might not occur infrequently in habitats in which population densities of one (or more) of these woodpeckers are great. The occurrence of copulations under these circumstances suggests, as has the work of Blume (1955, 1961), that initial sexual recognition facilitates rapid accommodation between the sexes, and that few or even no intrinsically reproductive displays may be required in at least occasional rapid mating of these woodpeckers.

Kilham (1966) has noted that Hairy Woodpecker pairs of a previous year may mate the following year with little "pair-formation" behavior. It seems likely that situations involving prolonged encounters, "trios" (see above), and intense encounters between the sexes will prove to involve mainly first-year birds and older birds which have lost their mate of the previous year. As data concerning mortality in these woodpeckers are lacking, it is impossible to consider the rate of turnover of individuals in populations at my study sites. At any rate, the difficulty in detecting pair-formation activities may be in part because of the prevalence of older birds in woodpecker populations (it might be noted that

woodpeckers are strong and tough-skinned, and scientific collectors generally agree that they are difficult to kill—it is conceivable they are longer-lived generally than comparable-sized birds of other groups).

PRE-COPULATORY BEHAVIOR AND COPULATION

Pre-copulatory displays in woodpeckers are rather few, and perhaps limited to the female; she solicits by crouching, often perching crosswise on a branch, and drooping her wings loosely. The female uplifts the tail just prior to the mounting of the male, and sometimes she holds her head up and to the rear (resembling the Head Raised Posture, perhaps a submissive display in this case). Males usually raise their crests as they prepare to mount. These actions have been described (Kilham, 1962) in the Downy Woodpecker and in the Hairy Woodpecker (Lawrence, 1967).

Copulations observed in the Nuttall's and Ladder-backed woodpeckers during March and April were relatively few (17 and six instances, respectively) and most were almost perfunctory. On March 14 a female Nuttall's Woodpecker gave a Queek Call, and a nearby male (its mate, presumably) flew to her and mounted as she turned crosswise, lifted her tail, and maintained her head slightly above the horizontal. The copulation lasted but 1 to 2 seconds, then the male flew off. In most instances the preliminary behavior passed unnoticed, or I came upon the birds as copulation ensued. One copulation occurred (April 6) after a low Wicka Call exchange between a male and a female Nuttall's Woodpecker; the male flew directly to the female and mounted, holding its crest moderately erect, then flew off as the female uttered a Rattle Call. Copulations of the Ladder-backed Woodpecker were observed only in April, and no Crest Raising was observed in males. One instance occurred following an encounter between a male *scalaris* and a male *nuttallii* in the presence of a female Ladder-back. The male Ladder-back left the Nuttall's Woodpecker, flew to its presumed mate, which half turned and crouched, and the Ladder-back male mounted very briefly. The female then flew off, and the male Ladder-back returned to the Nuttall's Woodpecker and resumed the encounter.

Although Wicka Calls, Tewk Calls, and Rattle Calls were heard just prior to copulation at one

time or another, I was unable to detect a special vocalization associated with copulation, either by males or females. Nor does one or another of the agonistic vocalizations especially seem associated with copulation. Miller (field notes) remarked on the utilization of a "yipe" call possibly to invite copulation by female Nuttall's Woodpeckers. The "yipe" he mentioned is apparently a Queek Call, and it is not confined to situations when copulation occurs. Miller found pairs to copulate two or three times each morning during the nesting period and even late in nesting (May 20). I did not follow individual pairs through the nesting cycle, but rather observed copulation purely by chance. Observations during my studies of Flickers (*Colaptes auratus*) indicated frequent copulations, up to 30 per day during the height of the nesting season and continuing at a lesser rate while young are in the nest. It seems likely that copulation in woodpeckers plays an important role in the maintenance of the pair-bond, beyond its primary (reproductive) role.

Only a few of the observed copulations occurred in proximity to nest sites. Rather, they seemed to occur when the mated pair happened to be close together, or when one member of a pair responded to the Drumming, Rattle Call, or Queek Call of its mate by approaching it closely.

Copulation is generally similar among the four species considered above. Although occurring commonly during nest-construction and egg-laying periods, it may occur sporadically during pair formation (as early as January in *villosus*; Kilham, 1966), as well as during incubation and even thereafter.

NESTING ACTIVITY

Information concerning the nest-construction and egg-laying of *scalaris* and *nuttallii* in northern Baja California has been summarized previously (Short and Crossin, 1967, pp. 292–293). Nest construction in the areas visited in California generally began in February. February specimens of *nuttallii* include a female with an ovary as large as 6.5 by 5.5 mm. on the second of the month, and with ova beginning to enlarge (to 1.5 mm.), but five males have testes only as great as 3.5 mm. in length and 2 mm. in width. March specimens collected prior to March 23 in California had larger gonads, but ova of the females were no larger than 2 mm. in diameter, except

for one female taken on March 17 (ova to 4 mm.). Freshly constructed nests were found in early March, and birds collected showed incipient brood patches. These data suggest that egg-laying commences in late March to early April in California *nutallii*. Miller (field notes) reports fresh eggs of this species in San Diego County from April 12 to May 10.

In Baja California egg-laying was detected as early as April 6 for *nutallii*, and by the end of April most but not all pairs had eggs. Nests contained young birds from April 21 onward.

No nests of Ladder-backed Woodpeckers were studied in California. The few California specimens collected in mid-March had large gonads (testes to 5 mm. in length, ovary to 10 mm. in length), but the female had small ova and brood patches were only beginning to form. It appears that the nesting period of *scalaris* approximately coincides with that of *nutallii* in California. In Baja California the nesting period seems also to coincide with that of *nutallii* (Short and Crossin, 1967, p. 293).

Examination of the ovaries of collected females indicates that both species lay a clutch of three or four eggs. No nests were examined for their contents, except as noted below.

Miller (field notes) mentioned 11 nests of *nutallii* in southern California constructed in willows (6), cottonwoods (1), sycamores (1), alders (1), elderberry (1), and fence post (1). I observed 30 definite or probable nests of *nutallii* in California and in Baja California. Of these, 16 were in willows, 12 in cottonwoods, and two in sycamores. Although the bulk of these nests are from riparian areas, it is significant that not one of these nests was in an oak tree, although oaks are available in some areas (occasionally, even common, as at Arroyo Santo Tomás). Nests of Ladder-backed Woodpeckers were infrequently observed. Old holes, presumably of Ladder-backs, were seen in Joshua trees at various places in California (east of Onyx, south of Weldon, Joshua Tree National Monument, for example). Of seven *scalaris* nests in Baja California, six were in willows and one was in a cottonwood stub. Other holes presumably of this species were seen in agaves and in cardon cactuses (*Pachycereus pringlei*) in desert areas near San Quintin.

Nest construction was observed sporadically. It seemed that female Nuttall's Woodpeckers participated significantly in excavation of nest cavities, as Lawrence (1967) found in the Downy

TABLE 25
BREEDING ACTIVITY OF HYBRIDS, POSSIBLE HYBRIDS, AND INTROGRESSANTS

A.M.N.H. No.	Sex	Date	Gonads	Brood Patch	Breeding Activity
INTROGRESSANT OR POSSIBLY INTROGRESSANT <i>nutallii</i>					
791515	♂	Mar. 21	9 × 8 mm.	Slight	Mate <i>nutallii</i> (?)
791518	♂	Mar. 21	7 × 6 mm.	—	—
791519	♂	Feb. 21	3 × 1.5 mm.	—	—
791477	♂	Apr. 6	8 × 4 mm.	Slight	—
791444	♀	Apr. 21	5 burst follicles	Strong	At nest in willow
791474	♂	Apr. 26	9 × 6 mm.	Slight	Mate <i>nutallii</i> (?)
HYBRIDS					
791507	♀	Mar. 21	Ova to 3.5 mm.	Slight	Alone, near No. 791515 (above)
791508	♀	Feb. 27	6 × 4 mm., ova small	—	—
791485	♂	Apr. 15	10 × 6 mm.	Strong	Excavating nest. Mate No. 791502 (? , below)
INTROGRESSANT OR POSSIBLY INTROGRESSANT <i>scalaris</i>					
791501	♀	Apr. 6	1+ burst follicle	Strong	Mate <i>scalaris</i> . Nest in willow
791498	♀	Apr. 6	Ova to 4 mm.	Slight	—
791502	♀	Apr. 15	Ova to 5 mm.	Strong	Mate hybrid 791485 (? , above)
791497	♀	Apr. 18	Ova to 3 mm.	Strong	Mate <i>scalaris</i> . Nest in willow
791499	♀	Apr. 18	Ova to 3 mm.	Strong	Mate <i>scalaris</i> . Nest in willow
791496	♂	Apr. 23	8 × 5 mm.	Strong	Mate <i>scalaris</i> . Nest, 4 eggs, in agave
791503	♀	Apr. 26	11 × 7 mm., ova 2 mm.	Strong	Mate <i>nutallii</i> (?)
791495	♂	Apr. 28	12 × 8 mm.	Strong	—

Woodpecker. Of five Ladder-backs actively working at their nests, none was a female. However, too few observations were obtained of the latter species to indicate any difference from *nutallii*.

Data concerning the condition of the gonads, and the breeding activity of hybrids, possible hybrids, and introgressant and possibly introgressant woodpeckers are summarized in table 25. Their gonadal condition and activities do not differ from temporally comparable data for *nutallii* and *scalaris*. Indeed all of the birds, even the February 27 female, had enlarged gonads. Those birds for which data concerning breeding activity are available appeared to be mated, or associated with a nest. One exception, the female hybrid A.M.N.H. No. 791507, was taken alone, adjacent to the territory of probable introgressant *nutallii* A.M.N.H. No. 791515, and its mate (A.M.N.H. No. 791531, *nutallii*). Other Nuttall's Woodpeckers were nearby, and the hybrid may have been mated. Of course, nothing can be said regarding the reproductive success of hybrid individuals, but there is every indication that they are successful at least to the extent of securing mates, excavating nests, and laying eggs.

BEHAVIORAL ISOLATING MECHANISMS

The investigations of behavior reported above (summarized in table 26) uncovered no conclusive evidence for the existence of ethological isolating mechanisms. From the fact that no massive hybridization occurs between *scalaris* and *nutallii*, we can infer that some partially effective reproductive isolating mechanisms are operating. It is likely that these mechanisms will prove to involve at least some of the external morphological features distinguishing these species, and possibly some of the behavioral differences (table 26) discussed above. It is well to note that the existence of differences does not mean that these are necessarily utilized for species recognition by the birds. One can cite some differences between the Downy and the Hairy woodpeckers, which overlap widely without interbreeding, but no one has demonstrated which of these differences are employed in conspecific mate selection, and hence in avoidance of interbreeding.

The following factors should be considered in relation to possible behavioral isolating mechanisms: 1) the importance of agonistic behavior and sexual recognition to these woodpeckers at

TABLE 26
COMPARISON OF BEHAVIOR PATTERNS OF NUTTALL'S AND LADDER-BACKED WOODPECKERS
(*Picoides nuttallii* and *Picoides scalaris*, respectively)

Behavior Pattern	Form of Pattern	Behavioral Context of Pattern
Bill Positioning Displays	Similar	Similar
Crest Raising Display	Less raised crest in <i>scalaris</i>	Similar
Head Bobbing Display	Similar	Similar
Head Turning Display	Similar	Similar
Head Swinging Display	Similar ^a	Similar
Wing Flicking Display	Similar	Similar
Wing Spreading Display	Similar	Similar
Flutter Display	Similar	Similar
Tail Spreading Display	Similar	Similar
Attack	Similar	Similar
Fleeing	Similar	Similar
Rustling Display	Similar	Similar ^a
Drumming	Different	Somewhat different? ^a
Call Notes	Different	Similar
Rattle Call	Different	Similar
Queek Call	Different	Somewhat different
Wicka Call	Different	Similar ^a
Tewk Call	Similar ^a	Different? ^a
Kwah Call	Only in <i>scalaris</i> ? ^a	? ^a

^aObservations very few in number. See text discussion.

all times of the year; 2) the occurrence of inter-specific agonistic encounters; 3) the morphological features of these woodpeckers as correlated with agonistic displays; and, 4) the dearth of pair-formation displays. Evidence from the occurrence of unisexual encounters corroborates Noble's (1936) experiments with the Flicker (*Colaptes auratus*) which showed the overriding primacy of sexual recognition features. Even the intimacy of the established pair bond is completely disrupted by a simple artificial change in the markings involved in sexual recognition. Considering the importance of sexual recognition, it is highly significant that most species of *Picoides* differ in the location and extent of male sexual markings. Such differences could act as reproductive isolating mechanisms at the time of pairing when a Crest Raising male exhibits its specific head markings to a female. An exception is the case of the Downy and Hairy woodpeckers, which have similar head markings (they may differ in their Crest Raising Displays, however). Other factors such as size differences, differences in bill size, lack of duet flights in the Downy, and vocalizations may be more important in the latter species.

Appropriate sex-to-sex responses during encounters between males and females would seem to play a role in furthering the establishment of a pair bond, considering the primacy of agonistic behavior in these woodpeckers. A failure or breakdown of communication during inter-specific encounters may account somewhat for the repeated interactions between *scalaris* and *nuttallii*, and between *nuttallii* and *villosus* described above. The use of improper visual cues or vocalizations during an otherwise appropriate display could confuse or disrupt an opponent. For example, the tail pattern difference between *scalaris* and *nuttallii* might have such an effect during Tail Spreading Displays between individuals of the two species. Or, the different Queek Calls of these species could have this effect even if uttered at an appropriate time during an appropriate display (e.g., during a Flutter Aerial Display). A complex of calls and color markings differing in the two species might effectively prevent interbreeding under normal circumstances, although unmated birds late in the breeding season may have their threshold of response so lowered by reproductive "urgency"

that they will accept even a non-conspecific mate.

The differences in call notes, Rattle Calls, Queek Calls, and Wicka Calls between *scalaris* and *nuttallii* appear as great as those occurring between various other species of the genus. Their color pattern differences are not as great as those existing among some sympatric species in this genus, but the plumage similarity between the widely sympatric *pubescens* and *villosus* suggests that the differences between *scalaris* and *nuttallii* are sufficient or nearly sufficient to function in species recognition. I suggest that we must consider the body size, and particularly habitat preferences with regard to reproductive isolation, as well as in relation to ecological competition. In northern California the Nuttall's and Downy woodpeckers differ in size (the Nuttall's is more than one-third heavier) and in habitat preference. In southern California, where they converge in habitat preference, the Downy becomes rare and drops out. It is in southern California that their reproductive isolation has broken down (albeit rarely). The sympatric Hairy and Downy woodpeckers show differences in habitat preference, size of territory and body size, and they do not interbreed. The Ladder-backed and Nuttall's woodpeckers are approximately equal in size, as are their territories, and their habitat preferences overlap considerably. As I have noted elsewhere (Short, 1970a), similarly sized, closely related woodpeckers occupy allopatric ranges, or, if sympatric, they tend to forage differently on different foods and to occupy different habitats. The Ladder-back and Nuttall's woodpeckers are largely allopatric. In their limited area of sympatry they exhibit some preference for different habitats, but their habits, being similar, bring them into frequent contact. Such contacts perhaps facilitate interbreeding.

We need to know more about pair formation in these species of woodpeckers. Further studies of their interactions and the behavior of hybrids in the area of sympatry are necessary to determine the factors responsible for their almost complete reproductive isolation. It is hoped that the above behavioral data and discussion will provide a background for future investigations of these factors.

THE PHYLOGENY OF NEW WORLD SPECIES OF *PICOIDES*

THE ORIGIN OF THE NEW WORLD GROUP

THERE ARE ELEVEN species of *Picoides* in the New World, including two species of three-toed woodpeckers to which *Picoides* was previously restricted (Bock and Short, ms.), and of course the Downy, Hairy, Nuttall's and Ladder-backed woodpeckers. The reasons for considering the New World species of *Picoides* as a distinct monophyletic group within this genus are discussed by Bock and Short (ms.). Goodwin (1968, p. 28) independently reached this conclusion, and he also believed that the three-toed woodpeckers (*Picoides*, *sensu stricto*) are closer phylogenetically to New World members of the genus "*Dendrocopos*" than to Old World forms in this genus (however, he does not merge the genera as do Bock and Short). It is unlikely that the three-toed woodpeckers are any more divergent from "*Dendrocopos*" than are some other distinct species (e.g., *hyperythrus*) and groups in this assemblage. The loss of one toe is no reason to separate the three-toed woodpeckers from other members of the genus (see Delacour, 1951), for the Oriental picid genus *Dinopium* contains three-toed and four-toed species that are universally considered congeneric. Needless to say, the separate derivation of "ladder-backed" and non-ladder-backed New World species by Voous (1947) is incorrect, for the white-backed *P. pubescens* is closely related to the barred-backed *scalaris* superspecies, there are distinctive white-backed ("*arizonae*") and ladder-backed populations within *P. stricklandi* (Davis, 1965), and even *P. villosus* has a population (*P. v. picoides*) that is barred on the back.

The *Picoides major* assemblage seems to be the most recently evolved, adaptively radiating group of Eurasian species of *Picoides* (Bock and Short, ms.). These large-sized species are mainly white-faced, white-backed, and red-bellied. Radiation of this group probably resulted in the extinction of older Palearctic species that were more closely related to the New World group. At any rate the relatives of the latter group are to be found among small- and medium-sized species of *Picoides* in the Oriental Region (one is in Africa as well). These

species (*P. kizuki* group) lack red below, have facial patterns more nearly like the New World species, and many have barred backs and streaked sides. It is likely that ancestors of the New World species lacked red below, or it would have been retained or reappeared in one or more New World species. Although some or most of the facial pattern has been lost in *P. albolarvatus* and *P. borealis* (fig. 1) among the New World species, most have a pattern distinctly like those of such Oriental (and Ethiopian) species as *P. kizuki*, *P. moluccensis*, *P. maculatus*, and *P. obsoletus*. There are resemblances in details of color pattern between these species (New World species first, Old World species second in each case): *P. borealis* and *P. mixtus*, and *P. moluccensis* and others (reduced nuchal); *P. stricklandi*, and *P. obsoletus* and others (brown replacing black); and, *P. lignarius* and *P. mixtus*, and *P. moluccensis* (tail barring and virtually all details of pattern). The streak-sided, barred backed, New World superspecies *P. scalaris* and *P. lignarius* (see fig. 1) bear strong resemblance in all respects to such Oriental species as *P. moluccensis*. No species of the *major* group exhibits marked resemblance to any New World species. I accept the remarkable similarities of the groups just mentioned as results of parallelism, reflecting their rather close relationship.

Thus at some time in the past (Pliocene?) Asian woodpeckers of this genus were able to enter North America where they later were, and have since remained, isolated geographically. At some subsequent time the ancestor of the *P. major* group evolved, was eminently successful, and underwent adaptive radiation in Asia. Some of these species entered the Palearctic, there to replace species of older groups, but they failed to reach North America (although the ancestor of one species, namely *tridactylus*, evolved simultaneously in North America and was able to reinvade the Old World successfully). Hence the extant Old World relatives of the New World group are restricted to the southern part of the Old World, where many species still inhabit the forest edges, brushland, and savannas.

THE HISTORY OF THE NEW WORLD GROUP

The ancestral New World species of *Picoides* probably was a ladder-backed, ventrally streaked species of woodlands and woodland edges, resembling closely the modern *P. scalaris* or *P. mixtus*. The early history of the group involved the evolution in eastern North America or northern Mexico of a less barred species perhaps somewhat resembling the modern *P. stricklandi azteca*, and a barred species largely retaining the features of the ancestral species (see fig. 26). The newly evolved barred species, perhaps in competition with its sister species, adapted to the woodland edge and arid scrub habitats associated with the Madro-Tertiary woodlands of the Southwest (Axelrod, 1958, 1960). This xeric-adapted species was able to extend its range into and through Central America, ultimately to reach arid scrub habitats in temperate South America. Fluctuations in climate eventually cut off the South American populations, and were

perhaps sufficiently severe to eliminate the species from northern South America (competition from species of *Veniliornis* may also have been a factor). It is noteworthy that the arid scrub vegetation of south-central Argentina is remarkably similar in its conspicuous elements to the shrub deserts of southwestern North America; cognate elements include superficially very similar species of creosote bush, *Larrea*, and palo verde, *Cercidium*, as well as acacia trees and cacti (Short, personal observ.). Intervening shrub deserts, such as in the valleys of east-central Bolivia and Peru indicate a previously continuous connection with such vegetation in northern South America and Central America. In any event, *P. mixtus* in south-central Argentina exists today in a habitat very similar in its botanic elements to the desert scrub occupied by the closely related *P. scalaris* in southwestern North America. The South American form reached the false beech (*Nothofagus*) forests of southern South America, where an isolate

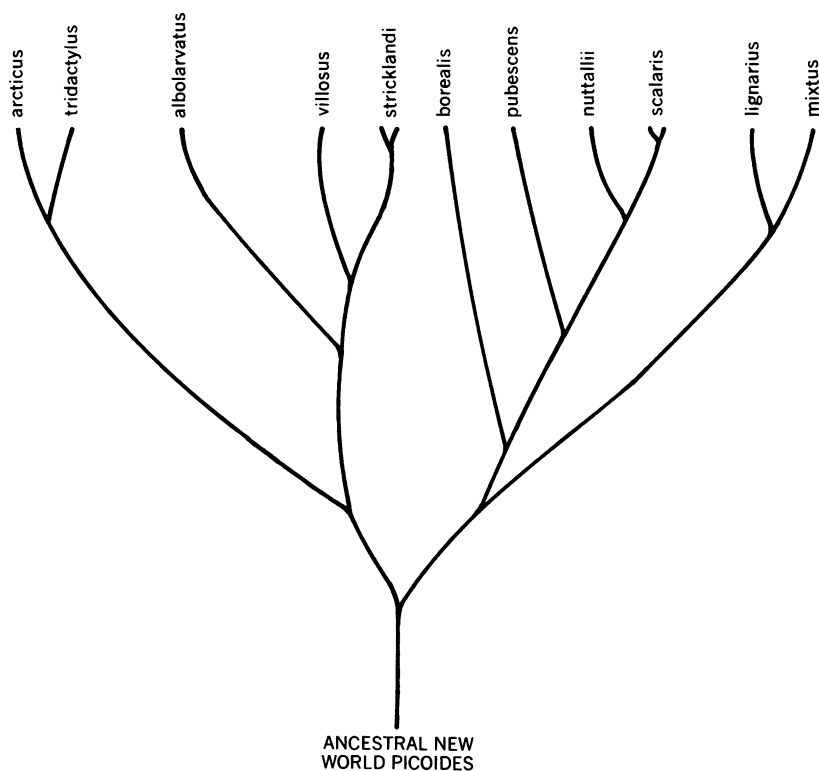


FIG. 26. Hypothesized phylogenetic diagram showing evolution and relationships of extant New World species of *Picoides* (see text).

FIG. 27. Modified phylogenetic diagram (see fig. 26) showing evolution of certain features of New World species of *Picoides* (see text).

TABLE 27

SOME CHARACTERS OF NEW WORLD SPECIES OF *Picoides*

(Parentheses indicate variation is considerable, or only part of the population has this feature, or that the feature is partly present)

Character	<i>mixtus</i>	<i>lignarius</i>	<i>scalaris</i>	<i>nuttallii</i>	<i>pubescens</i>	<i>borealis</i>	<i>stricklandi</i>	<i>villosus</i>	<i>albolavatus</i>	<i>arcticus</i>	<i>tridactylus</i>
PRIMITIVE											
Mixed malar patch	X	X	X	—	X	—	(X)	(X)	—	(X)	X
Dusky, nondistinct nasal tufts	X	X	X	—	—	—	X	—	—	X	X
Streaks in crown	(X)	(X)	X	(X)	—	—	—	—	—	(X)	(X)
Broad nuchal patch (♂)	—	—	X	X	—	—	(X)	—	—	—	—
Narrow auricular patch	X	X	X	—	—	—	—	—	—	—	—
Barred back	X	X	X	X	—	X	(X)	(X)	—	—	(X)
Streaked, barred, spotted underparts	X	X	X	X	—	X	X	—	—	X	X
Dusky cast on white	(X)	—	X	—	(X)	—	—	(X)	—	—	—
Barred rectrices, especially outer ones	X	X	X	—	—	—	(X)	(X)	—	—	(X)
Thin, moderately long bill	X	X	X	X	X	—	(X)	—	—	—	—
Low tail/wing ratio	X	X	(X)	—	—	—	—	—	—	—	—
DERIVED											
Black malar patch	—	—	—	X	—	X	(X)	—	—	(X)	—
White, well-defined nasal tufts	—	—	—	X	X	X	—	X	—	X	X
Black (or brown) crown, no spots	—	—	—	—	X	X	X	X	—	—	—
Narrow nuchal patch	X	X	—	—	X	X	(X)	X	X	—	—
Full auricular patch	—	—	—	X	X	—	X	X	—	X	X
White back	—	—	—	—	X	—	(X)	(X)	—	—	(X)
Unmarked underparts	—	—	—	—	(X)	—	—	(X)	—	—	—
White with no cast	—	X	—	X	(X)	X	X	(X)	—	X	X
Reduced markings on white outer rectrices	—	—	—	X	X	X	(X)	X	—	X	(X)
Longer, heavier bill	—	—	—	—	—	—	(X)	X	(X)	X	X
Moderate tail/wing ratio	—	—	(X)	X	X	—	X	X	X	X	X
VERY SPECIALIZED											
Loss of head pattern	—	—	—	—	—	—	—	(X)	X	(X)	(X)
Loss of tail pattern	—	—	—	—	—	—	—	—	X	—	—
Wing patch	—	—	—	—	—	—	—	—	X	—	—
Loss of auricular patch	—	—	—	—	—	X	—	—	X	—	—
Extreme melanism	—	—	—	—	—	—	—	—	X	X	(X)
Very wide bill	—	—	—	—	—	—	—	—	—	X	X
3 toes	—	—	—	—	—	—	—	—	—	X	X
Crown patch instead of nuchal (♂)	—	—	—	—	—	—	—	—	—	X	X
Great tail/wing ratio	—	—	—	—	—	X	—	—	—	—	—

The latter was extremely successful, spreading throughout North America (perhaps in the process affecting adversely the numbers and distribution of three-toed woodpeckers, and *P. albolavatus*, and *P. borealis*). *Picoides villosus* is ecologically the most broadly tolerant of all North American *Picoides*, requiring some large trees,

but existing in diverse woodlands at various altitudes. This species is also very variable (variation involves over-all color, size, facial pattern, streaking below, back color and bars, and tail pattern). The similarly patterned but brown-colored *P. stricklandi*, isolated in the Mexican highlands, parallels the development of traits of

villosus. *Picoides s. stricklandi* is moderately long-billed, barred-backed, and has a moderate-sized nuchal patch, but it is brown. The more northerly *P. s. arizonae* is long-billed, like *villosus*, and it also has a white back like the latter; its nuchal is narrow like that of *villosus*. *Picoides s. azteca* is a restricted montane Mexican race similar to the subspecies *stricklandi*, but black, and with a broader nuchal patch; it thus resembles *P. nuttallii* in appearance. The southern races *azteca* and *stricklandi* have more white in the outer rectrices than does *arizonae*—*azteca* especially resembles *nuttallii* in this feature. *Picoides s. azteca* is less barred and more streaked below (approaching *mixtus*) than are the other races, and it probably more nearly resembles the ancestral phenotype. *Picoides stricklandi* appears to have retained more primitive characters than any other member of its subgroup (which also includes *villosus*, *arcticus*, *tridactylus*, and *albolarvatus*) and its variation in so many features may be related to its age. For example it has dusky nasal tufts, narrow auricular patches, a barred back, spotted and streaked underparts (latter "scalloped" partially, very like *P. lignarius*), variable outer rectrices (barred as *scalaris* to white as *villosus*), an extremely variable pattern of rectrix 6 (patterns include some typical of *lignarius* or *scalaris*, *nuttallii*, *villosus*, etc.) and a variable bill (see table 27 and also fig. 27). This woodpecker is now sympatric with *villosus* in highland Mexico, *villosus* having successfully invaded the highlands of Central America as far south as Panama. The *stricklandi* and *arizonae* groups of *P. stricklandi* are distinct and do not meet, but I agree with Davis (1965) that they have not yet attained reproductive isolation, hence are conspecific.

The southern North American and Central American barred-back group evolved more slowly, and three of the four species of this group are considered to be very recent in their origin. An early offshoot of this line, evolving after ancestral three-toed woodpeckers, *albolarvatus*, and the South American species had evolved, was the ancestor of *P. borealis*. This may have originated as an eastern isolate of the main ladder-backed line. It probably occupied a rather broad range in eastern North America, where it came into contact with the evolving ancestor of *villosus*. Much later, with the advent of pre-*pubescens* in the East as an offshoot of the same line, the ancestral *borealis* either became

specialized, or continued along a line of specialization for pine-foraging and nesting in southeastern pine forests. Its range became restricted and it is now (partly or mainly due to man's influence in selectively removing older trees) uncommon. In its predilection for pinewoods it parallels the western *albolarvatus*. The characters of *borealis* are both primitive and derived (table 27), and some of its special features are probably a reflection of interactions with *pubescens* and *villosus*. It shows some resemblance to *nuttallii*, particularly in its back pattern, and ventral markings. A hybrid of *P. scalaris* and *P. villosus*, described by Miller (1955), somewhat resembles *P. borealis*, but I do not find the similarity nearly so remarkable as did Miller. The hybrid, which I have examined, resembles *nuttallii* quite strongly as well. These similarities reflect: the rather close interrelationship of all New World *Picoides*; and the fact that a hybrid between a species with primitive patterns and one with specialized (derived) patterns will by its intermediacy resemble species which have evolved some specialized features.

More recently the ancestor of *pubescens* evolved from the southwestern ladder-backed stock. Smaller size was probably a feature of the evolution of this isolate, which perhaps took place in the Northwest. It probably was very *scalaris*-like in appearance early in its history (the juvenal plumage of *pubescens*, as of *villosus*, often shows the streaked pattern below and very barred rectrices), perhaps even retaining a barred back for some time. Apparently its small size and effective reproductive isolating mechanisms enabled it to become sympatric with *villosus*, and eventually with *borealis*. The smaller size of *pubescens* and larger size of *villosus* may have placed some stringent limits on *borealis* in its recent evolution. Although *pubescens* overlaps broadly with *villosus* in North America, it fails to enter Mexico, and I believe that Davis (1965) is correct in concluding that the presence of *scalaris* (closely related to *pubescens*) has prevented the southward expansion of *pubescens*. In the Southeast *pubescens* is sympatric with *borealis*, but the two species prefer different habitats. Throughout most of the continent *pubescens* and *villosus* occur together in the same habitats, although *pubescens* is more an edge species (preadapted for suburban living). In the West and South, where species of *Picoides* other than *villosus* occur, *pubescens* is virtually restricted to riparian situations, although this

tendency is evident throughout its range. It is noteworthy that the close relatives (*nutallii*, *scalaris*, and to a lesser extent *borealis*) of *pubescens*, occurring around the periphery of the range of *pubescens* all have barred backs, whereas *pubescens* has a white back like the larger, not so closely related *villosus* with which it is sympatric. Nothing is known of the interaction among *pubescens*, *villosus*, *arcticus*, and *tridactylus* in the limited northern area of sympatry where they locally occur together.

Most species of *Picoides* that occur sympatrically are ecologically separated. Thus, where *nutallii*, *albolarvatus*, and *villosus* are sympatric in the highlands of southern California, *nutallii* occurs in oaks, *albolarvatus* in pines, and *villosus* in other coniferous forest and mixed woods. I have elsewhere (Short, 1970a) indicated that species of woodpeckers inhabiting the same area and in direct contact frequently either differ greatly in size, or in foraging habits, or both. Similarly sized woodpeckers with similar foraging habits are usually allopatric (*nutallii* and *scalaris* form a good example). I believe that the similarity in pattern of *pubescens* and *villosus* is the result of: their broadly sympatric occurrence; some degree of competitive and behavioral interaction; and their relationship—close enough to allow parallel evolution, yet sufficiently distant so that they will not interbreed. Their behavior patterns are similar and they do interact (see below). Their foraging habits may overlap to some degree so that competition for food, and possibly competition for nest sites may occur. Under these conditions it may be advantageous for both species to have similar color patterns to

facilitate agonistic interactions. Aggressive behavior of territorial birds may tend to space individuals of the two species, as well as conspecific individuals. If this is true, the tendency for the two species to occupy different habitats may be enhanced behaviorally (see Moynihan, 1968). The remarkable similarity of these species is not the only case of its kind in woodpeckers (Cody, 1969; Bock and Short, ms.), but usually such parallelism involves species of closely related genera (e.g., *Dryocopus-Campephilus*, *Dinopium-Chrysocolaptes*). However, "mimic" species of these genera are relatively of the same size, whereas the Hairy Woodpecker may be more than twice (even three times, by weight) the size of the Downy.

Some of the characters used in analyzing the relationships and phylogeny of the New World species of *Picoides* are modifiable, and subject to the diverse effects of selection relating to predation and various kinds of interactions that can occur among related species. The combination of characters that I have used is helpful, although genetically simple changes (such as melanism, which may obscure an array of features) can greatly reduce their number. I am sure that the history of these woodpeckers suggested above will have to be modified following further studies, especially detailed anatomical studies. Nonetheless, I believe that the major features of this hypothetical history (summarized in fig. 26), and especially the consideration of the New World group as monophyletic, will be corroborated by evidence resulting from future studies.

THE EVOLUTION OF NUTTALL'S AND LADDER-BACKED WOODPECKERS

There remains only the discussion of the origin of the modern *P. scalaris* and *P. nutallii*. The latter is almost certainly strongly divergent from its more *scalaris*-like ancestor (although their ancestor may at one time have exhibited more traits now found in *nutallii*). None of the diverse races of the widespread *scalaris* approaches the distinctness of *nutallii*, and tendencies toward the latter are evident only where the ranges of the two species approach each other.

Picoides nutallii evolved from pre-*scalaris* after the latter had given rise to *P. pubescens*. The ori-

gin of *P. nutallii* was probably as a California isolate of their ancestral desert-edge species. The magpie, *Pica nuttalli*, and the blackbird, *Agelaius tricolor*, may owe their origins to factors similar to those responsible for the origin of *Picoides nuttalli*. Perhaps exceedingly arid conditions during one of the late Pleistocene interglacial periods caused the isolation of pre-*nuttalli* from its sister population to the south and east. Some time during its isolation it came into contact with *P. pubescens*, and these two species ultimately were able to adapt to each other sufficiently to permit

their sympatry. Interaction with *pubescens* may have influenced the evolution of some distinctive features of *nutallii*. It is remotely possible that *nutallii*, which is rather intermediate morphologically between *scalaris* and *pubescens*, originated as a hybrid population in an area of secondary contact between the latter two species.

At some time after its isolation and divergence, *nutallii* expanded its range to enter into secondary contact with *scalaris*, which presumably was extending its range following amelioration of conditions that originally had isolated parts of their ancestral population. There possibly followed several periods of contact and isolation. More recently, unfavorable environmental conditions in northeastern Baja California and southeastern California led to the isolation of the peninsular Baja California and mainland (Arizona, western Mexico) populations of *P. scalaris*. *Picoides nutallii* was out of contact for some time with *scalaris* populations in California, but it may have remained in contact, perhaps hybridizing frequently with the Baja California portion of *P. scalaris*. This would account for the indications of introgression in Baja California populations, and for the reinforcement of isolating mechanisms and evolution of gene combinations enabling the two species to coexist, at least over a small part of that region. The peninsular Baja California populations of *scalaris*, diverging from the mainland populations of that species, evolved into the modern races *eremicus* and *lucanus*. More recently, populations of *P. s. cactophilus* reinvaded southeastern California, or at least the western fringes of that area, coming into contact with *nutallii*. Tenuous contact also was established with *P. s. eremicus* along the eastern base of the Sierra Juárez (a few intermediate specimens are known; see Short, 1968). The different interaction of the two species in California and Baja

California under this interpretation would be the result of an older contact in the latter area, and a more recent contact in California.

An alternative interpretation would be to assign responsibility for the different interactions of *scalaris* and *nutallii* in California and Baja California entirely upon a contracting range of *P. pubescens* and a strong *pubescens-scalaris* interaction. Under this view, the entire *scalaris-nuttallii* contact would date from the same time, and the absence of *pubescens* in Baja California and its presence in California would account for the different interactions of *nutallii* with *scalaris*. However, *pubescens* is rare in southern California, especially in the areas where *nutallii* and *scalaris* meet or approach each other closely. There is no apparent difference in the interaction of the last two species around Kernville, where *pubescens* occurs, and near Victorville, where *pubescens* is absent. I am sure that the presence of *pubescens* has (and perhaps has had) some effect on the nature of the *scalaris-nuttallii* interaction. It also undoubtedly influenced the evolution of some traits of *nutallii*, perhaps precluding *nutallii* from evolving a white back or smaller size which might be advantageous with respect to *nutallii-scalaris* interactions. However, the rarity or absence of *pubescens* in much of southern California means that it cannot be having an important effect on the *nutallii-scalaris* contact in much of this region at the present time. If the presence of *pubescens* were the deciding factor in whether *nutallii* and *scalaris* could coexist, I would expect *nutallii* and *scalaris* to coexist somewhat frequently in southern California (except at Kernville). That they fail to do so indicates that the presence of *pubescens* is not of overriding consequence, however important it may be.

THE CLASSIFICATION OF NEW WORLD SPECIES OF *PICOIDES*

The classification of the New World species of *Picoides* presented below is that of Bock and Short (ms.). It follows from the phylogenetic discussions above (see fig. 26), and from an evaluation of other characters (e.g., juvenal plumages; see Bock and Short, ms.). Super-species are indicated by brackets as suggested by Amadon (1966).

- Picoides [lignarius] lignarius* (Molina) 1782
- Picoides [lignarius] mixtus* (Boddaert) 1783
- Picoides [scalaris] scalaris* (Wagler) 1829
- Picoides [scalaris] nuttallii* (Gambel) 1843
- Picoides pubescens* (Linné) 1766
- Picoides borealis* (Vieillot) 1807
- Picoides stricklandi* (Malherbe) 1845
- Picoides villosus* (Linné) 1766
- Picoides albolarvatus* (Cassin) 1850

Picoides tridactylus (Linné) 1758

Picoides arcticus (Swainson) 1831

This group of species should be placed together within *Picoides*. Difficulties inherent in any linear arrangement preclude placing the group exactly where it should be placed, namely

near *P. moluccensis*. I prefer to place the New World group following the various Old World groups also derived from the ancestors of *P. moluccensis* and its close relatives. However one may arrange the diverse Old World groups, the New World group should follow them (see, e.g., Bock and Short, ms.).

SUMMARY AND CONCLUSIONS

STUDIES OF MORE THAN 2000 specimens of southwestern North American species of *Picoides* reveal limited hybridization between the morphologically similar Downy and Nuttall's woodpeckers (three known hybrids), and the Nuttall's and Ladder-backed woodpeckers (at least eight hybrids). The Downy and Nuttall's woodpeckers are broadly sympatric in California, where they generally occupy somewhat different habitats. In southern California, however, both inhabit riparian woodlands; there the Downy diminishes in numbers, and its range terminates in San Diego County. The two hybrids of these species for which locality data are available come from San Diego County. It is likely that the hybrids resulted from restricted availability of mates for Downy Woodpeckers in that region.

The desert-inhabiting Ladder-backed Woodpecker is parapatric with the Nuttall's Woodpecker in southern California. Contact between these species occurs at a few sites, probably through the wandering of post-breeding Ladder-backed Woodpeckers. Sporadic hybridization occurs at present, but perhaps it was more prevalent in the past for there is evidence of introgression greater than that expected from the limited interbreeding of today.

In northwestern Baja California the Nuttall's Woodpecker is sympatric with the Ladder-backed Woodpecker over a 100- by 25-mile area. Within this area these woodpeckers predominantly inhabit isolated or semi-isolated riparian woodlands along different streams. More extensive riparian woodlands, those at higher elevations, and those surrounded or partly surrounded by chaparral vegetation are apt to be inhabited by Nuttall's Woodpeckers. Isolated, smaller woodlands, those at lower elevations and those surrounded by xeric vegetation tend to be occupied by Ladder-backed Woodpeckers. Various intermediate areas are inhabited by both species, and hybrids are apt to occur in such areas. Tiny isolated riparian woods may be occupied by one or the other species, or by a few individuals of each, and hybridization also may occur.

Thirty-six specimens (19 from Baja California) other than the eight (four from Baja California) believed to represent Nuttall's and Ladder-back

hybrids are likely to represent hybrid or introgressant individuals. Variation in the two species indicates that introgression is affecting 10 per cent or less of their southern California populations, and 12 per cent (*nuttallii*) to as much as 30 per cent (*scalaris*) of their populations in northwestern Baja California. Character displacement seems to be occurring only in *scalaris*, affecting bill length, and possibly wing length, bill depth, and tail barring. The Nuttall's Woodpecker's extensive sympatry with the Downy Woodpecker may be responsible for its lack of character displacement with respect to *scalaris*. Differences between the situation in California and that in Baja California are probably owing to differences in the time of the original contacts, in the climatic events since the contacts were established, and in the particular populations of Ladder-backed Woodpeckers that are involved. The California and northern Baja California Ladder-backs represent different racial groups (*cactophilus* of the *cactophilus* group, and *eremicus* of the *lucasanus* group, respectively) of that species, and hence distinct gene pools. There is little gene flow between these populations of *P. scalaris*.

Modes of foraging are similar in the Nuttall's and Ladder-backed woodpeckers. Plants used for foraging in the area of sympatry are similar as well, at least in the breeding season. Studies are needed during those times of the year when population densities are greater and food supplies more limited. There is evidence for sexual differences in foraging sites in both of these species. Females tend to feed on smaller branches and branchlets of trees (*nuttallii*), or on smaller shrubs and cacti (*scalaris*) than do males. Such differences in desert-inhabiting Ladder-backed Woodpeckers may favor better exploitation of food resources. In the shrub desert the diversity of plants and spacing of conspecific plants make it likely that such sexual differences may minimize conflicts over foraging sites, as the birds utilize different sites; and promote visual and vocal contact, as the birds can forage closer together by utilizing different plants than if they used the same plant species. The evolution of sexual foraging differences in the Ladder-back

probably was facilitated by the lack of competitors, as no other closely related woodpecker inhabits the deserts occupied by the Ladder-backed Woodpecker.

The Ladder-backed, Nuttall's, Downy, and Hairy woodpeckers have similar agonistic displays. They differ in some of their vocalizations. These differences, plus the visual cues offered by differences in color pattern (especially of the face, wings, and tail; perhaps also bill size) may enable species recognition either without accompanying displays, or during interspecific encounters involving displays. Their pair formation probably is intricately bound to agonistic behavior. Sexual recognition may determine the nature and intensity of displays in an initial encounter between individuals of the opposite sex. If nonconspecific vocalizations and color markings accompany these displays, they may preclude further agonistic interactions ultimately leading to pair formation and even hybridization. The similarity in plumage patterns between the broadly sympatric Downy and Hairy woodpeckers, and the differences in their vocalizations suggest that the latter may play a primary role in reproductive isolation of these and the other species of *Picoides* under consideration.

The four species of woodpeckers mentioned above generally exhibit territorial overlap *inter se* wherever they overlap. An exception is the interspecific territoriality of *scalaris* and *nuttallii* in the area of their sympatry in Baja California. It is hypothesized that this interspecific territoriality is furthered by the increased contacts between individuals of these woodpeckers where they occur together in an ecologically simple situa-

tion (e.g., cottonwood–willow riparian woods), and where they of necessity forage similarly. A single instance of apparent interspecific territoriality of Hairy and Nuttall's woodpeckers under such circumstances lends support to this view. Interspecific territoriality is furthered by the relative similarity of the plumaged patterns (basic black and white) of these woodpeckers, and particularly by their similar displays. At the same time, such similarities may through habituation retard the reinforcement of isolating mechanisms in secondary contacts between closely related woodpeckers.

The New World species of *Picoides* comprise a close-knit group within that genus. Among species of the New World group the South American *P. mixtus* and *P. lignarius*, as well as *P. stricklandi* and *P. scalaris*, most closely approach morphologically the probable ancestor of the group. The Hairy Woodpecker is closely related to Strickland's Woodpecker and the White-headed Woodpecker, and the three-toed woodpeckers are related to this sub-group. Another line is comprised of the Red-cockaded, Downy, Nuttall's, and Ladder-backed woodpeckers. The last two species are still actively undergoing speciation, and they comprise a superspecies. The Downy Woodpecker is very closely related to *nuttallii* and to *scalaris*, as indicated by its morphology, largely allopatric distribution (and apparent interaction with *nuttallii* where they are sympatric), and hybridization with *P. nuttallii*. Nevertheless, all of the New World species of *Picoides* are sufficiently closely related that rare hybrids may occur between any two of them, particularly those that are mainly allopatric.

LITERATURE CITED

- AMADON, D.
1966. The superspecies concept. *Syst. Zool.*, vol. 15, pp. 245–249.
- AXELROD, D. I.
1958. Evolution of the Madro-Tertiary geoflora. *Bot. Rev.*, vol. 24, pp. 433–509.
1960. The evolution of flowering plants. In Tax, S. (ed.), *Evolution after Darwin*, vol. 1, The evolution of life. University of Chicago Press, pp. 227–305.
- BANKS, R. C.
1967. Birds and mammals of La Laguna, Baja California. *Trans. San Diego Soc. Nat. Hist.*, vol. 14, pp. 205–232.
- BEAL, F.
1911. Food of the woodpeckers of the United States. U.S. Dept. Agr., Biol. Surv. Bull., no. 37, pp. 1–64.
- BLUME, D.
1955. Über einige Verhaltensweisen des Grünspechts in der Fortpflanzungszeit. *Vogelwelt*, vol. 76, pp. 193–210.
1956. Verhaltensstudien an Schwarzspechten (*Dryocopus martius*). *Ibid.*, vol. 77, pp. 129–151.

1957. Verhaltensstudien an Grünspechten (*Picus viridis*). *Ibid.*, vol. 78, pp. 41-48.
1958. Verhaltensstudien an Buntspechten (*Dendrocopos major*). *Ibid.*, vol. 79, pp. 65-88.
1961. Über die Leberweise einiger Spechtarten. *Jour. Ornith.*, vol. 102 (Sonderheft), pp. 1-115.
- BOCK, W. J., AND L. L. SHORT
[MS.] A revision of the genera of woodpeckers (Aves: Picidae).
- BROWN, J.
1964. Goals and terminology in ethological motivation research. *Animal Behaviour*, vol. 12, pp. 538-541.
- BROWN, J., AND R. W. HUNSPERGER
1963. Neuroethology and the motivation of agonistic behavior. *Animal Behaviour*, vol. 11, pp. 439-448.
- CODY, M. L.
1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor*, vol. 71, pp. 222-239.
- DAVIS, J.
1965. Natural history, variation and distribution of the Strickland's Woodpecker. *Auk*, vol. 82, pp. 537-590.
- DELACOUR, J.
1951. The significance of the number of toes in some woodpeckers and kingfishers. *Ibis*, vol. 93, pp. 60-62.
- GRINNELL, J.
1908. The biota of the San Bernardino Mountains. *Univ. California Publ. Zool.*, vol. 5, pp. 1-170.
- GRINNELL, J., AND A. H. MILLER
1944. The distribution of the birds of California. *Pacific Coast Avifauna* no. 27, pp. 1-608.
- JOHNSON, N. K.
1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondi-oberholseri-wrightii* complex. *Univ. California Publ. Zool.*, vol. 66, pp. 79-238.
- KILHAM, L.
1960. Courtship and territorial behavior of Hairy Woodpeckers. *Auk*, vol. 77, pp. 259-270.
1962. Reproductive behavior of Downy Woodpeckers. *Condor*, vol. 64, pp. 126-133.
1965. Differences in feeding behavior of male and female Hairy Woodpeckers. *Wilson Bull.*, vol. 77, pp. 134-145.
1966. Reproductive behavior of Hairy Woodpeckers. I. Pair formation and courtship. *Ibid.*, vol. 78, pp. 251-265.
1969. Reproductive behavior of Hairy Woodpeckers. III. Agonistic behavior in relation to courtship and territory. *Ibid.*, vol. 81, pp. 169-183.
- KLOPMAN, R. B.
1968. The agonistic behavior of the Canada Goose (*Branta canadensis canadensis*). I. Attack behavior. *Behaviour*, vol. 30, pp. 287-319.
- KÜCHLER, A. W.
1964. Potential natural vegetation of the conterminous United States (Manual to accompany the map). *Amer. Geogr. Soc., Special Publ.* no. 36, pp. 1-156.
- LAWRENCE, L. DE K.
1967. A comparative life-history study of four species of woodpeckers. *Amer. Ornith. Union Monogr.*, no. 5, pp. 1-156.
- MAILLIARD, J., AND J. GRINNELL
1905. Midwinter birds on the Mohave Desert. *Condor*, vol. 7, pp. 71-77.
- MAYR, E.
1942. Systematics and the origin of species. New York, Columbia University Press, xiv+334 pp.
1963. Animal species and evolution. Cambridge, Belknap Press of Harvard University Press, xvi+797 pp.
1969. Principles of systematic zoology. New York, McGraw-Hill Co., xiv+428 pp.
- MILLER, A. H.
1955. A hybrid woodpecker and its significance in speciation in the genus *Dendrocopos*. *Evolution*, vol. 9, pp. 317-321.
- MOYNIHAN, M.
1968. Social mimicry; character convergence versus character displacement. *Evolution*, vol. 22, pp. 315-331.
- NOBLE, G. K.
1936. Courtship and sexual selection of the flicker (*Colaptes auratus luteus*). *Auk*, vol. 53, pp. 269-282.
- ORIAN, G. H., AND M. F. WILLSON
1964. Interspecific territories of birds. *Ecology*, vol. 45, pp. 736-745.
- PHILLIPS, A. R., J. T. MARSHALL, AND G. MONSON
1964. The birds of Arizona. Tucson, University of Arizona Press, xx+220 pp.
- RIDGWAY, R.
1887. On a probable hybrid between *Dryobates nuttallii* (Gamb.) and *D. pubescens gairdnerii* (Aud.). *Proc. U.S. Natl. Mus.*, vol. 9, pp. 521-522.
- RUGE, K.
1968. Zur Biologie des Dreizehenspechts *Picoides tridactylus* L. 1. Beobachtungsgebiet, Aktionsgebiet, Nahrungserwerb, Trommeln, Pendelbewegungen. *Ornith. Beob.*, vol. 65, pp. 109-124.
- SELANDER, R. K., AND D. R. GILLER
1963. Species limits in the woodpecker genus *Centurus* (Aves.). *Bull. Amer. Mus. Nat. Hist.*, vol. 124, pp. 213-274.

SHORT, L. L.

- 1965a. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist., vol. 129, pp. 307-428.
- 1965b. Specimens of Nuttall Woodpecker from Oregon. Condor, vol. 67, pp. 269-270.
1968. Variation of Ladder-backed Woodpeckers in southwestern North America. Proc. Biol. Soc. Washington, vol. 81, pp. 1-10.
1969. Taxonomic aspects of avian hybridization. Auk, vol. 86, pp. 84-105.
- 1970a. Notes on the habits of some Argentine and Peruvian woodpeckers. Amer. Mus. Novitates, no. 2413, pp. 1-37.
- 1970b. Reversed sexual dimorphism in tail length and foraging differences in woodpeckers. Bird-Banding, vol. 41, pp. 85-92.

SHORT, L. L., AND R. C. BANKS

1965. Notes on birds of northwestern Baja California. Trans. San Diego Soc. Nat. Hist., vol. 14, pp. 41-52.

SHORT, L. L., AND R. S. CROSSIN

1967. Notes on the avifauna of northwestern Baja California. Trans. San Diego Soc. Nat. Hist., vol. 14, pp. 282-299.

SHREVE, F.

1951. Vegetation of the Sonoran Desert. Carnegie Inst. Washington Publ. 591, pp. 1-192.

VOOUS, K. H.

1947. On the history of the distribution of the genus *Dendrocopos*. Amsterdam, Zool. Mus., pp. 1-142.

