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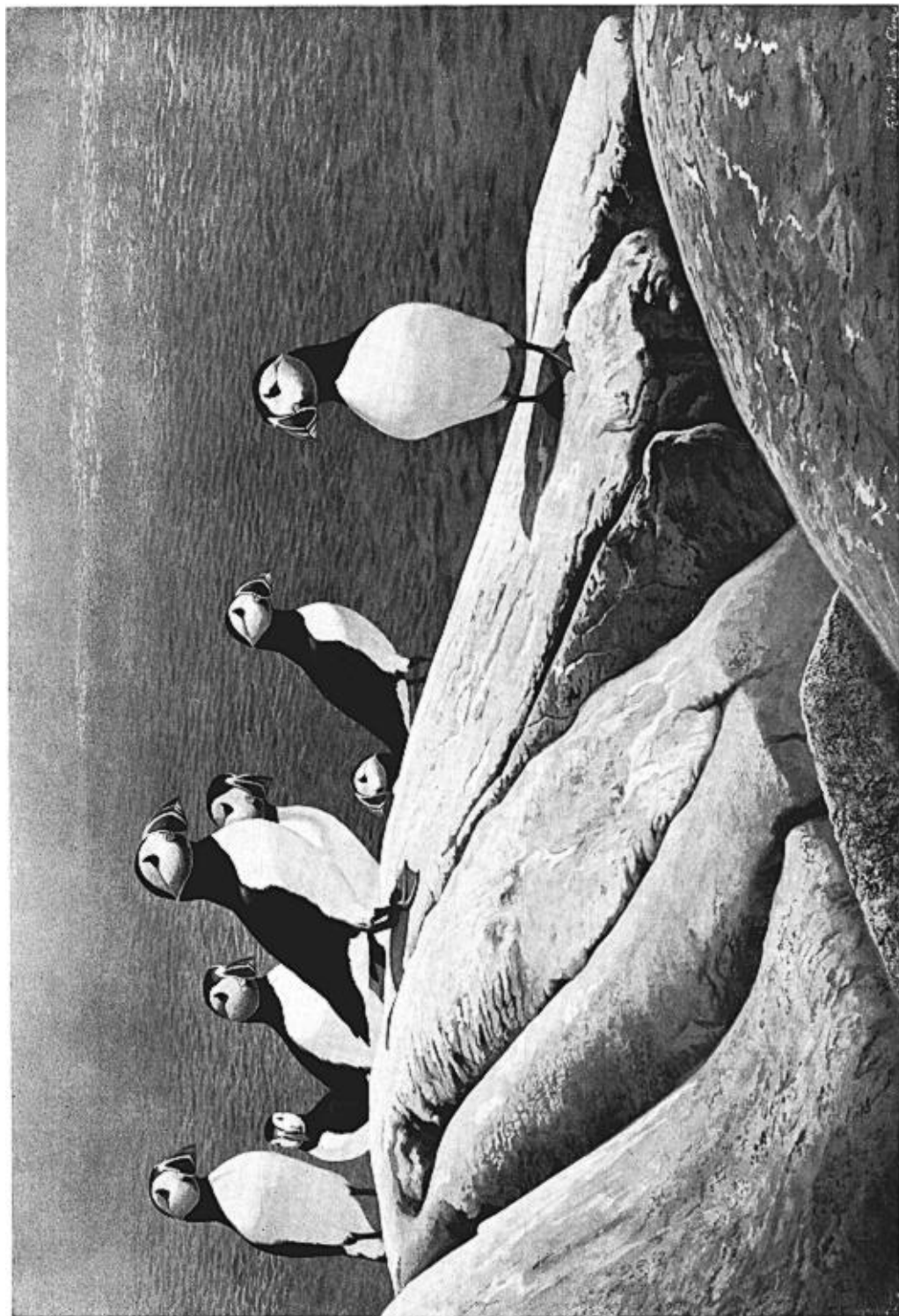
NATURAL HISTORY, VARIATION, AND DISTRIBUTION OF THE STRICKLAND'S WOODPECKER

JOHN DAVIS

AMONG the New World members of the woodpecker genus *Dendrocopos*, two forms are sharply differentiated from their congeners in that they are brown and white rather than black and white. One form is widely distributed, extending from the mountains of southeastern Arizona and southwestern New Mexico south in the middle and upper middle elevations of the great Sierra Madre Occidental of western Mexico to the state of Jalisco, and thence east in the mountains rimming the south edge of the Mexican plateau to east-central Michoacán. Separated from this wide-ranging form by an airline distance of about 50 miles is a more restricted series of populations of brown-backed *Dendrocopos* occupying high elevations in the mountains from the Michoacán-México boundary east to Puebla and Veracruz. The populations of the north and west, characterized in typical form by medium brown coloration, immaculate or nearly immaculate dorsum, and spotted and barred underparts, have been considered by most ornithologists to be a distinct species, the Arizona Woodpecker (*Dendrocopos arizonae*). The more restricted populations of the south and east, characterized by very dark, sooty brown dorsal coloration, heavily barred dorsum and rump, and streaked and barred underparts, have been considered by most ornithologists to represent a second species, Strickland's Woodpecker (*Dendrocopos stricklandi*). This paper presents information on the natural history of these woodpeckers, describes their morphologic variation, and attempts to evaluate the relationship between the major components of the complex.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to a number of persons who have helped me in the course of this study. My wife, Betty, gave assistance with some of the fieldwork in Mexico. Robert K. Selander read the manuscript and made a number of valuable suggestions. Herbert G. Deignan, M. D. F. Udvardy, Philip S. Humphrey, William E. Duellman, Doris M. Cochran, and James A. Peters supplied information



Puffins, Maimicus Rock, Maine

*Reproduced through the courtesy of Mr. and Mrs. Samuel D. Bogan
(See p. 681)*

from a painting by Robert Verity Clem

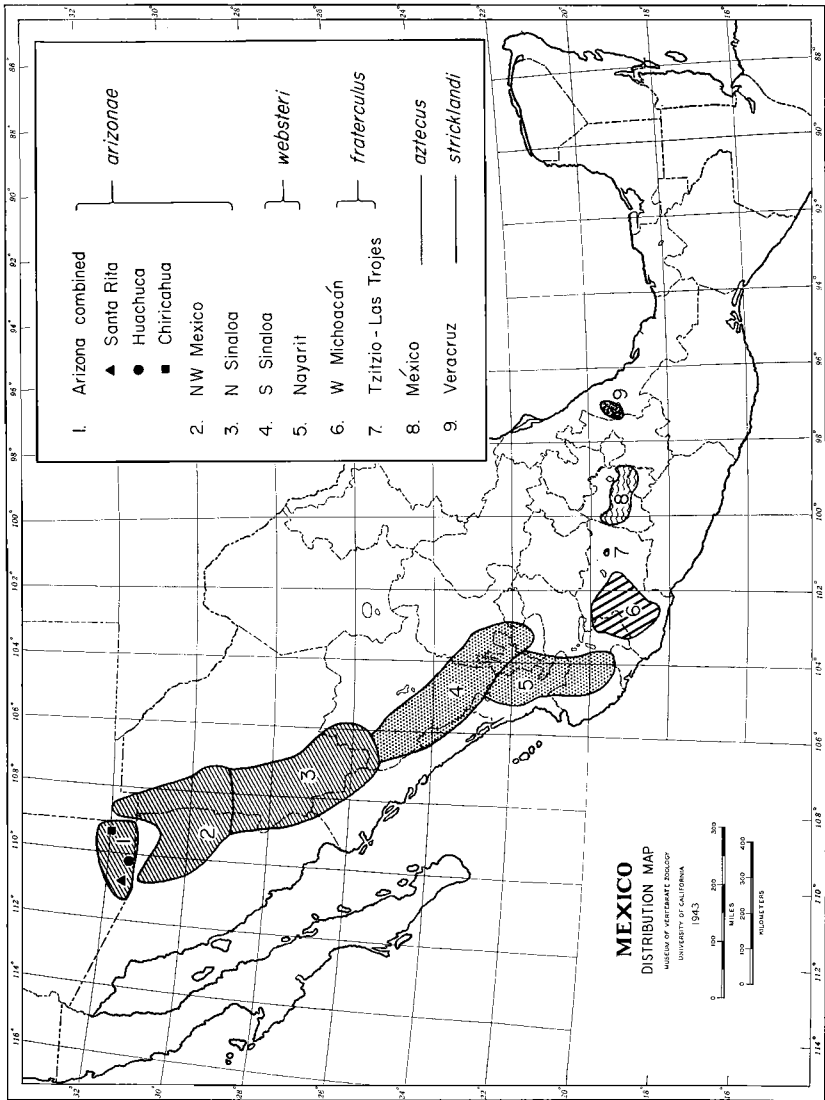


Figure 1. Map showing geographic distribution of subspecies and of the samples used in the analysis of geographic variation.

on the travels of, and specimens collected by, John Xántus in Michoacán. Ing. Norberto Sanchez Mejorada identified specimens of trees which I collected in Michoacán. Alden H. Miller measured and took notes on specimens in the British Museum (Natural History). Mont Cazier extended many courtesies to me in the course of my stay at the Southwestern Research Station and, as did also E. Gorton Linsley and Ronald W. Stark, gave me valuable information on the distribution and emergence

of forest insects. Bruce G. Elliott generously turned over to me notes which he made on the foraging of *Dendrocopos stricklandi* near Mexico City. Gene M. Christman made the illustrations accompanying this paper and Don Harvey took the photographs of specimens.

Finally, I would acknowledge the great debt I owe the veteran collector, the late Chester C. Lamb. It was he who discovered the southeasternmost population of the Arizona Woodpecker near Tzitzio, Michoacán, in 1939, and it was he who discovered the westernmost population of the Strickland's Woodpecker on the Michoacán-México boundary in 1941, thus extending the distribution of these forms to the present limits. In addition, the extensive series in the Moore Collection, the greatest single source of information available on these birds in Mexico, was collected almost entirely by him.

I borrowed material from the following collections: American Museum of Natural History through Dean Amadon; British Museum (Natural History) through J. D. Macdonald; California Academy of Sciences through Robert T. Orr; Carnegie Museum through Kenneth C. Parkes; Chicago Natural History Museum through E. R. Blake; Cornell University through Charles G. Sibley; Dickey Collection through Thomas R. Howell and O. M. Buchanan; Los Angeles County Museum through Kenneth E. Stager; Louisiana State University Museum of Natural Science through George H. Lowery, Jr.; Minnesota Museum of Natural History through Dwain W. Warner; Moore Collection through John William Hardy; Museum of Comparative Zoology through Raymond A. Paynter, Jr.; Museum of Zoology, University of Michigan, through Robert W. Storer; New Mexico State University through Ralph J. Raitt; Peabody Museum of Yale University through S. Dillon Ripley; Texas Cooperative Wildlife Museum through William B. Davis; United States National Museum through George E. Watson; and University of Kansas Museum of Natural History through Richard F. Johnston. To all of these institutions and to the staff members who made these loans, I am most grateful.

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MATERIALS AND METHODS

Although I consider the Arizona and Strickland's woodpeckers as members of the species *Dendrocopos stricklandi*, I shall use the names *arizonae* and *stricklandi* throughout this paper to refer to the two major assemblages described in the introduction. A total of 512 specimens of *arizonae* and 97 specimens of *stricklandi* was used in this study. These specimens were divided into the following samples for analysis of morphologic variation:

<i>arizonae</i>	<i>stricklandi</i>
Arizona Combined	México
Santa Rita	Veracruz
Huachuca	
Chiricahua	
Northwestern Mexico	
Northern Sinaloa	
Southern Sinaloa	
Nayarit	
Western Michoacán	
Tzitzio-Las Trojes	

The geographic distribution of these samples is shown in Figure 1.

The following measurements were taken: culmen, from the anterior edge of the nostril; wing, the chord; tail; and tarsus. These measurements are described by Baldwin, Oberholser, and Worley (1931: 16, 76, 92-93, and 107, respectively). The wings and tails of excessively worn birds were not measured. Birds in juvenal plumage were not measured, but since the postjuvenal molt is complete in these woodpeckers it was impossible to separate first-year birds from older individuals, and therefore all age groups exclusive of juvenals were combined.

The seasonal variation in bill length was not great enough to require purification of samples on a seasonal basis for analysis of this character. The following data show mean bill lengths for the three periods of the year in which bill length was greatest, intermediate, and smallest, for the males of the Arizona Combined sample:

Period	Number	Mean with Standard Error
December-March	13	22.86 ± .37
May-June	30	22.54 ± .23
August-October	32	22.07 ± .17

As can be seen, the differences in mean bill length among these three samples are not statistically significant.

For each sample of 10 specimens or more, mean, range, standard error, standard deviation, and coefficient of variation were calculated for each of the four measurements used. Samples of fewer than 10 were analyzed in this fashion for the Tzitzio-Las Trojes sample only. In addition, coefficient of difference (C. D.) was calculated for each measurement between every combination of pairs of samples of males for which measurement data had been treated statistically. Coefficient of difference was calculated according to the formula given by Mayr, Linsley, and Usinger (1953: 146), the difference between the means of two samples being divided by the sum of their standard deviations. When the value of coefficient of difference is 1.28, joint non-overlap of the two samples being compared is 90 per cent. Joint nonoverlap of 90 per cent or more is considered by many taxonomists to indicate subspecific difference between populations represented by the samples being analyzed, and it is so considered in this study.

Field work was carried out in the states of Michoacán and México, Mexico, from 20 January to 31 May 1961, and at the Southwestern Research Station (of the American Museum of Natural History), near Portal, Cochise County, Arizona, between 20 June and 20 July 1961.

HABITAT PREFERENCE AND FORAGING BEHAVIOR

In the northern part of its range, *arizonae* is associated primarily with oaks, although it also uses pine-oak woodland and riparian vegetation, the latter including such trees as sycamores (*Platanus occidentalis*), cottonwoods (*Populus*), walnuts (*Juglans*), and willows (*Salix*). In many places it occurs in woodlands composed of mixtures of two, and rarely of all three, of these vegetation types. Ornithologists who have studied this woodpecker in Arizona and New Mexico almost invariably note it as being primarily a bird of the oaks (F. M. Bailey, 1928; V. Bailey, 1913; Brandt, 1951; Fowler, 1903; Henshaw, 1875; Monson, 1937; Monson and Phillips, 1964; Scott, 1886; Swarth, 1904, 1908, 1914, 1929; van Rossem, 1936; Visher, 1910). In his study of the birds of pine-oak wood-



Figure 2. Encinal, lower Cave Creek Canyon, Chiricahua Mountains, Cochise County, Arizona, with taller, riparian trees along Cave Creek in the background. Photographed on 19 July 1961.

land in southeastern Arizona, southwestern New Mexico, and adjacent northwestern Mexico, Marshall (1957: 85) states that the Arizona Woodpecker "is limited to woods in which oaks are plentiful." He gives the principal foraging site as branches and trunks of oaks (*op. cit.*: 52), and he lists the preferred montane habitats of this woodpecker in order of decreasing preference as encinal and pine-oak woods (*op. cit.*: 55).

In the period 21 June to 14 July 1961, I found Arizona Woodpeckers commonly in the Chiricahua Mountains of southeastern Arizona. These birds were distributed between Portal Ranger Station, elevation 4,800 feet, and a point 0.4 miles by road below Onion Saddle, 7,400 feet. The breeding season was over and all young birds seen were full-grown and capable of doing at least some foraging for themselves. Thus, the season was advanced and some post-breeding wandering may have taken place before my observations began.

I found the woodpeckers in riparian vegetation, either containing some oaks or immediately adjacent to oaks on the lower canyon walls; in encinal (Figure 2); and in pine-oak woodland. The 114 foraging stations used by individual birds between 21 June and 14 July were as follows: oaks (*Quercus*), 47; pines (*Pinus*), 26; sycamores, 16; agaves (*Agave*), 14; dead trees, species not determined, 5; walnuts, 3; willow, 1; locust (*Robinia*), 1; and cottonwood, 1. Oaks were used more frequently

than any other kind of tree, and this agrees with the observations of other workers.

As regards height of foraging station, this apparently depends on the over-all height of the tree being used. As can be seen from Table 1, the mean estimated heights of foraging sites in oaks, pines, and sycamores, for which most data are available, varied almost exactly in relation to the mean over-all heights of the trees in which the foraging sites were located. In each type of tree, foraging individuals worked about two-thirds of the way up, despite the fact that the pines and sycamores, on the one hand, averaged considerably taller than the oaks. This does not take into account agaves, which represent quite specialized foraging stations.

Between 21 June and 14 July, there was a noticeable shift from the use of living wood to the use of dead wood as a foraging substrate. From 21 to 27 June, woodpeckers foraged on living wood 25 times, and on dead wood, either on dead trees or the dead parts of trees still alive, only 6 times. From 28 June to 14 July, they foraged 36 times on living wood and 47 times on dead wood. This shift is highly significant (Yates' corrected Chi-square 8.10, d. f. 1; $P < .005$). After the birds were using mainly dead wood, their manner of foraging also appeared to change, although I have no quantitative data to support this. Periods of hammering at one spot seemed shorter, and especially noticeable was the much more frequently observed habit of tapping very lightly a few times, as though testing, and then, after a brief pause, either hammering vigorously or moving to another spot and "testing" again. These changes in foraging site and method were correlated with the explosive emergence of adult insects in late June and early July, and presumably with a movement of insects, especially larvae, to more peripheral positions in the wood of trees, which accompanied the emergence of adults.

According to Dr. Mont Cazier, these shifts in the distribution of the insect population are triggered by the pattern of late spring and early summer rainfall, with the first heavy rain of the late spring setting up a situation in which the next ensuing rainfall, whether light or heavy, will stimulate the emergence of adult insects and the movement of larvae to peripheral locations. The larval shift would be especially prominent in dead wood, with larvae moving from heartwood to sapwood to pupate. Dr. Cazier also suggested that the increased use of "testing" by light tapping may have served to induce movements on the part of peripherally located larvae or pupae, such movements being sensed by the woodpecker as it clung to the tree. If movements were detected, hammering would follow. If none was detected, the bird would shift to another spot and test again. Linsley (1961: 31) states that the sound of cerambycid beetle

TABLE 1
FORAGING HEIGHT RELATIVE TO TREE HEIGHT, CHIRICAHUA MOUNTAINS, ARIZONA

Tree	Tree height		Bird height	
	Mean (feet)	N	Mean (feet)	N
Oaks	21.9	15	13.5	21
Pines	42.9	19	28.5	20
Sycamores	42.2	9	28.1	11

larvae boring in wood "is frequently discernible at a distance of several feet and probably helps birds to locate them." After pupation had occurred, presumably following a move from heartwood to sapwood, this auditory cue would be lacking, and some other method of location, such as that described above, would have to be used.

Dr. E. Gorton Linsley stated (in conversation) that a shift similar to that just described for insects in general in the Chiricahuas, would undoubtedly occur specifically in cerambycid beetles, at least in those located in dead wood. This is not to say that such a shift might not also occur in cerambycid larvae in live wood, but little information is available concerning the seasonal movements of beetles so located. Cerambycids would be of particular importance as all developmental stages would undoubtedly be prominent in the diets of woodpeckers. Linsley (1961: 31) states that "Many birds . . . derive a part of their food from adult cerambycids . . . Woodpeckers in particular are especially fond of the larvae."

The weather records at the Southwestern Research Station show that the first heavy rain of the late spring came on 16 June (1.27 inches). The next rain came on 27 June (.06 inch), with a trace (less than .01 inch) reported on 28 June, and again on 30 June. The great shift in the distribution of the insect population, with a very evident and explosive emergence of adults, especially noticeable in certain families of beetles, that occurred at the end of June and the beginning of July was apparently triggered by the rains of 27 June. Presumably, the insect larvae, especially those in dead heartwood, moved to peripheral locations at the same time, and the woodpeckers adjusted their selection of foraging sites and choice of foraging methods accordingly.

Another noticeable shift affected the use of agaves (*Agave palmeri*) as foraging stations. Between 21 and 27 June, agaves were used only once, but between 28 June and 14 July, Arizona Woodpeckers foraged on them 13 times. Individuals used living agaves 6 times, foraging on the flower clusters only. Sometimes they perched on the large clusters of fleshy flowers and probed down into the corollas. At other times they perched

next to flower clusters and probed between the flowers. In the first instance it was not possible to tell whether they were feeding on nectar or on insects which had been attracted to it; in the second instance they were probably feeding on insects crawling between the flowers. Dead agaves were used 8 times, the foragers ignoring the old, dry flower clusters and hammering on the dead flowering stems.

The longest observations of Arizona Woodpeckers foraging on agaves were made on 28 June and 10 July. On 28 June, two full-grown young were watched as they hammered on dead agave stalks for nine minutes. Since the birds were already foraging when I found them, they may have been working in this manner for some time. After they had left I examined one of the stalks. Pecking had been confined to an area between three feet eight inches and five feet seven inches above ground. A number of holes had been punched through the hard, outer "shell" of the stem into the pith. Only once did I see a bird actually extract a prey item from the pith and this appeared to be a large insect larva of some sort. On 10 July, an adult male, accompanied by a begging juvenile, foraged vigorously on a dead agave stem for a total of 26 minutes between 0619 and 0650 hours. The juvenile foraged for a few minutes only and spent most of its time begging for food. The adult fed it several times, although I could not see what prey items were involved. After the birds had left, examination showed that all pecking had been confined to an area between 18 and 30 inches above ground. Many holes and slits had been punched through to the pith; the largest measured $2\frac{1}{2}$ by $\frac{3}{4}$ inches. I stripped away the outer "shell" and found two adult histerid beetles (*Hololepta* sp.) and an adult curculionid beetle (*Scyphophorus acupunctatus*), these identified by Dr. Cazier, and a number of large pupae and larvae, presumably of the curculionid. In cross section, one could see that the larvae had recently cut tunnels from the central pith to the peripheral situations which they and the pupae now occupied. Noticeable was the manner in which both larvae and pupae rotated or wiggled on being disturbed, behavior consistent with Dr. Cazier's suggestion as to the function of exploratory pecking.

Marshall (1957: 85) observed a young Arizona Woodpecker probing into agave blossoms and he noted that Acorn Woodpeckers (*Melanerpes formicivorus*) also feed on these flowers (*op. cit.*: 53), presumably on nectar. I noted both Acorn Woodpeckers and Red-shafted Flickers (*Colaptes cafer*) foraging on agaves in much the same ways as those used by *arizonae*. Marshall's observations, and mine, suggest that, especially after the onset of insect emergence and larval shift, agaves are used regularly by a variety of woodpeckers representing birds of rather different foraging habits.

Henshaw (1875: 389), who encountered Arizona Woodpeckers in the Chiricahuas in the period 3 to 29 August 1874, stated that these birds appeared "to prefer to secure their food by a careful search rather than by the hard labor of cutting into the wood in the way the Hairy Woodpecker [*Dendrocopos villosus*] employs its strength." However, the foraging that I noted before 28 June was strictly comparable to what Henshaw considered as typical of the Hairy Woodpecker. In short, it seems evident that this species in the northern part of its range varies its foraging stations and methods according to seasonal shifts in the abundance and distribution of prey items of one sort or another.

These northern populations are not dependent on any particular kind of tree for nest sites. Bent (1939: 92-93), reviewing some of the literature pertinent to the nesting of this species in Arizona, mentions seven nests. Three were found in oaks, and one each in a sycamore, a walnut, a maple, and "a mescal stalk" [= *Agave* sp.]. Brandt (1951: 450) notes finding a nest in an apple tree, and states that the "selection for a home site . . . is often an agave pole wherever one of sufficient dimensions can be found." Later (*op. cit.*: 660), he states that "those occupied cavities that I could find were betrayed by the numerous, tell-tale chips about the base of the nesting tree, which most often was a walnut . . ." I was shown a nest hole in a large sycamore on Cave Creek which had been used earlier in 1961.

At the southernmost point in its distribution, the locality three miles north of Tzitzio, 6,500 feet, and the nearby settlement of Las Trojes, 7,100 feet, Michoacán, the habitat occupied by *arizonae* is markedly different than that which it occupies in Arizona and New Mexico. Here, in east-central Michoacán, the woodland in which *arizonae* occurs is composed almost entirely of pines; oaks of any kind are relatively rare. The almost complete dominance of pines is attested to by the fact that the entire economy of the region is based on the gathering of pine resin; this is a Mexican counterpart of the "turpentine" areas of southeastern United States. At the locality three miles north of Tzitzio, *arizonae* occupied a large stand of *Pinus teocote* on a flat-topped, mesa-like ridge. Oaks were very rare and no other species of pine was noted. There was virtually no understory, and what little there was consisted chiefly of young pines. The open nature of the woods, the almost complete absence of trees other than *Pinus teocote*, and the flatness of the terrain, made for great homogeneity of habitat (Figure 3). At Las Trojes, the woods in which I found *arizonae* were located on a slope falling away sharply to the south. This slope was not uniform but consisted of a series of alternating north-south ridges and canyons. My hunting was confined to two steep ridges and the broad, open canyon between them. The woodland in this canyon was



Figure 3. Open *Pinus teocote* woodland, three miles north of Tzitzio, Michoacán, Mexico, photographed in May, 1961.

dominated by *Pinus teocote* with occasional large *Pinus michoacana* var. *cornuta* interspersed. The western ridge was dominated by *Pinus tenuifolia*, with occasional *P. teocote*, *P. montezumae*, and *P. michoacana* var. *cornuta* interspersed. The eastern ridge was covered by a nearly pure stand of *P. michoacana* var. *cornuta* on its upper end and a nearly pure stand of *P. teocote* on its lower end. Oaks were very rare throughout the entire area. A few patches of brush, especially *Baccharis* sp., were present, but the woods were open, as at the locality north of Tzitzio.

On 44 occasions I recorded the trees in which individual *arizonae* were

seen, whether foraging or not; the birds were seen in pines 42 times and in oaks only twice. Foraging birds were seen 21 times, 20 times in pines and only once in an oak. In the Chiricahuas, foraging *arizonae* were recorded 26 times in pines and 47 times in oaks. The difference between the proportions of pines and oaks used as foraging sites at the two localities is highly significant (Yates' corrected Chi-square 20.87, d. f. 1; $P < .005$).

As regards height of foraging stations, *arizonae* in the Tzitzio-Las Trojes area seemed to have two well-marked preferences; birds foraged either near the ground or at relatively high levels, with infrequent use of intermediate stations. Of the 16 stations for which height was estimated, 7 were between 2 and 15 feet above ground, averaging 5.9 feet, and 9 were between 30 and 60 feet up, averaging 40.6 feet. None was recorded foraging between 15 and 30 feet. Thus, most of the records were either very close to the ground or well up in the crowns. All records but one of foraging at the 30-foot level or higher were for branches; one bird foraged 45 feet up on the main trunk of a pine. Males were seen drumming twice; the drumming stations were 45 and 50 feet up on the main trunks of tall pines. It seems obvious that *arizonae* at the northwestern part of its range is primarily a bird of the oaks, whereas at the southeastern extreme it is almost entirely associated with pines. No information is available to indicate whether or not there is a clinal shift from the use of oaks to pines by the birds from northwest to southeast.

As regards *stricklandi*, it is a bird of higher elevations, ranging from about 8,500 feet to 13,500 feet. Although *stricklandi* is found in woods dominated by pines, other elements are also present, such as firs, oaks, cypresses, and alders. Most observers have associated this woodpecker primarily with pines and other conifers (W. B. Davis, 1945: 277, under *Balanosphyra formicivora formicivora*; Davis and Russell, 1953; Goldman, 1951; Paynter, 1952; Sutton and Burleigh, 1940, 1942). Moore (1946: 105) noted that: "Although true *stricklandi* generally seems to be found as a breeding bird in pure stands of evergreens, chiefly pines, the Puerta [= Puerto] Lengua de Vaca series of *aztecus* was taken . . . around 9,400 feet, where oaks occur occasionally among the firs and some of the individuals were actually collected as they foraged on oak trees." Fourteen specimens of *stricklandi* collected in the states of México and Morelos (Texas Cooperative Wildlife Museum) had the following notations on their labels: "upland pine" (5), "climax pine" (4), "*Pinus-Abies*" (3), "pines" (1), and "rocky hillside" (1).

I observed *stricklandi* at Puerto Lengua da Vaca, on the México-Michoacán boundary, on 23, 24, and 25 May 1961. The forest was primarily pine-fir (*Pinus pseudostrobus-Abies religiosa*), with scattered oaks, alders (*Alnus acuminata*), and cypresses (*Cupressus* sp.). Individ-

uals were seen foraging in pines, alders, and oaks. Some hammering at bark was noted, but most of the foraging consisted of probing at and gleaning from leaves and tufts of needles. The almost complete lack of calls and the primary dependence on gleaning rather than hammering made it very difficult to locate individuals. Hairy Woodpeckers seen in the same woods also foraged both by gleaning and by vigorous hammering. In view of the sudden and very noticeable shift in foraging habits noted in *arizonae* in the Chiricahuas later in the season, it is not possible to generalize on the foraging habits of *stricklandi* on the basis of these limited observations. However, observations made on *stricklandi* near the Morelos-Distrito Federal boundary by Bruce G. Elliott on 11 and 12 April 1964 again suggest dependence on foraging methods other than vigorous hammering. He noted a male foraging on some stumps by probing without any sustained hammering; another male foraged on the lichen-covered undersides of the lower boughs of four pines. "Much gentle probing with taps apparently directed at an angle to dislodge the greenish-white lichen adhering to the bark. The picid was feeding on something under this growth."

The available information on mere occurrence strongly suggests that *stricklandi* occurs in woodland dominated by conifers, and especially by pines. If these birds showed no particular preference for any one genus of trees, most of their foraging over the range from the state of México to the state of Veracruz would be in pines, since they are the most numerous of the trees occurring in the habitats occupied by these woodpeckers.

In summary then, there appears to be more in common ecologically between *arizonae* of the Tzitzio-Las Trojes area and *stricklandi* than between the northwestern and southeastern populations of *arizonae*. *Stricklandi* is, of course, set apart from all populations of *arizonae* by its restriction to higher elevations and, concomitantly, to a colder and more humid climate.

INTRAGENERIC CONTACTS

Two species of *Dendrocopos*, *D. villosus* and the Ladder-backed Woodpecker, *D. scalaris*, come into contact with *Dendrocopos stricklandi* in various parts of its range. The relations of *stricklandi* to these other species serve to define, at least in part, some of the factors which determine its distribution.

In the northern part of its range *arizonae* is almost, if not entirely, separate from *villosus* in the breeding season, apparently because "the Hairy Woodpecker requires coniferous forest for its early nesting season in this area After the downhill trek of Hairy Woodpeckers in early summer, the two postbreeding species jointly inhabit pine-oak woods

in fall and winter; occasionally they feed in the same tree together" (Marshall, 1957: 85). In the Chiricahuas between 21 June and 14 July 1961, I found occasional *villosus*, adults, young, and single adults accompanied by begging juveniles, throughout the range of *arizonae*, but Hairy Woodpeckers were not common at any one place in these middle elevations. In the coniferous forest above the range of *arizonae*, *villosus* was still very common, and the postbreeding movement to lower elevations had apparently just gotten under way. In New Mexico, the same separation between these woodpeckers apparently prevails, as Bailey (1928) assigns *D. v. icastus* of southwestern New Mexico to the "Transition and Canadian zones" and *arizonae* of the same region to the "Upper Sonoran Zone."

As regards *D. scalaris*, there is apparently no contact between it and *arizonae* in the breeding season in the Chiricahuas. I found that *arizonae* ranged down to the Portal Ranger Station at 4,800 feet, and I recorded *scalaris* once in mid-July as high as Cave Creek opposite the ranger station. The two thus came barely into contact at that season. Monson and Phillips (1964: 34) state that *arizonae* is found rarely in winter in the lowlands adjacent to the live oaks in southeastern Arizona, and I have examined six specimens of *arizonae* collected at or near Portal, within the range of *scalaris*. Five of these were collected between 22 July and 10 October, and thus after the breeding season. A female collected on 22 April was presumably a breeding bird, but it was probably a temporary visitor. In the Chiricahuas in June and July, 1956, Tanner and Hardy (1958: 5) recorded *scalaris* from the desert up to 5,200 feet; *arizonae* from 5,200 to 7,200 feet; and *villosus* from 6,500 feet up. The overlap between *arizonae* and *villosus* was similar to the postbreeding overlap between the two in the same months in 1961, and it undoubtedly resulted from the down-mountain movement of *villosus* after the breeding season.

Little has been published on the distributions of *arizonae*, *villosus*, and *scalaris* relative to each other in Mexico. *D. villosus* ranges considerably higher than *arizonae* within the geographic range of the latter, as it has been collected at 10,000 feet on Mt. Mohinora and Laguna Juanota, both in Chihuahua (specimens in Moore Collection), and the species was recorded up to 11,300 feet on Cerro de Tancitaro, in western Michoacán, by Blake and Hanson (1942: 534). Yet, some overlap between the two might be expected at lower elevations. Such overlap is apparently rare. Excluding a few localities for *arizonae* visited in the course of an expedition to the Barranca de Cobre at which collecting was so limited that *villosus* might have been overlooked, there are 17 localities represented by specimens of *arizonae* in the Moore Collection. No seasonal segregation of these localities is made here, so that both breeding and non-breeding

localities are represented. This sample impurity should increase the chances of the two being found together, if the separation between them is primarily in the breeding season, as in Arizona. Yet at only two of these localities were both *villosus* and *arizonae* recorded. Even at those Chihuahuan localities excluded from consideration, it seems likely that *villosus* and *arizonae* do not occur together, as Stager (1954: 27) recorded only *arizonae* in the same general area between 7 and 30 May 1950. The two localities at which both woodpeckers were found were one mile north of Tapalpa, 7,800 feet, Jalisco, in March and April, and 17 miles east of La Junta, 7,500 feet, Chihuahua, in June. Both *villosus* and *arizonae* were definitely breeding at the locality near Tapalpa. Of the 17 localities, 14 were at or below 7,000 feet, and 13 were at or below 6,500 feet. Only three stations were at or above 7,500 feet, including the localities near Tapalpa and La Junta. These are apparently unusually high stations of occurrence for *arizonae* in Mexico, and this probably explains why the two woodpeckers overlapped there.

J. H. Batty collected single female specimens of *arizonae* and *villosus* at Arroyo del Buey, northwestern Durango, on 23 and 28 May, respectively (Miller, 1906: 166). The altitude of this station is given as 7,500 feet, but this may be too high. The altitude at La Cienega de las Vacas, at which Batty collected six specimens of *arizonae* on this same trip, between 30 March and 3 April, and where he recorded this woodpecker as "rather common," is given as 8,500 feet, which would be an unusually high station of record for this form. Batty also collected three specimens of *scalaris* at this locality between 30 March and 1 April, and this would be an extremely high locality at which to find that species, especially in, or perhaps just prior to, the breeding season. It seems likely that all of the altitudes given by Miller (1906: 161) for Batty's camps were too great. The fact remains that there was some overlap between *arizonae* and *villosus* at Arroyo del Buey in late May, either in or just past the breeding season, and considerable overlap between *arizonae* and *scalaris* at La Cienega de las Vacas at a time when these birds were either breeding or getting ready to breed. Thus, the situation was considerably different from that in the Chiricahuas.

On the Volcán de Nieve, on the boundary between Colima and Jalisco, Schaldach (1963: 53-54) found *villosus* mainly in the Humid Pine-Oak Forest, ranging in the cold, dry season downslope to the Arid Pine-Oak Forest; *scalaris* in the Arid Pine-Oak Forest but more common in the Thorn Forest of lower elevations; and *arizonae* in both the Arid and Humid pine-oak forests. Thus, there was some overlap among all three in the Arid Pine-Oak Forest, but this was outside the breeding season of *villosus*. *D. villosus* and *arizonae* apparently overlap in the Humid

Pine-Oak Forest in the breeding season, as *villosus* is resident there and *arizonae* was observed there in June and July; although these months are undoubtedly outside the breeding season, it seems unlikely that *arizonae* moved upmountain following its breeding.

In the Sierra de Autlán, western Jalisco, Schaldach (1963: 53–54) recorded *arizonae* in February and April, 1959. Zimmerman and Harry (1951: 307) collected a single specimen of *arizonae* in these mountains in pine-oak woodland at 8,000 feet, but they recorded *scalaris* only in scrubland at much lower elevations about the city of Autlán proper.

On Cerro de Tancítaro, western Michoacán, Blake and Hanson (1942: 533–535) recorded only one specimen of *arizonae* collected in two seasons of intensive field work. It was collected at Tancítaro, which is described as a village located on a plateau adjacent to the southern base of Cerro de Tancítaro; the elevation appears to be about 5,500 feet (1942: 517, figure 40). *D. villosus* was apparently at least fairly common and ranged from the plateau up to 11,300 feet. Three *scalaris* were collected on “Cerro de Tancítaro,” with no elevations specified. This locality designation apparently indicates stations higher than the village of Tancítaro, since this is at the base of the Cerro. Seemingly, then, the three species overlap in the non-breeding season, as all field work was done in late June, July, and August. *D. villosus* ranges considerably higher than the other two.

To summarize, in the northern part of the range of *arizonae*, there seems to be virtually complete, or complete, separation of the three species of *Dendrocopos* in the breeding season. Farther south, in central western Mexico, the relations of the three forms vary locally, but there seems to be a definite tendency for *scalaris* to range to higher elevations, with consequent overlap at some localities with *arizonae*, and even with *villosus*. *Arizonae* may also overlap with *villosus* in the breeding season, although apparently uncommonly, as judged by the rather small number of localities at which both have been collected. It may be that the two occur together somewhat more frequently, since most collectors would undoubtedly collect *arizonae* in preference to *villosus*. This background serves to introduce the situation in the Sierra de Ozumatlán, east of Morelia in east-central Michoacán, in which the terminal population of *arizonae* occurs in the Tzitzio-Las Trojes region.

In 1939, Chester C. Lamb made a general collection three miles north of Tzitzio, 6,500 feet, from 4 to 10 August; two specimens of *arizonae* were collected but *villosus* was neither collected nor recorded in his field notes. In 1951, Mr. Lamb and I worked at this locality from 13 to 30 July, collecting or recording every species encountered; five *arizonae* were collected but again, *villosus* was not recorded. Thus, in a total of 43

man-days spent at this locality, no record of *villosus* was made. In 1961, I spent a total of 13 days collecting and observing in the Tzitzio-Las Trojes area between 20 January and 20 May. *Arizonae* was recorded many times and 18 specimens were collected. The only evidence of *villosus* was a single bird heard at Las Trojes on 21 January. At these two localities occupied by *arizonae*, it is evident that *villosus* was so rare that its presence must be regarded as casual, or even accidental. Yet, *villosus* was recorded at elevations both above and below Las Trojes.

The relation of *arizonae* to *villosus* in the area of Las Trojes can best be understood by describing their distributions along a transect traversing the Sierra de Ozumatlán east of Morelia, along the main highway to Mexico City. References to kilometer markers indicate the highway distance to Mexico City and the road distance in kilometers between the various localities to be mentioned may be determined by simple subtraction. Morelia itself is at Kilometer 312 and lies at an elevation of 6,204 feet.

Kilometer 291, 6,800 feet, was visited on 31 January 1961. The woodland here was pine-oak, with oaks predominant, and considerable underbrush below the trees. Only *Dendrocopos scalaris* was noted here; it was common.

Kilometer 288, 6,900 feet, was visited on 7 April. The woodland here was dry pine-oak, with pines and oaks present in about equal numbers. A pair of *villosus* and a pair of *scalaris*, both obviously mated judging from their actions, were seen in the same area, and no antagonism between them was noted. Once the female *villosus* fed in an oak and the male *scalaris* fed in the same tree shortly after the female had left.

Las Trojes, Kilometer 282, 7,100 feet, was visited on 20, 21, 24, 25, and 27 January; 29 and 31 March; and 15 April. The terrain at this locality has already been described. *D. villosus* was recorded only once, on 21 January. *Arizonae* was common and apparently resident; breeding specimens were collected in March and April. *D. scalaris* was common and it was seen on every visit; on 29 March one was watched for several minutes as it excavated a nest cavity in an isolated pine in the middle of a cornfield. The species was apparently resident and breeding. The territories of *arizonae* lay wholly within the pine woodland whereas those of *scalaris* routinely included some open, treeless area, perhaps a cornfield or pasture, a patch of scrub or brush, or the dooryards of houses in the settlement. Thus, *scalaris* was a bird of the edge whereas *arizonae* was strictly a bird of the woodland. The overlap between the two was marginal and no interaction between them was noted.

Las Peras, Kilometer 272, 7,800 feet, was visited on 2, 4, 7, and 9 February, and 10 March. Several types of woodland and forest were

present: seemingly virgin pine-fir forest, the trees tall and closely spaced; pine-fir-oak forest; almost pure pine woodland at elevations below the settlement; and almost pure oak woodland on the drier ridges. The pine woodland appeared to be similar to that at Las Trojes. The locality was noticeably colder and more humid than was Las Trojes and the duff in the forests and woodlands was quite moist, whereas that at Las Trojes was very dry. Several times the clouds had descended on Las Peras, whereas they were still above Las Trojes when I passed through it on my way up or down the Sierra. *Arizonae* was recorded only once, a single bird heard calling a few times on 9 February; I consider this record only fairly reliable at best. *D. villosus* was common in all types of woodland and forest. Steller's Jays (*Cyanocitta stelleri*), Gray-barred Wrens (*Campylorhynchus megalopterus*), Red Warblers (*Ergaticus ruber*), and Mexican Chickadees (*Parus sclateri*), all absent at Las Trojes, were present here, indicating the effect of increased altitude on the climate at Las Peras. *Dendrocopos scalaris* was absent.

San Jose de las Cumbres, Kilometer 265, 8,450 feet, was visited on 21 and 23 February. The vegetation here was pine-fir forest with scattered oaks, much interrupted by clearings so that there were many small, separate tracts of forest. *D. villosus* was common here; no other *Dendrocopos* was recorded.

Puerto Morillos, Kilometer 260, 8,800 feet, was visited on 23, 25, and 28 February and 2 March. Two main forest types were noted, pine-fir forest with scattered oaks, alders, and cypresses, and almost pure pine woodland. *D. villosus* was common throughout the area; no other *Dendrocopos* was noted. Chester Lamb collected here from 23 June to 5 July 1954; *villosus* was the only *Dendrocopos* that he recorded.

Puerto Garnica, Kilometer 258, 9,200 feet, was visited on 7, 9, 16, and 25 March. This is the highest point in the Sierra de Ozumatlán traversed by the highway to Mexico City. The forest here was mainly pine-fir-alder, the trees of great size, with scattered oaks and cypresses. One restricted area of open pine woodland was also visited. *D. villosus* was common everywhere; no other *Dendrocopos* was noted.

Sixteen miles by road south-southeast of Zinapécuaro, six miles north of Kilometer 237, 8,000 feet, was visited on 26 February and 9, 15, 16, and 22 March. The woodland at this locality east of the Sierra de Ozumatlán was extensive and consisted of dry, open pine woods strongly reminiscent of those in the Tzitzio-Las Trojes area. *D. villosus* was the only species of *Dendrocopos* encountered; it was common everywhere.

In the Sierra de Ozumatlán, *villosus* was the most wide-ranging, and *arizonae* the most restricted, of the three *Dendrocopos*. Both *scalaris* and *arizonae* reached the upper limit of distribution at Las Trojes, excluding

the single record of *arizonae* at Las Peras. *D. scalaris* was also found below *arizonae* and probably reaches its peak of abundance at lower elevations. *D. villosus* was by far the most tolerant of the three as regards habitat preference; it is best thought of as being more common at elevations above Las Trojes but ranging marginally to elevations below it. It occupied many types of habitat, from xeric pine and pine-oak woodland to moist pine woodland to the moist pine-fir, pine-fir-oak, and pine-fir-alder of higher elevations. *Arizonae* seems to be restricted to xeric and virtually pure pine woodland at 7,100 feet or below. Both it and *scalaris* are probably stopped in their eastward distribution in the Sierra de Ozumatlán by the colder, more humid climatic conditions that prevail at higher elevations. At Las Peras, 700 feet higher and only 10 kilometers by a very twisting road to the east, and thus probably only 6 or 7 kilometers airline, *arizonae* was at best a casual visitor, if my single voice record was valid, but *villosus* was common in all types of habitat present. From Las Peras to the summit, only *villosus* was present.

The absence of *arizonae* in seemingly ideal habitat near Kilometer 237 apparently resulted from one or more of three factors. First, the elevation of 8,000 feet may indicate climatic conditions unsuitable for *arizonae*. This seems unlikely since the woodland at this locality was almost pure pine and very dry and it appeared very similar to the pine woodland at Las Trojes. The most likely possibility seems to be either that the Sierra de Ozumatlán acts as an absolute barrier to *arizonae* or that *arizonae* and *villosus* are competitors and that *villosus* is more successful at this locality. Although the two forms differ somewhat in size, *villosus* being larger, the differences are not so great as to preclude the possibility that they compete. This possibility is strengthened by the almost complete replacement of *villosus* by *arizonae* in the Tzitzio-Las Trojes area.

In other localities near Morelia, *villosus* occurred in what seemed to be ideal *arizonae* habitat. I visited San Miguel del Monte, seven miles airline southeast of Morelia, 7,000 feet, on 8 March. That habitat was a very dry, second growth, nearly pure pine woodland with occasional tall trees, very much reminiscent of the habitat three miles north of Tzitzio. Only *villosus* and *scalaris* were recorded. Puerto de Chalcayotes, about 12 miles southeast of Morelia, 8,000 feet, was visited on 18 March and 28 April. The habitat was very dry pine woodland with scattered oaks. Only *villosus* was noted.

I collected at Rancho La Cofradía, four miles east of Uruapan, 5,200 feet, western Michoacán, on 11 and 12 May. Chester Lamb had collected four *arizonae* at that locality in June and July, 1939; he did not collect *villosus* nor did he include it in the list of 110 species which he recorded in his field notes. At the time of my visits the mature pine woodland had

been reduced to a narrow strip, perhaps one-third of a mile long and averaging about 150 yards wide, running along the base of a high ridge. This ridge was nearly devoid of trees but one could see from the presence of many stumps and from scattered patches of small pines 3 to 10 feet high that the entire ridge had been covered with a pine woodland which had been cut within the past decade or so. Thus the *arizonae* habitat which had been present when Mr. Lamb visited the locality in 1939 had been so reduced that any woodpecker territory would of necessity be located peripherally and would include, or be contiguous to, open, almost treeless terrain. In other words, this was now *scalaris* habitat and only that species was recorded. On 13 May, I spent several hours hunting two miles east of Uruapan in pine woodland between Rancho La Cofradía and the town. This tract was about one mile long and perhaps 300 yards wide and represented the only fairly extensive pine woodland in the entire region about Rancho La Cofradía. I located one pair of *villosus* and recorded *scalaris* commonly; the latter was largely restricted to peripheral areas along the down-slope margin of the tract, with open fields containing scattered trees contiguous. *Arizonae* had apparently disappeared from the area because of the destruction of its habitat. The presence of *scalaris* was to be expected from the nature of the terrain and because Mr. Lamb had collected seven *scalaris* at Rancho La Cofradía in 1939 and recorded the species in his field notes as common there. However, it was surprising to find an established pair of *villosus*; this is further evidence of the tolerance of *villosus* for a variety of habitats and suggests that *arizonae* is relatively intolerant. Disturbance of *arizonae* habitat where *villosus* is present or nearby would undoubtedly favor the latter over the former.

One other feature of the distribution of *arizonae* should be mentioned, and that is its apparent association with the Coppery-tailed Trogon (*Trogon elegans*) rather than with the Mexican Trogon (*T. mexicanus*). *T. elegans* is more of a lowland species but in the higher parts of its range it overlaps with *arizonae*. *T. mexicanus* is distributed at higher elevations than *T. elegans* and would be expected to overlap broadly with *arizonae*. In the Tzitzio-Las Trojes area, *T. elegans* was the only trogon recorded by Chester Lamb and myself in the course of our combined field work carried out in 1939, 1951, and 1961. At Las Peras and above I found only *mexicanus*. The reason for the association between *arizonae* and *T. elegans* may be the apparent preference of these two species for drier sites. Edwards and Martin (1955: 175), working in the area about Lake Pátzcuaro, Michoacán, stated that "The local distribution of *Trogon elegans* was somewhat puzzling. It seemed to completely replace *Trogon mexicanus* in the dry pine-oak woods north of the lake but was absent in the humid pine-oak woods and fir forest, where *Trogon mexicanus* was

common." At the 17 localities in the Moore Collection represented by specimens of *arizonae*, *Trogon mexicanus* only was recorded at four, *elegans* only at eight, both species at two, and neither at three. The northern limits of the distribution of *mexicanus* are in the Sierra Madre Occidental in central western Chihuahua. *T. elegans*, on the other hand, reaches the Santa Rita, Huachua, and Chiricahua mountains of Arizona (Monson and Phillips, 1964: 32). In June and July, 1961, I found *elegans* and *arizonae* in riparian vegetation and adjacent encinal in Cave Creek Canyon in the Chiricahuas. Marshall (1957: 45), discussing certain species which reach their northern limits in southwestern and south-central Arizona, stated that *arizonae* reaches north as far as encinal and pine-oak woodland are found, whereas some other species, including *Trogon elegans*, "are suspected of sensitivity to climate because their distribution shows little correspondence with changes in vegetation from south to north." I agree and would suggest that both *arizonae* and *T. elegans* prefer a relatively dry climate as compared with *Trogon mexicanus*.

One aspect of the distribution of *arizonae* in the Tzitzio-Las Trojes area is most puzzling. If, in fact, *villosus* and *arizonae* are ecologically incompatible, one may well wonder how the small, isolated populations of *arizonae* persist at Las Trojes and in the area three miles north of Tzitzio in such close contact with the far larger population of *villosus* which ranges down to elevations below Las Trojes and which occupies a variety of habitats, including types which closely resemble those occupied by *arizonae* in the Tzitzio-Las Trojes area. Why these small, isolated populations have not yielded before the pressure of *villosus* is a mystery. One must invoke the presence of subtle and as yet undetected ecological characteristics differentiating the Tzitzio-Las Trojes area from the adjacent parts of the range of *villosus*, surely an erudite way of admitting ignorance.

As regards *stricklandi*, the only other member of the genus with which it comes into contact is *villosus*. The two overlap, especially in the lower parts of the range of *stricklandi*. I recorded both in the same area at Puerto Lengua de Vaca and twice saw individuals of both species foraging together in the same trees without any apparent interaction between them. Nelson and Goldman collected a male and female *stricklandi* at Huitzilac, Morelos, on 31 December 1892, and 1 January 1893, respectively. Davis and Russell (1953: 97) list three specimens of *villosus* in the Biological Survey Collection collected at Huitzilac between 29 December 1892 and 1 January 1893, and the two species undoubtedly overlap at that locality. On the other hand, Paynter (1952: 295), collecting above 3,000 meters on Popocatepetl and Ixtaccihuatl between 31 October and 5 November 1950, stated that *stricklandi* was "very abundant" at the foot of Popo

but he did not record *villosus* there. The limited information available suggests that *stricklandi* is found at considerably greater elevations than *villosus* but ranges down into the upper parts of the distribution of that form. The apparent failure of one species to exclude the other where they come together may perhaps be the result of differences in foraging behavior. Since *stricklandi* has such a small bill compared with that of *villosus* it seems probable that these two forms are using rather different food sources. *Arizonae*, on the other hand, has a significantly larger bill than *stricklandi* and this suggests that *arizonae* and *villosus* may overlap to a greater degree in their diets.

However, I investigated seemingly ideal habitat for *stricklandi* in Michoacán but found it occupied only by *villosus*. The forest at Puerto Garnica was similar to that at Puerto Lengua de Vaca, and at about the same elevation, but only Hairy Woodpeckers occurred there. I spent a total of 10 days in March, April, and May collecting on Cerro San Andrés, about 10 miles north-northwest of Ciudad Hidalgo in eastern Michoacán. This is the highest mountain in the state, with an elevation of just under 13,000 feet, and it is only 25 miles airline from Puerto Lengua de Vaca. I hunted in several types of habitat between 8,000 and 10,000 feet, including what appeared to be ideal habitat for *stricklandi*, but found only *villosus*. It seems possible that *stricklandi* is adapted primarily to elevations above 10,000 feet, but ranges marginally to lower elevations. *D. villosus* may be adapted to middle elevations, perhaps from 7,000 to 9,000 feet, but ranges marginally above and below these limits. Thus, *villosus* and *stricklandi* overlap marginally at some localities. The failure of *stricklandi* to occur west of its present limits is difficult to explain in terms of competition with *villosus* since the two are sympatric at a number of places. It may be that climatic factors limit the range of *stricklandi*, as habitat which appears suitable occurs west of its present range.

The last member of the genus to be considered here, *scalaris*, does not seem to influence the distributions of *arizonae*, *stricklandi*, or *villosus*. However, the mere fact that the breeding range of *scalaris* overlaps at all with the breeding range of *arizonae*, and especially with that of *villosus*, represents a situation so different from its intrageneric relations in the United States that a few remarks may not be inappropriate. Voous (1947: 96-97), noting that this species has been recorded in riparian woodland, city parks, and other wooded situations, in addition to the deserts which constitute its nearly exclusive habitat in the United States, concluded that *scalaris* was originally a forest bird that had been driven from its original forest home and into the desert regions by successive woodpecker invasions from the north during glacial periods. He also briefly mentioned possible competition with the Downy Woodpecker (*Dendrocopos pubes-*

TABLE 2
MEAN RATIOS OF DIMENSIONS TO CUBE ROOT OF BODY WEIGHT
(EXPRESSED AS PERCENTAGES OF THE GREATEST)

<i>Sample</i>	<i>Wing</i>	<i>Tail</i>	<i>Bill</i>	<i>Tarsus</i>
Arizona Combined and Northwestern Mexico	95.5 (7) ¹	93.5 (4)	100.0 (11)	100.0 (10)
Tzitzio-Las Trojes	95.4 (9)	87.5 (9)	92.6 (9)	97.3 (9)
México	100.0 (16)	100.0 (15)	76.8 (15)	96.0 (18)

¹ N in parentheses; males only.

dens), as noted in Bent (1939: 84), as a possible factor in limiting its range. I think that this last point could be elaborated further.

The ranges of *scalaris* and *pubescens* in the United States are mutually exclusive if one overlooks the overlap, in California, between *pubescens* and *nuttallii*, which is surely a very close relative of *scalaris*. Even between these two, however, there is a well-marked ecologic separation. Grinnell and Miller (1944: 243, 245) state that *D. p. turati*, the race of the Downy Woodpecker that is sympatric with the Nuttall's Woodpecker, is "markedly restricted to riparian soft-woods, willow and cottonwood" and that *nuttallii* inhabits "typically, interior, rather dry, foothill belts of oaks." They note that there is occasional local invasion of the habitat of one species by the other, and also that there is local use of orchards by both species (orchards, of course, representing man-made habitat), but the great majority of individuals is separated ecologically. In United States *scalaris* is primarily a bird of the desert regions, areas into which penetration by *pubescens* is marginal, at best. But south of the United States, in the absence of *pubescens*, *scalaris* occupies a wide variety of habitats other than the deserts. It has been recorded in the thorn scrub of the Sinaloan lowlands (El Molino, Reforma), on the humid coast of Nayarit (San Blas), and in pine-oak and pine woodland, as on Cerro de Tancítaro and at Las Trojes in Michoacán, and it ranges from sea level to at least 7,100 feet. On the Yucatán Peninsula it "ranges from the coastal scrub to moderately high deciduous forest, and occasionally into the zone of rain forest, where there are clearings" (Paynter, 1955: 168). It seems likely that the absence of competition with *pubescens* has allowed *scalaris* to occupy a wider variety of habitats than it does to the north and that this has brought the species into occasional contact with both *arizonae* and *villosus* in the breeding season.

VARIATION IN SIZE

Table 2 shows the ratios of dimensions to cube root of body weight for the three samples for which sufficient weight data were available. The

ratios were calculated for each specimen and for ease of comparison the mean ratios for each sample were multiplied by the factor necessary to increase the largest to 100 (Amadon, 1943: 172-173). The data presented in Table 2 thus indicate the relative, not absolute, development of the lengths of wing, tail, bill, and tarsus in the three samples.

Considering bill length first, it is evident that the bill is relatively long in the northwesternmost sample, of moderate length in the Tzitzio-Las Trojes sample, and extremely short in the México sample. The most probable factor affecting geographic variation in bill length in *arizonae* is the restriction of that form to woodland increasingly dominated by oaks, and less by pines, from southeast to northwest. In the northwestern part of its range, *arizonae* forages to a large degree, perhaps primarily, on an oak-inhabiting entomofauna. Larval and adult insects inhabiting oaks tend to be relatively deeply buried, since they do not favor the bark and cambium of oaks as sites of residence. Insects inhabiting pines, on the other hand, tend to a much greater degree to occur in bark and cambium. Thus, the birds in the northwest must dig more deeply for a substantial part of their food and presumably this accounts for the relatively greater development of the bill in the birds of that area. In the southeastern part of the range, in Michoacán, where the birds occupy virtually pure pine woodland, a great part of the diet is obtained from relatively superficial sites.

The significant decrease in mean bill lengths between the Arizona Combined and Northwestern Mexican samples (Table 3) suggests that the latter population depends more on pines as foraging sites. Vegetationally, at least, this suggestion is supported by the surveys made by Marshall (1957). His figures 18 and 20 (1957: 32, 34) show the increasing prominence of pine-oak woodland and the decreasing prominence of encinal from north to south. In extreme northeastern Sonora and extreme northwestern Chihuahua, encinal has become much restricted and coniferous forest has become more prominent. Brand (1936: map) shows in less detailed fashion a similar shift in the proportions of "oak-agave-juniper" and "pine forest" from northern Sonora and northern Chihuahua southeast to southern Sinaloa and southern Durango. Presumably, then, there is almost a steadily increasing dependence on pines as foraging sites to the southeast, with a concomitant decrease in bill length. Although adequate information is lacking on the foraging sites used by *arizonae* in the area from Sonora to Jalisco, the terminal population, in the Tzitzio-Las Trojes area, with the smallest bill of all, is confined to virtually pure pine woodland and almost all individuals recorded foraging were doing so in pines.

TABLE 3
BILL LENGTH IN MILLIMETERS

Sample	Sex	N	Mean	Standard error	Standard deviation	Coefficient of variation
Arizona Combined	♂	126	22.43	0.10	1.16	5.17
	♀	79	19.25	0.10	0.89	4.62
Santa Rita	♂	30	22.65	0.21	1.17	5.17
	♀	17	18.98	0.27	1.12	5.90
Huachuca	♂	55	22.37	0.16	1.18	5.27
	♀	40	19.32	0.13	0.81	4.19
Chiricahua	♂	41	22.36	0.18	1.12	5.01
	♀	22	19.34	0.18	0.83	4.29
Northwestern Mexico	♂	20	21.60	0.16	0.73	3.38
	♀	14	18.98	0.17	0.64	3.37
Northern Sinaloa	♂	29	20.28	0.18	0.97	4.78
	♀	27	17.84	0.20	1.06	5.94
Southern Sinaloa	♂	11	19.48	0.33	1.10	5.65
	♀	15	16.49	0.14	0.55	3.34
Nayarit	♂	15	18.96	0.27	1.06	5.59
	♀	9	16.49	—	—	—
Western Michoacán	♂	9	18.59	—	—	—
	♀	8	15.30	—	—	—
Tzitzio	♂	11	18.46	0.20	0.66	3.58
	♀	10	16.26	0.26	0.81	4.98
México	♂	34	15.94	0.11	0.66	4.14
	♀	23	14.55	0.14	0.68	4.67
Veracruz	♂	5	16.24	—	—	—
	♀	8	14.69	—	—	—

This same difference in relative dependence on oaks versus pines may account for similar variation in bill size between other species of *Dendrocopos*. For example, according to measurements given by Ridgway (1914), 10 "adult" (that is, not in juvenal plumage) male Nuttall's Woodpeckers, oak-dependent birds, had mean wing, tail, tarsal, and bill (exposed culmen) lengths of 102.7, 63.8, 18.4, and 20.8 mm, respectively, whereas 21 "adult" Red-cockaded Woodpeckers (*D. borealis*) from all parts of the range of that pine-dependent species had corresponding measurements of 118.7, 75.5, 20.2, and 21.4 mm. The wing length of *nuttallii* is 86.5 per cent that of *borealis*, tail length is 84.5 per cent, tarsal length is 91.1 per cent, but bill length is 97.2 per cent. Since *borealis* is a heavier bird than *nuttallii* (see Norris and Johnston, 1958: 116, for weights of *borealis*, and Grinnell, Dixon, and Linsdale, 1930: 261, for weights of *nuttallii*), it is evident that the bill is relatively much smaller in *borealis*, presumably because this species obtains a large percentage of its diet from pines (Beal, 1911: 22-23; Beal, McAtee, and Kalmbach, 1927).

The still further decreases in bill length in *stricklandi*, absolute and relative (Tables 2 and 3), may be a result of the primarily coniferous nature of its habitat, reinforced by the influence of higher altitude and

TABLE 4
WING LENGTH IN MILLIMETERS

Sample	Sex	N	Mean	Standard error	Standard deviation	Coefficient of variation
Arizona Combined	♂	107	115.04	0.18	1.90	1.65
	♀	77	111.75	0.23	1.98	1.77
Santa Rita	♂	27	114.34	0.32	1.67	1.46
	♀	16	111.46	0.47	1.88	1.69
Huachuca	♂	44	114.84	0.31	2.05	1.79
	♀	39	111.53	0.32	2.00	1.79
Chiricahua	♂	36	115.80	0.30	1.82	1.57
	♀	22	112.35	0.42	1.96	1.74
Northwestern Mexico	♂	16	115.11	0.58	2.33	2.02
	♀	13	111.62	0.34	1.21	1.08
Northern Sinaloa	♂	22	110.80	0.37	1.73	1.56
	♀	23	109.53	0.45	2.17	1.98
Southern Sinaloa	♂	8	109.17	—	—	—
	♀	11	108.88	0.60	1.99	1.83
Nayarit	♂	10	110.43	0.72	2.26	2.05
	♀	5	106.06	—	—	—
Western Michoacán	♂	11	107.53	0.65	2.15	2.00
	♀	6	105.53	—	—	—
Tzitzio	♂	11	105.40	0.45	1.49	1.41
	♀	12	103.02	0.34	1.19	1.16
México	♂	34	114.19	0.35	2.05	1.80
	♀	23	111.13	0.48	2.31	2.08
Veracruz	♂	5	114.34	—	—	—
	♀	8	111.42	—	—	—

concomitant lower environmental temperatures, in conformity with "Allen's Rule," which states that blood-supplied protruding parts such as bill or tarsus are shorter in warm-blooded vertebrates in colder than in warmer climates (for a discussion of the validity of the "ecological rules," see Mayr, 1956). In view of the lack of vigorous hammering done by the birds observed by Elliott on the Morelos-Distrito Federal boundary and by the birds I observed at Puerto Lengua de Vaca, I am tempted to add that foraging method may also exert an important selective force toward small bill size in *stricklandi*, but lengthy observations on foraging at different seasons would have to be made in order to determine this. However, the possibility warrants further investigation.

Wing length in *arizonae*, decreasing clinally from northwest to southeast (Table 4, Figures 4 and 5) is apparently correlated with a general decrease in body size (Table 2). Tail length, decreasing clinally from northwest to southeast in *arizonae* (Table 5, Figures 4 and 5), is relatively shorter in the Tzitzio-Las Trojes sample than in the northwestern sample. The reason for this is not clear.

The sharp reversal in *stricklandi* of the clines of decreasing wing and tail lengths (Tables 4 and 5, Figures 4 and 5) is apparently independent of any weight difference between the Tzitzio-Las Trojes and México

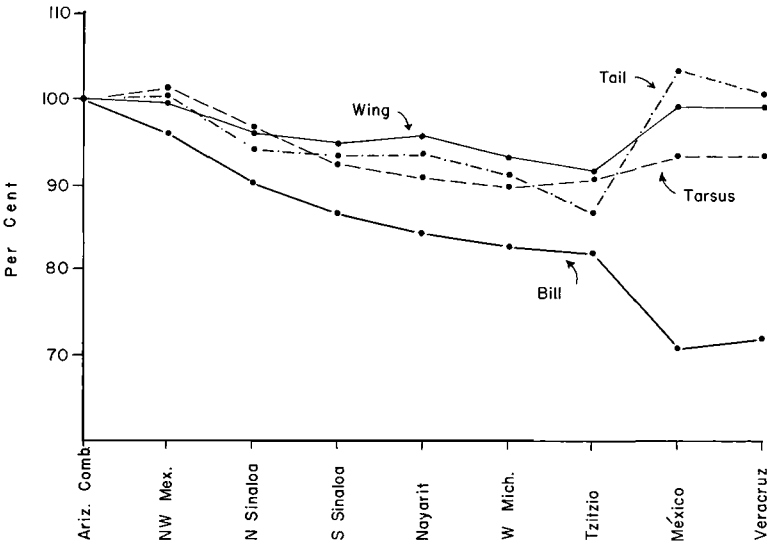


Figure 4. Geographic variation in dimensions, expressed as percentages of the mean lengths of the Arizona Combined sample (= 100 per cent). Males only.

samples (Table 2). The most likely explanation for the relatively great development of the wing and tail in *stricklandi* is that the greater expansion of these flight surfaces may represent an adaptation for flight in the thinner atmosphere of high altitudes (see Hamilton, 1961: 185 for a discussion of air pressure as a selective force on wing size).

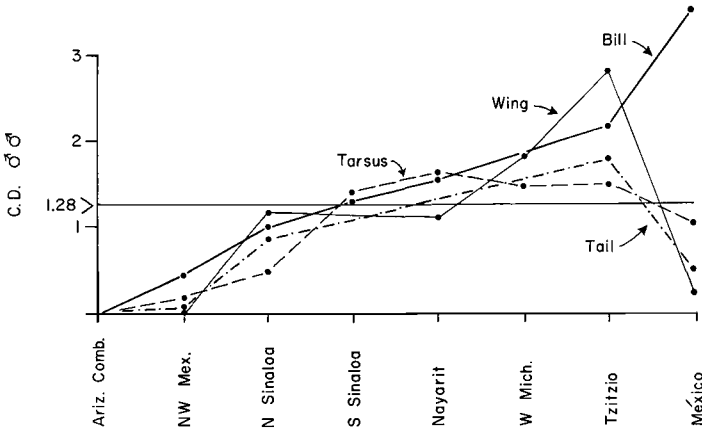


Figure 5. Geographic variation in dimensions expressed as coefficients of difference between the Arizona Combined sample and each successive sample to the southeast. Males only.

TABLE 5
TAIL LENGTH IN MILLIMETERS

Sample	Sex	N	Mean	Standard error	Standard deviation	Coefficient of variation
Arizona Combined	♂	88	68.11	0.28	2.61	3.83
	♀	58	67.30	0.32	2.45	3.64
Santa Rita	♂	22	67.20	0.46	2.16	3.21
	♀	8	66.72	—	—	—
Huachuca	♂	38	68.10	0.41	2.50	3.67
	♀	34	67.17	0.41	2.38	3.54
Chiricahua	♂	28	68.84	0.55	2.90	4.21
	♀	16	67.87	0.72	2.89	4.26
Northwestern Mexico	♂	11	68.25	0.68	2.25	3.30
	♀	7	67.13	—	—	—
Northern Sinaloa	♂	17	64.29	0.46	1.91	2.97
	♀	21	64.76	0.50	2.28	3.52
Southern Sinaloa	♂	6	63.68	—	—	—
	♀	12	65.02	0.67	2.33	3.58
Nayarit	♂	6	63.93	—	—	—
	♀	2	61.65	—	—	—
Western Michoacán	♂	6	62.32	—	—	—
	♀	4	59.92	—	—	—
Tzitzio	♂	9	59.21	0.79	2.37	4.00
	♀	8	60.20	0.99	2.81	4.67
México	♂	26	70.63	0.47	2.41	3.41
	♀	20	69.24	0.51	2.30	3.32
Veracruz	♂	3	68.83	—	—	—
	♀	3	67.50	—	—	—

Geographic variation in tarsal length is less pronounced than in any other dimension considered (Table 6, Figures 4 and 5). The cline in tarsal length coincides, in general, with those in other dimensions in *arizonae*. The very slight differences in relative tarsal length among the three samples for which data are presented in Table 2 are probably not significant.

As regards weight, which may be considered a reasonably good indicator of over-all body size, there are wide differences among the three samples which have been considered (Table 7). There is a highly significant difference in weight between the Arizona Combined-Northwestern Mexican sample on the one hand and Tzitzio-Las Trojes on the other (C. D. = 2.35, joint nonoverlap 99.1 per cent). Between the northwestern-most sample and México, the difference is somewhat less but it is still highly significant (C. D. = 1.52, joint nonoverlap 93.6 per cent). Between Tzitzio-Las Trojes and México, the amount of joint nonoverlap is not significant, but there is a significant difference in mean weight between the two samples.

The considerable difference in weight between the northwestern and Tzitzio-Las Trojes samples may result from any one, or any combination,

TABLE 6
TARSAL LENGTH IN MILLIMETERS

Sample	Sex	N	Mean	Standard error	Standard deviation	Coefficient of variation
Arizona Combined	♂	121	19.48	0.06	0.65	3.34
	♀	74	18.43	0.07	0.61	3.31
Santa Rita	♂	28	19.64	0.12	0.61	3.11
	♀	18	18.40	0.09	0.38	2.07
Huachuca	♂	52	19.54	0.09	0.67	3.43
	♀	37	18.44	0.13	0.79	4.28
Chiricahua	♂	41	19.30	0.10	0.62	3.21
	♀	19	18.42	0.08	0.34	1.85
Northwestern Mexico	♂	18	19.73	0.16	0.67	3.40
	♀	14	18.28	0.13	0.49	2.68
Northern Sinaloa	♂	29	18.77	0.17	0.94	5.01
	♀	26	17.96	0.16	0.84	4.68
Southern Sinaloa	♂	11	18.00	0.12	0.41	2.28
	♀	14	17.19	0.10	0.39	2.27
Nayarit	♂	12	17.72	0.13	0.46	2.60
	♀	9	17.30	—	—	—
Western Michoacán	♂	11	17.54	0.20	0.66	3.76
	♀	8	17.04	—	—	—
Tzitzio	♂	11	17.75	0.15	0.50	2.82
	♀	12	17.18	0.08	0.29	1.69
México	♂	35	18.19	0.09	0.56	3.08
	♀	22	17.74	0.14	0.64	3.61
Veracruz	♂	5	18.26	—	—	—
	♀	6	17.78	—	—	—

of three factors. First, the increased weight of the northwestern birds may be a reflection of selection pressures operating in accordance with "Bergmann's Rule," which states that individuals of a species of warm-blooded vertebrate in the cooler portions of the species' range are on the average larger than individuals resident in the warmer parts of the range, in line with conservation of heat because of a more favorable surface/volume ratio. It seems likely that a gradient of increasingly cooler climate exists along the range of *arizonae* from southeast to northwest, with an accompanying parallel increase in weight of the populations distributed along the gradient. Second, Salt (1963) has recently brought forward evidence that in some 53 species of western North American birds there is a "species center," at which the birds are least in weight, and that there are gradients of increasing weight radiating out in all directions from the species center. Salt presents evidence that "the greatest degree of specific adaptation to habitat conditions exists at the center, and that larger size represents a mechanism for nonhabitat specific increase in efficiency as a temporary adaptation to new conditions pending evolution of specific adaptation to the individual conditions in the newly occupied habitat" (1963: 905-906). Since it seems probable that the *stricklandi*

TABLE 7
WEIGHTS IN GRAMS OF THREE SAMPLES OF MALES

<i>Sample</i>	<i>N</i>	<i>Mean</i>	<i>Standard error</i>	<i>Standard deviation</i>	<i>Coefficient of variation</i>
Arizona Combined and Northwestern Mexico	11	48.95	0.77	2.54	5.19
Tzitzio-Las Trojes	9	37.89	0.72	2.17	5.73
México	19	40.75	0.66	2.86	7.02

complex originated in the highlands of central Mexico, as will be suggested in more detail later, the northwestern populations would be recently arrived in their present range, and the presumed history of *arizonae* is thus compatible with the hypothesis advanced by Salt. Third, as has been demonstrated, the bill of *arizonae* is relatively better-developed in the northwesternmost populations in accordance with the nature of their primary foraging sites. It may well be that at least part of the increase in size at the northwestern extreme of the range is associated with this greater development of the bill. In other words, the greater size of the oak-dependent birds of the northwest may be in part to provide the strength needed to operate the relatively large bill efficiently.

The increase in weight of the México sample over Tzitzio-Las Trojes may represent an increase in body size in response to the cooler climate at the higher elevations at which *stricklandi* is found, in accordance with Bergmann's Rule.

SEXUAL DIMORPHISM IN SIZE

Selander and Giller (1963: 261-266) have discussed sexual dimorphism in size in a number of species of woodpeckers, especially in the genus *Centurus*. In the great majority of these species, sexual dimorphism in bill length is greater than that in any other size character. The same is true of *Dendrocopos stricklandi* (Figure 6). It is also true of the populations of *D. villosus* and *D. scalaris* resident in southwestern United States and adjacent Mexico, and of *D. nuttallii* (representing another oak-dependent species) and *D. borealis* (representing another pine-dependent form), as shown in Figure 7. In *nuttallii* and *borealis* sexual dimorphism in bill size is not as great as in *villosus* and *scalaris* but dimorphism in wing and tail lengths is also sharply reduced; indeed, in the three cases in which the difference between males and females in bill length falls below 10 per cent (*nuttallii*, *borealis*, and *D. v. icastus*), difference in wing length falls below 1 per cent, and in *nuttallii* and *borealis* there is no difference between males and females in tail length, so that relatively the disparity between the sexes in bill length is as great as in the other populations considered.

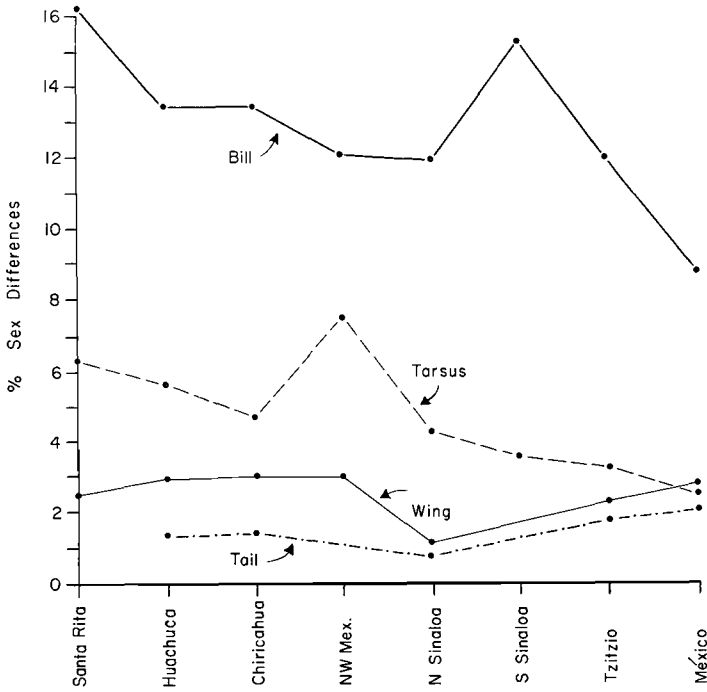


Figure 6. Percentages of sex difference in four dimensions in *Dendrocopos stricklandi* for samples in which there were at least 10 specimens of each sex.

Some workers have regarded accentuated sexual dimorphism in the size of structures associated with foraging and feeding as adaptive in that such differences would serve to decrease competition for food between the sexes and would broaden the spectrum of size of food items usable by a given population as a whole. In most birds, bill size would probably be the most important size character involved. The evolution of accentuated sexual dimorphism in a given character is one means of increasing the variability of that character in any population. But another method would be the evolution of accentuated individual variability within each sex in the character concerned, with presumably increased variability of diet. It is of interest, then, that of the four size characters analyzed in this study, bill length is nearly always the most variable individually no matter what species is involved. To cite some carefully analyzed cases of variability in bill, wing, tail, and tarsal lengths, in jays of the genus *Aphelocoma*, variability was least in wing length, greater in tail length, still greater in tarsal length, and greatest in bill length (Pitelka, 1951: 363). Exactly the same order holds true for the brown towhees of the genus *Pipilo*

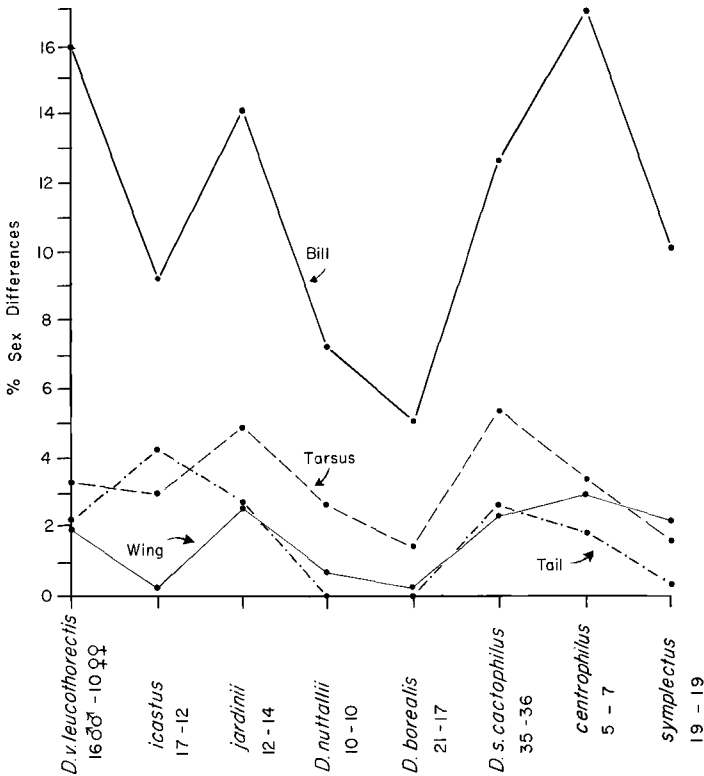


Figure 7. Percentages of sex difference in four dimensions in three races of *Dendrocoptes villosus*, *D. nuttallii*, *D. borealis*, and three races of *D. scalaris*. Hyphenated pairs of numbers indicate numbers of males and females in each sample. Data from Ridgway (1914).

(Davis, 1951: 92). In sparrows of the genus *Junco*, the order is only slightly different: wing, tarsus, tail, and bill (Miller, 1941: 365-367). In *Dendrocoptes stricklandi* the order is the same as that in *Junco* (Table 8). No doubt many other examples could be cited.

Since it has been shown that there can be significant seasonal variation in bill length in a number of passerine species that shift their diets seasonally (Davis, 1954), one might conclude that such high coefficients of variability in samples analyzed for bill length result from the use of impure samples for analysis. However, samples used for analysis of variation in wing and tail lengths are rarely pure, either, because of wear, and it seems unlikely that the greater variability in bill length found in so many species is based on a sampling artifact. Surely in *D. stricklandi* it is not, as it has been demonstrated that the seasonal

TABLE 8
MEAN COEFFICIENTS OF VARIATION

<i>Dimension</i>	<i>Sex</i>	<i>N</i>	<i>Mean C.V.</i>
Wing	♂	9	1.74
	♀	8	1.67
Tarsus	♂	10	3.27
	♀	8	2.89
Tail	♂	7	3.54
	♀	6	3.81
Bill	♂	9	4.73
	♀	8	4.58

variation in bill length is not significant (page 540). It would seem, rather, as though we are dealing with a population characteristic of adaptive value, and that this variability may perhaps be the basic means of minimizing competition for food in most populations of birds. In species that have more specialized foraging niches, with a concomitant narrowing of the spectrum of usable food items, and surely woodpeckers are more specialized foragers than *Aphelocoma*, *Pipilo*, and *Junco*, the accentuated sexual dimorphism in bill length may serve to supplement individual variability as a method of lessening competition for food.

VARIATION IN COLOR AND PATTERN

Phillips (1961: 343) stated that the population of *arizonae* from Zacatecas to the Nevado de Colima, on the boundary between Colima and Jalisco, and thence presumably east to Michoacán, is darker and sootier (less brown) than are the birds from Arizona south to Jalisco. I agree that there is a slight tendency for the birds at the southeastern extreme of the range to be somewhat darker than specimens collected farther north, but this is an ill-defined tendency at best. When I compared specimens of similar wear and date of collection, I found considerable variation in dorsal coloration in nearly every sample and I was unable to make out any well-marked cline in increasing darkness from northwest to southeast.

In pattern, three characters may be discussed in *arizonae*: the amount of ventral spotting, the size of the white spots on the outer webs of the primaries, and the nature of the white markings on the back and rump. Ridgway (1914: 263) redescribed the race *fraterculus*, which includes the southeastern populations of *arizonae*, as "Similar to *D. a. arizonae* [of the northwest], but smaller, averaging more heavily spotted beneath, and with white spots on outer webs of primaries smaller (sometimes obsolete)."

As regards the amount of ventral spotting, I can see no consistent difference among the samples from all parts of the range when birds in a

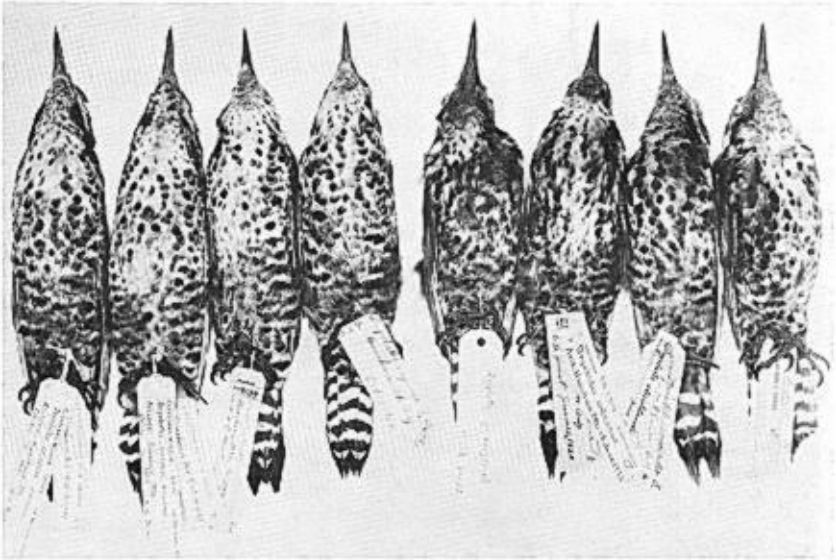


Figure 8. Specimens of *D. s. arizonae* from the Huachuca Mountains, Cochise County, Arizona, the four on the left collected in October, the four on the right collected in June. The accentuation of ventral spotting because of wear is clearly shown.

similar stage of wear are compared. As Swarth (1904: 12) noted correctly, the effect of wear on the appearance of ventral spotting is pronounced, and birds in fresh plumage appear much paler and far less heavily spotted below than do worn birds (Figure 8). As feather wear proceeds, the broad white edges of the outermost layer of spotted feathers are eroded, exposing the spots on the underlying feathers. The process continues from layer to layer of the spotted feathers until the entire ventral aspect of the individual appears darker and more heavily spotted. I suspect that Ridgway compared birds in different stages of wear.

As regards the size of the white spots on the outer webs of the primaries, here again there is a great amount of individual variation within all samples and I cannot make out any particular trend in the variation of this character.

The best marked geographic variation in pattern is found in the nature of the white tipping, barring, or spotting on the feathers of the back (exclusive of the scapulars) and rump (Figures 9 and 10). In a few specimens of both *arizonae* and *stricklandi* I found some white markings on the scapulars; such marks are characteristic of such species of *Dendrocopos* as *muttallii* and *scalaris* (which are, of course, also heavily barred

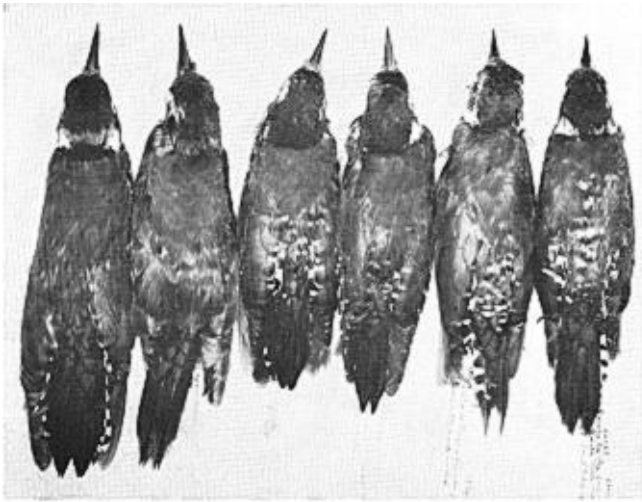


Figure 9. White-barred variants in the *arizonae* complex. From left to right: a "pure" individual from the Huachuca Mountains, Arizona; a male from northern Chihuahua; two females, La Pisagua and Volcán de Nieve, both in Jalisco; two females, from near Tinguindín and from near Ario de Rosales, western and central Michoacán, respectively.

on the interscapular region, lower back, and rump). I think these scapular markings in *arizonae* and *stricklandi* are the infrequent expression of genetic factors common to many species of *Dendrocoptes*, and I do not believe that they are significant in any other regard.

Although *arizonae* was described by Hargitt (1886: 115) as uniformly colored above, and although nearly all subsequent authors have described the bird in this fashion, the presence of white-marked variants in the northwestern populations has been known for many years. J. A. Allen (*in* Scott, 1886: 426, footnote), stated: ". . . it may be remarked that in his series of 21 specimens [Scott's series of *arizonae* from the Santa Catalina Mountains, Arizona], about one-fourth of them show more or less distinct white bars on the rump, irrespective, apparently, of sex or age. In some examples these bars are quite conspicuous; but none of them show [*sic*] any white bars on the interscapulars." Swarth (1904: 12) stated: "Of twenty-four specimens from this region [the Huachuca Mountains of Arizona] four show more or less traces of white bars across the rump; one of these is a male in nuptial plumage, one a male in freshly acquired autumnal plumage, one a female in nuptial plumage (this specimen has some faint indications of white bars on some of the scapulars as well), and one is a young male. Another spring female has some white bars on the scapulars but none on the rump. Presumably this is a tendency toward the Mexican species *Dryobates stricklandi*."

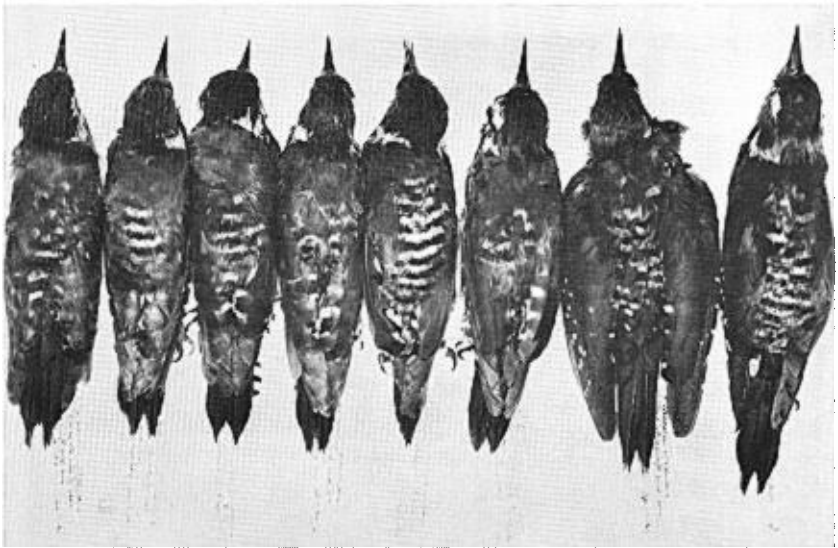


Figure 10. Seven white-barréd variants from the Tzitzio-Las Trojes area, and on the right, a specimen of *D. s. aztecus* from Huitzilac, Morelos.

In a previous paper (Davis, 1953: 92), I noted that five of the seven specimens of *arizonae* that had been collected three miles north of Tzitzio in 1939 and 1951 had barring on the back, rump, or both; two of these were described as having dorsal bars nearly as wide as those of *stricklandi*. These latter specimens are the sixth and third from the left of those shown in Figure 10. I also described three white-barréd specimens in a series of four in the Moore Collection that had been collected near Uruapan, western Michoacán, and I noted that 10 of 64 specimens in the Moore Collection, ranging from Chihuahua to Jalisco, showed some white marking on the back, rump, or both.

In the present study, any specimen of *arizonae* showing white tipping, barring, or spotting on even a single feather of the back (exclusive of the scapulars) or rump was considered to show variation toward the back or rump pattern of *stricklandi*. This "all or none" approach was considered necessary, since all degrees of white back and rump marking could be found, from specimens with only a single white-marked feather to the most extreme of those shown in Figure 10; it would be completely arbitrary to decide on a particular number of feathers as a minimum indication of variation towards *stricklandi*. Specimens with white marks on the scapulars only were not considered. Undoubtedly the totals to be presented would have been higher if each specimen had been seen in fresh plumage, as the extreme wear to which woodpeckers are subjected in

the course of the year would be more than enough to remove the white tip or subterminal bar from a single feather.

Of 488 specimens for which the presence or absence of white dorsal marking was recorded, 291 of both sexes and both age groups (juvenal plumaged birds and "adults"), or 59.6 per cent, showed one or more white-marked back or rump feathers. Of 394 "adults," 243, or 61.7 per cent, showed white markings. Of 94 juvenals, 48, or 51.1 per cent, were positive for this character. Of "adult" males and females, 55.0 and 70.9 per cent were positive, respectively; the corresponding percentages for juvenal males and females were 44.3 and 63.6, respectively. These figures suggest strongly that the expression of white dorsal markings is sex-influenced. Further evidence of this is found in the fact that of the seven heavily marked specimens from the Tzitzio-Las Trojes area shown in Figure 10 five are female, one is a male, and one is of undetermined sex, although in male plumage. At best, the ratio of males to females is two to five. Figures 9 and 10 show 12 of the 13 most heavily marked specimens of *arizonae*; of these 13, 4 are male (including the one of undetermined sex) and 9 are female. One must assume either that the frequency and strength of expression of white dorsal marking in *arizonae* is sex-influenced or that the white-marked males are selected against. I found no evidence of any imbalance in sex ratio in the Tzitzio-Las Trojes population and it seems more likely that sex influence, possibly through hormonal control, is the controlling factor.

The geographic variation in the frequency of occurrence of "adult" white-marked variants is presented in Table 9. The only samples that are out of line are Northwestern Mexico and Nayarit. Otherwise, there is a well marked trend toward increasing frequency of white-marked variants from northwest to southeast. This trend parallels that for strength of expression of white marking; of the 13 most heavily marked specimens, 1 is from Chihuahua, 3 are from Jalisco, and 9 are from Michoacán.

The pattern of geographic variation in the *stricklandi* group is relatively simple. Moore (1946: 104), describing *Dendrocopos stricklandi aztecus* from Puerto Lengua de Vaca, stated that this form differed from the nominate race of Puebla and Veracruz in having much reduced streaking on the underparts, blacker (less brownish) upper parts, and the white of the anterior back extending farther forward. The only differentiation that I can see, which is quite noticeable, involves the first character. The blacker upper parts probably resulted from comparison of the type series of *aztecus*, collected in October, 1941, and therefore in fresh plumage and only five years in the tray at the time *aztecus* was described, with specimens collected in 1892 and 1893, and therefore undoubtedly somewhat foxed. (Although Moore did not give the year in which these specimens

TABLE 9
FREQUENCY OF WHITE-BARRED VARIANTS
ADULTS ONLY, BOTH SEXES

<i>Sample</i>	<i>Sample (N)</i>	<i>Variant (N)</i>	<i>Per cent variants</i>
Arizona Combined	211	121	57.3
Northwestern Mexico	34	26	76.5
Northern Sinaloa	55	32	58.2
Southern Sinaloa	26	18	69.2
Nayarit	23	10	43.5
Western Michoacán	20	16	80.0
Tzitzio	25	20	80.0

were collected, he noted that they were in the Biological Survey Collection and gave the months and days of collection, from which information I have been able to figure out the years.) Moore (1946: 105) noted a possible additional character differentiating the population at Puerto Lengua de Vaca, the "Apricot-Orange" coloration of the terminal fourth of the three outer rectrices, and he stated his belief that this coloration was not stain, since the birds were in fresh plumage. I have seen other specimens from farther east in Mexico with the same type of coloration, or, more likely, discoloration, and I feel that it is purely adventitious, perhaps resulting from tannin in the bark of oaks on which the birds were known to have foraged (Moore, *loc. cit.*).

VOCALIZATIONS

At Las Trojes and also three miles north of Tzitzio, the call note of *arizonae* was a clear, high-pitched *sweeek*, sometimes followed by a harsh rattle. The single call note could be differentiated from that of the associated *D. scalaris*, which was a less clear *chirk*. The rattle of *arizonae* was much harsher than a comparable whinnying series of notes sometimes given by *scalaris*, and the rattle maintained an even volume throughout whereas the whinny decreased in amplitude toward the end. The loud *chirk* and whinnying series of *D. villosus* also differed considerably from the corresponding calls of *arizonae*.

At Puerto Lengua de Vaca, although I had never met *stricklandi* in the field, I detected its presence at once as soon as it called, as its calls sounded exactly like those of *arizonae* in the Tzitzio-Las Trojes area. And again, I was able to detect the presence of *arizonae* the first time I heard one call at the Southwestern Research Station because the notes sounded identical to those I had heard given by both *arizonae* and *stricklandi* in Mexico. To my ear there was no detectable difference in call notes among these three populations. I agree with Phillips (1961: 343), that at least some of the calls of both forms are similar.

The drumming of both *arizonae* and *stricklandi* consists of a single, even roll. The very limited drumming of *stricklandi* in late May was noticeably weaker than that of *villosus* in the same area. Although the substrate against which the birds were drumming may have had something to do with this, I suspect that the considerable difference in bill size between the two species was responsible for most of the difference in volume.

SPECIES LIMITS

Since the description of *Picus arizonae* by Hargitt (1886: 115), the brown-backed populations of *Dendrocopos* distributed from Arizona to the state of Veracruz have been considered by most ornithologists to pertain to two species, *D. arizonae*, ranging from Arizona to Michoacán, and *D. stricklandi* (*P[icus]*. [*Leuconotopicus*] *Stricklandi* Malherbe 1845), found from the Michoacán-México boundary east to Puebla and Veracruz. In 1953, on the basis of heavily white-barred specimens which I collected three miles north of Tzitzio, Michoacán, and reported as *Dendrocopos arizonae* × *D. stricklandi*, I stated (Davis, 1953: 92): "In my opinion *arizonae* and *stricklandi* are geographic representatives of a single polytypic species." Later, Phillips (1959: 27), in listing a long series of genera and species which subspeciate to a greater degree in western United States and Mexico than in the north and east of North America, included in this list "*Dendrocopos scalaris* and *stricklandi* (including 'arizonae')." Although he presented no additional evidence on the relationships of *arizonae* and *stricklandi*, and indeed mentioned these birds nowhere else in this paper, he did agree tacitly with the opinion which I had expressed some years earlier. Most other authors have preferred to maintain *arizonae* and *stricklandi* as distinct species.

Phillips (1961: 343-345) presented what he considered important additional evidence supporting the thesis of conspecificity of *arizonae* and *stricklandi*. The first piece of evidence consisted of a specimen of *arizonae* with distinct traces of white bars on its rump ("con distintos trazos de barras blancas sobre la rabadilla . . .") collected in Jalisco. A full-page photograph of this specimen is presented (*op. cit.*: 344), legended "Ejemplar excepcional de *Dendrocopos stricklandi* procedente de Jalisco." I have examined this photograph carefully and I can make out two, and possibly three, white-barred rump feathers. Since such variants in *arizonae* were reported as early as 1886 (Allen *in* Scott, 1886), since far more conspicuously white-barred specimens were reported from Michoacán in 1953 (Davis, 1953), and since 291 of 488 specimens examined in this study show white barring (the great majority being at least as strongly marked as the specimen figured by Phillips), it is evident that the

“ejemplar excepcional” from Jalisco is anything but that and actually provides no additional information bearing on the problem of species limits in this complex of woodpeckers.

A second type of variation which Phillips felt constituted “mayor evidencia de coespecificidad” consisted of variation in dorsal color, with a presumed cline of increased darkness running from Arizona southeast and culminating in *stricklandi*. Thus, according to Phillips, there is a color cline connecting *arizonae* and *stricklandi* (“corriendo a través de las 2 ‘especies’”). As I stated previously, I can make out no well-defined cline of increasingly dark dorsal coloration in *arizonae*. I can see only a small increase in the frequency of occurrence of slightly darker individuals to the southeast. To try to express my views more specifically, as a taxonomist I would not recognize the race *fraterculus* of the southeastern part of the range of *arizonae* as valid if it were based on differences in dorsal color alone. Perhaps more importantly, the dorsal color of *stricklandi* is so dark and sooty that it is in a different class from that of *arizonae*. The darkest specimens of *arizonae* do not come anywhere near *stricklandi* in this character. This can be seen at once, even when 5 molting specimens of *arizonae* collected three miles north of Tzitzio in July, 1951 (Moore Collection)—and therefore individuals drawn from the southeasternmost population of *arizonae* (and bearing areas of the freshest possible dorsal plumage)—are compared with 11 specimens of *stricklandi* collected four miles by road southwest of Río Frío, México, in August, 1952 (Moore Collection). The latter, in fresh plumage, are strictly comparable as regards freshness of dorsal plumage and year of collection. The color difference between *arizonae* and *stricklandi* is so great that even if a cline of increasingly dark dorsal coloration did exist in *arizonae*, and culminated in *stricklandi*, there would be such a pronounced step in this cline between the two, and this step would coincide with such pronounced differences in pattern and size, that the difference in dorsal color could as well be used as an argument against, as for, conspecificity.

Schaldach (1963: 53–54), who listed specimens from the Volcanes de Colima, on the Colima-Jalisco boundary, and from the Sierra de Autlán, Jalisco, as *Dendrocopos arizonae fraterculus*, stated:

The Jalisco birds demonstrate an intermediate condition of the white barrings on the rump [italics mine], between these Lengua de Vaca *stricklandi* and typical *arizonae* of further [sic] north and west. It is the author's considered opinion, concurred in by Dr. [Allan R.] Phillips, that when more specimens become available from the mountain systems between Jalisco and the State of México, *arizonae* and its races will be found to be only subspecifically distinct from *stricklandi*, and that a cline culminating in the boldly barred birds of Puebla and Veracruz (typical *stricklandi*) will be found to exist.

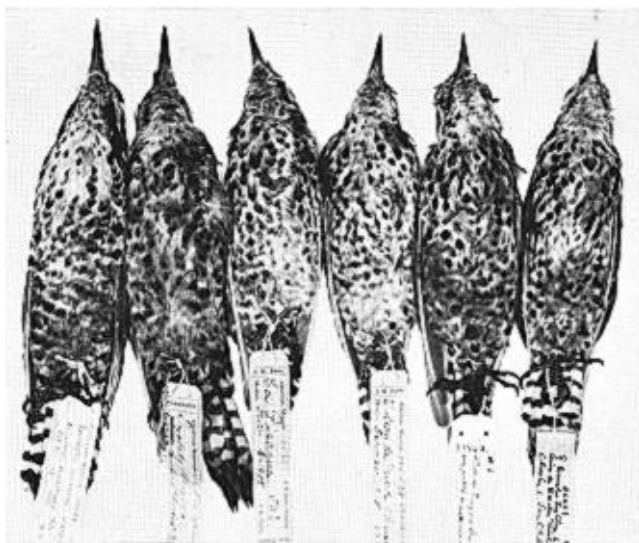


Figure 11. The birds shown in Figure 9, in ventral aspect; the order is the same.

In a sense, there is a cline of increasing dorsal barring from northwest to southeast, both in increasing frequency of white-barred variants (Table 9) and in the pronounced increase of heavily white-barred variants in Jalisco and Michoacán. As regards frequency, the cline is fairly regular. As regards heaviness of barring, there are really three discrete populations: a population with very few extreme variants, from Arizona to Nayarit; a population with a low frequency of such variants in Jalisco and Michoacán; and a population in which all individuals are heavily white-barred, *stricklandi*. One must not lose sight of the fact that heavily white-barred birds include only 28 per cent (7 of 25) of all specimens collected in the Tzitzio-Las Trojes area. To use a purer sample, of the 18 specimens collected in this area in 1961 (and this may be considered a very good sample of the population concerned), 5, or 27.8 per cent, were heavily white-barred.

Of the remaining 13 specimens, 4 have no white markings, and 9 have slight to moderate barring comparable to that shown by 59.6 per cent of all *arizonae* examined for this character. Thus, over 70 per cent of the specimens taken from this southeasternmost population of *arizonae*, located only 50 miles from the nearest population of *stricklandi*, have at best white markings comparable to those found in almost 60 per cent of *arizonae* from all parts of its range. If the frequency of occurrence of heavy dorsal barring could be considered clinal in any way, again there would be a major step in the cline between Tzitzio-Las Trojes and México.

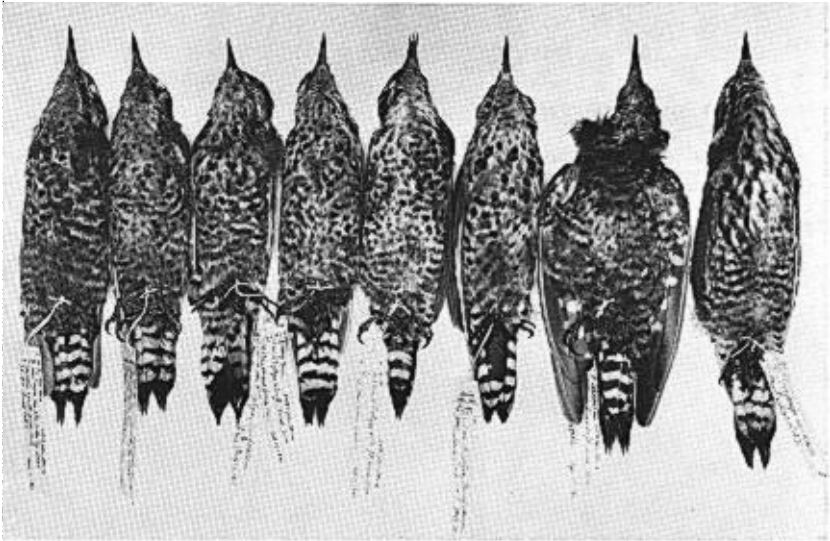


Figure 12. The birds shown in Figure 10, in ventral aspect; the order is the same.

In correspondence with Dr. Kenneth C. Parkes in 1953, shortly after I had described the heavily barred specimens collected near Tzitzio and reported the occurrence of variants showing weak expression of this character as far north as Chihuahua, I expressed the opinion that the pattern of variation in dorsal barring resulted from secondary contact between *arizonae* and *stricklandi* with subsequent introgression of *stricklandi* genes into the populations of *arizonae* to the north and west. Dr. Parkes, on the other hand, thought that white-barréd variants were so frequent and widespread in *arizonae* that it was more logical to think of genes for white barring as a normal component of an *arizonae* gene-pool. I now agree with Dr. Parkes. First, the presence of white-barréd variants is so frequent in the much more abundant material used in this study that one must conclude that most specimens of *arizonae* show this character to some degree. Second, no approach to *stricklandi* in pattern of the underparts is evident in any specimen of *arizonae*, including the most heavily barréd ones (Figures 11 and 12). Third, if secondary contact had occurred between *arizonae* and *stricklandi*, one might expect unusually great variability in dimensions in the Tzitzio-Las Trojes sample. But the coefficients of variation for lengths of culmen, wing, tail, and tarsus in this sample are within the ranges of the coefficients of variation for these dimensions in the other samples of *arizonae*. Actually, the coefficient of variation for bill length in the Tzitzio-Las Trojes sample is the next to lowest in the eight samples in which the measurements of this dimension

were treated statistically; that for wing length is the lowest of eight; that for tail length is the next to highest of six; and that for tarsal length is the third lowest of nine. Only in tail length does variability seem unusually high, and in general the Tzitzio-Las Trojes sample shows less variability in size than any other. In other words, if we are to assume secondary contact and subsequent introgression to the northwest, then this would involve only dorsal barring and neither dimensions nor ventral pattern. This seems quite unlikely.

The increase in dorsal barring from northwest to southeast, both in frequency of occurrence and intensity of expression, presumably follows an environmental gradient or set of gradients in much the same fashion as do the clines which have been demonstrated for size characters in *arizonae*.

Another point of difference between *arizonae* and *stricklandi* is in the more extensive red on the heads of adult males of the latter group. As pointed out by Ridgway (1914: 259, 261), the occiput and upper nape of male *stricklandi* are red, whereas the red in male *arizonae* is restricted to a nuchal crescent. There is some variation in both populations, but most individuals can be separated on the basis of this character.

A character that may be indicative of close relationship between *arizonae* and *stricklandi* is the darkness of the crown and nape of *arizonae*, exclusive of the red head markings of males. This contrasts sharply with the paler brown of the rest of the dorsum; it can be discerned in the specimens in Figures 9 and 10. "Make" of skin can cause variation in the extent of the dark area on the nape. Ridgway (1914: 261) mentions this character in his description of *arizonae*. Swarth (1904: 12) stated that birds in fresh fall plumage are of practically uniform coloration above, but that the pileum and nape do not seem to fade as the dorsum does, so that the contrast results from differential fading. I do not agree with this, as the great majority of freshly molted birds that I have examined show a decided contrast between the darker pileum and nape on the one hand, and paler dorsum on the other. There is no recognizable geographic trend in the darkness of the pileum and nape, but there is considerable variation within all samples. Nevertheless, this darker coloration is a character of the entire *arizonae* group and it mitigates the idea that *arizonae* is entirely pale above as opposed to *stricklandi*, which is entirely dark and sooty dorsally. Some of the darker specimens of *arizonae* actually approach the dorsal coloration of *stricklandi* on their crowns and napes. If head color is controlled by one set of genes, and back color by another, then the darker head coloration of *arizonae* may represent another point of genetic similarity between that form and *stricklandi*.

As evidence in favor of conspecificity of these two forms, one may cite the following points:

1. The wide distribution and frequent occurrence of white-barred variants throughout the range of *arizonae* indicate genetic similarity between the two groups in this character.
2. The head and nape of *arizonae* approach the dorsal coloration of *stricklandi* in darkness and sootiness, suggesting that the two groups are genetically similar as regards ground color of the head.
3. At least some of the vocalizations of the two are similar.
4. Ecologically, *arizonae* shows a greater range of variation from northwest to southeast than exists between *arizonae* in the southeast and *stricklandi*.
5. The difference in dorsal pattern between the unbarred individuals of *arizonae* on the one hand, and *stricklandi* on the other, would not interfere with pair formation should the two groups ever come together, at least as far as *arizonae* is concerned, since two mixed pairs of *arizonae* were collected near Tzitzio. One consisted of a heavily barred male and an unbarred female, and the other consisted of an unbarred male and a heavily barred female.

As evidence for retaining the two groups as distinct species, one may cite the following points:

1. There is complete discontinuity between the two forms in ventral pattern.
2. The clines of decreasing wing and tail lengths from northwest to southeast in *arizonae* are strongly and significantly reversed in *stricklandi*. There is also a marked decrease in bill length between the southeasternmost population of *arizonae* and *stricklandi*.
3. There is a marked difference between *arizonae* and *stricklandi* in body proportions.
4. There is a marked difference between *arizonae* and *stricklandi* in dorsal coloration, exclusive of the pileum and nape.
5. Males of *stricklandi* have more extensive red on the head than males of *arizonae*.
6. *Stricklandi* is restricted to much higher altitudes than *arizonae* throughout its range.

In this case, without the test of sympatry, the determination of species limits becomes arbitrary and subjective and it depends in large part on whether one wishes to emphasize differences or similarities. The matter is not simple and it cannot be decided on the variation in one or two characters of color or pattern, as I attempted to do in 1953 and as others have attempted to do more recently.

To consider these two forms as conspecific discounts the great morphological differences between them, differences which rise abruptly in two populations barely 50 miles apart. Yet, to treat them as distinct species discounts the ecologic similarities between the nearest representatives of the two groups, discounts the similarities in the vocalizations of the two, and conceals the fact that we are *not* dealing simply with a plain-backed form (*arizonae*) versus a barred-backed form (*stricklandi*). This is a concept held by most ornithologists, to be sure, but is founded primarily

on older published descriptions based on limited material. Rather, it seems that dorsal pattern represents a point of similarity rather than difference. My feelings can best be presented by a paraphrase of Pitelka's (1951: 375) discussion of his consideration of the Scrub and Florida jays as conspecific (*Aphelocoma coerulescens*): Placement of all [of these brown-backed *Dendrocopos*] in one species emphasizes morphologic, behavioristic, and ecologic similarities, close phylogenetic relationship, and the fact of allopatric distribution; it unfortunately obscures the fact of advanced phylogenetic divergence of the [*arizonae* and *stricklandi* groups].

More or less arbitrarily, then, I would regard *arizonae* and *stricklandi* as representatives of a single, polytypic species. At the same time, I would emphasize the fact that the differences between the *arizonae* and *stricklandi* groups are far greater than the differences between any of the populations within either group. This is, of course, another illustration of the truism that all subspecies are not equivalent in the evolutionary sense. The *arizonae* and *stricklandi* groups represent populations which are well on the way to achieving reproductive isolation, if, indeed, they have not already achieved it.

One other treatment of these two forms should be discussed here, namely that of Voous (1947). Voous, working without the benefit of the more plentiful and critical material now available, and without the important distributional information acquired since his monograph was written, treated *arizonae* and *stricklandi* as separate species pertaining to widely separated sections of *Dendrocopos*. He placed *stricklandi* in the group of "North American White-backed Woodpeckers" along with *villosus* and *pubescens*. *Arizonae* was placed in the section of "Aberrant Species," along with *Dendrocopos (Desertipicus) dorae*, a brown-backed species of Arabia; although no direct relationship between these two was implied, they were considered "to be the offspring of a formerly generally distributed form." Voous (1947: 65) stated that "the present range of *arizonae* coincides with the distribution of the glacial sonoran forest refugium" and he noted that the species is partial to oaks. However, the range that he gave for *arizonae* is that given by Ridgway (1914) and extends from Arizona and New Mexico south only to Colima; the eastward occurrence to east-central Michoacán was not then known. Similarly, the range of *stricklandi* (1947: 81), taken from the same source, did not extend that form west to Puerto Lengua de Vaca. Thus, three important facts were not known: first, that *arizonae* and *stricklandi* approach to within 50 miles of each other; second, that *arizonae* is a bird of nearly pure pine woodland in Michoacán; and third, that the dorsal cross-barring of *arizonae* is not confined to the lateral rectrices only (1947: 64) but that at least traces of such barring are found on the

dorsum, rump, or both of most specimens and that it is quite prominent on some. The relationship of *arizonae*, on the basis of evidence available at this time, is clearly with *stricklandi*.

Considering especially geographic variation in size, it seems likely that a *stricklandi*-like population of woodpeckers, inhabiting coniferous forest at high elevations in the central Mexican highlands, was ancestral to the *stricklandi-arizonae* complex. Such an ancestral population may have been originally isolated from *villosus* and became adapted to higher elevations. This hypothesized derivation from *villosus* is supported by certain features of color and pattern, as pointed out by Voous (1947: 73-81). *Arizonae* may well have been derived from a population segregated from ancestral early *stricklandi* at the lower altitudinal limits of its range in eastern Michoacán or western México. The hypothesized derivations of *stricklandi* from *villosus* and of *arizonae* from *stricklandi* are suggested by certain trends in color and pattern. Thus, dorsal color is black in *villosus*, dark, sooty brown in *stricklandi*, and brown in *arizonae*. *Villosus* has a broad, white mid-dorsal streak; *stricklandi* has mid-dorsal barring (an interrupted mid-dorsal streak?); and *arizonae*, with rare exceptions, has the dorsum immaculate or with very much reduced white markings. *D. villosus* has immaculate, white underparts or, in some populations, a little streaking on the sides of the breast. *D. stricklandi* has a moderate amount of streaking on the underparts (this much reduced in the westernmost populations of *stricklandi*), whereas *arizonae* is heavily spotted below. The two lateral rectrices of *villosus* are pure white; in *stricklandi* these feathers are mostly white with black bars on the distal portion, these bars narrower than the white interspaces, and often irregular in shape, and incomplete; in *arizonae* these feathers are heavily and regularly barred, the black bars sometimes broader than the white bars.

After its presumed origin from an ancestral early population of *stricklandi*, *arizonae* may have been forced into pine woodland at lower elevations because of competition with *villosus*. Here, still foraging in coniferous woodland but occupying a region of warmer climate and denser atmosphere, bill length increased and wing and tail lengths decreased. Presumably, this population extended its range to the west and northwest along the major mountain axes, occupying middle elevations. These middle elevations may have been the most available areas for range expansion, with the bulk of *villosus* distributed above and the great bulk of *scalaris* below. Presumably, then, as these early populations of *arizonae* pioneered to the northwest, they encountered vegetation increasingly dominated by oaks, and bill size increased in response to the selection pressures exerted by the changing niche. Accompanying the increase in bill size may have been some increase in over-all body size. Further increase in body size

TABLE 10
PERCENTAGES OF JOINT NONOVERLAP BASED ON COEFFICIENTS OF DIFFERENCE
FOR BILL AND WING LENGTHS, MALES ONLY

Bill length (below place names)				Wing length (above place names)			
Ariz	50.8	87.9	—	86.6	96.8	99.8	58.7
67.0	NW Mex	85.5	—	84.6	95.4	99.4	58.3
84.4	78.2	N Sin	—	53.6	79.9	95.3	81.6
90.5	87.7	65.2	S Sin	—	—	—	—
94.1	92.9	74.2	59.5	Nayar	74.5	91.0	80.8
—	—	—	—	—	W Mich	72.2	94.4
98.5	98.8	86.9	71.9	61.4	—	Tzit	99.3
99.9	100.0	99.6	97.8	96.1	—	97.2	México

may have resulted in accordance with Bergmann's Rule or Salt's hypothesis, as previously discussed.

The culmination of this evolutionary history may be seen today in Arizona, where these three forms are sharply separated in the breeding season: *D. villosus* occupies the predominantly coniferous forests at high elevations; *arizonae* occupies encinal and pine-oak woodland at middle elevations; and *scalaris* occupies the desert vegetation at still lower elevations.

SUBSPECIES LIMITS

Three races have been proposed within the *arizonae* group of *D. stricklandi* as here defined. Hargitt (1886: 115) named *Picus arizonae* from the Santa Rita Mountains of Arizona. Ridgway (1887: 286) named *fraterculus* from the "Sierra Madre of Colima" and gave its range as "southwestern Mexico." He later (1914: 263) outlined the range of *fraterculus* in more detail, ascribing it to the states of Sinaloa, Jalisco, Colima, Zacatecas, and Nayarit ("Territory of Tepic"). This range was also given by Cory (1919: 495), and van Rossem (1934: 445) agreed with it at least to the extent of extending *arizonae* south at least to southern Sonora and Chihuahua. Most recent workers extend *fraterculus* north to the southern parts of Sonora and Chihuahua (Blake, 1953; Miller *et al.*, 1957; A.O.U., 1957); this is apparently based on a later concept held by van Rossem (1945: 140-141, and footnote 29). Phillips (1961: 343, 345) has recently named the race *websteri*; the five "cotipos" are from the "Sierra San Juan, al oeste de Tepic, Nayarit," and the range is given as "Sierras costeras de Nayarit y de Jalisco," with specimens examined by the describer from the type locality and from the Sierra de Autlán, Jalisco. *D. s. websteri* is described as being closely related to *D. s. arizonae* and *D. s. fraterculus* but smaller than the former and paler above than the latter.

Phillips divides the *arizonae* complex into two major color types, a

TABLE 11
PERCENTAGES OF JOINT NONOVERLAP BASED ON COEFFICIENTS OF DIFFERENCE
FOR TARSAL AND TAIL LENGTHS, MALES ONLY

Tarsal length (below place names)				Tail length (above place names)			
Ariz	51.2	80.2	—	—	—	96.3	69.1
57.5	NW Mex	82.9	—	—	—	97.5	69.5
67.4	72.6	N Sin	—	—	—	88.3	92.9
91.9	94.5	71.6	S Sin	—	—	—	—
94.4	96.2	77.3	62.5	Nayar	—	—	—
93.1	95.0	77.9	66.6	56.4	W Mich	—	—
93.3	95.4	76.1	60.6	51.2	57.1	Tzit	99.2
85.8	89.4	65.2	57.9	67.7	70.2	66.3	México

series of pale brown populations ranging from Arizona to western Jalisco, and a darker, sootier series ranging from Zacatecas to the Nevado de Colima and thence east to Michoacán. As stated previously, I cannot make out any well-defined geographic variation in color within the *arizonae* group. However, I think that there are grounds for recognizing *websteri* on the basis of geographic variation in size. As can be seen from Tables 10 and 11, the Nayarit sample differs significantly from the Arizona Combined and Northwestern Mexico samples in lengths of bill and tarsus, and from the Tzitzio-Las Trojes sample in wing length. Although *websteri* obviously represents a mid-point on a cline of decreasing size (Figures 4 and 5) and therefore recognition is more or less arbitrary, the cline is a long one, extending more than 1,200 miles, and it does not seem amiss to recognize this intermediate population. On this basis I propose the following distributions within the *arizonae* group:

I. *Dendrocopos stricklandi arizonae* (Hargitt). From southeastern Arizona (Baboquivari, Santa Catalina, and Pinaléño mountains) and extreme southwestern New Mexico (Peloncillo and Animas mountains) south in the Sierra Madre Occidental through Sonora and Chihuahua to northeastern Sinaloa and northwestern Durango.

II. *Dendrocopos stricklandi websteri* Phillips. From southeastern Sinaloa, west-central Durango, and western Zacatecas south to the Volcanes de Colima, Jalisco.

III. *Dendrocopos stricklandi fraterculus* (Ridgway). From the Sierra de Coalcomán, Michoacán, east and north through southeastern Jalisco to east-central Michoacán (three miles north of Tzitzio, Las Trojes).

A point of confusion involves the type locality of *D[ryobates]. arizonae fraterculus* Ridgway. The describer (1887) gave the type locality as "Sierra Madre of Colima." This was later given as "Sierra Madre, Colima" by Ridgway (1914) and Cory (1919). Phillips (1961: 345) restricted the type locality to "la vertiente oriental del Nevado de Colima." Subsequently, Deignan (1961: 288) gave the following information on the type specimen of *fraterculus*: "Sierra Madre (not Sierra Nevada) = Río Neshpa, State of Michoacán (not Colima), México. April 1863. Collected

by John Xántus. Original number 533." Phillips (1962: 332), taking cognizance of the information presented by Deignan, stated that the Río Neshpa (= Nexpa) represents a locality south of the previously known limits of distribution of this woodpecker, and that the species does not occur in the lowlands. However, the headwaters of the Nexpa are in the central part of the Sierra de Coalcomán near Aguililla, elevation 2,800 feet, southern Michoacán. Since Robert W. Storer collected three specimens of *fraterculus* two miles south-southwest of Coalcomán, at 4,500 feet (University of Michigan Museum of Zoology), it seems probable that the species ranges in suitable habitat throughout the Sierra de Coalcomán, and its occasional occurrence on the upper Río Nexpa, although somewhat low, seems quite possible. Dr. William E. Duellman (letter) states: "In that area [near Aguililla] at elevations of less than 1,000 meters pine-oak forest is developed, so [Xántus] could have obtained your bird there."

Mr. Herbert G. Deignan kindly forwarded to me Xántus' itinerary from January to May, 1863, as derived from his field registers preserved at the United States National Museum. In April, 1863, Xántus was at several localities, including "Sierra Madre in Michoacan/Neshpa River," where he collected specimens 526-550a, including 533, the type of *fraterculus*. Perhaps the question is not so much whether Xántus was in, or near, the range of *fraterculus*, but rather whether he actually took the trip on which he supposedly collected on the Río Nexpa. Madden (1949: 189-190), the best biographer of Xántus, stated:

The most extensive expedition which Xántus described to Baird is of very doubtful authenticity. He asserted that in April and May [of 1863], in company with a priest of Cualcomantlan (Coalcomán) he penetrated southern Michoacan to the village of Chacan (?) in the Sierra Madre. Going forward with two Indians, he followed the crest of the range to Tupila (?) and 'finally, after 19 days immense sufferings & hardships' reached the town of Lauria (La Orilla) at the mouth of the Zacatula River (Río Mexcala). To belie this extravagant tale is the fact that, although according to Xántus the exploration lasted at least thirty-five days, ending about 10 May, during this period between 5 April and 10 May Xántus wrote from the city of Colima to Captain Charles H. Poor, commanding U. S. S. *Saranac*, on 8 April, and dispatched two consular reports to Washington on 15 April and 7 May.

Peters (1960), discussing this problem, notes that two of the letters cited by Madden were mailed within little more than a week after Xántus' departure, and may well have been written before he left. The third letter was dated three days before his return to Colima on 10 May and may indicate a slightly earlier arrival date than Xántus admitted. Peters continues: "It seems to me, however, that Madden is allowing his knowledge of Xántus' actions in other situations and in other periods of his life

to influence his ideas concerning the Michoacán trip, and that he is unjustified in his statement that Xántus did not make the trip."

In support of Peters' views, the birds collected by Xántus on the Nexpa were of the "right" races for the area, according to identifications forwarded to me by Dr. Philip S. Humphrey. Especially significant is a specimen of Steller's Jay, *Cyanocitta stelleri purpurea*, Xántus original number 531. This race, as presently understood, is endemic to western and central Michoacán, although it may possibly occur on the Nevado de Colima (see Schaldach, 1963: 65). Further, Steller's Jay probably occurs high in the Sierra de Coalcomán; on Cerro de Tancítaro, Blake and Hanson (1942: 537) found this species almost entirely restricted to pine-alder-fir cloud forest (*op. cit.*: 520). Forest of this type is present on Cerro de Barolosa, presumably the highest mountain in the Sierra de Coalcomán (Duellman, 1961: 133). Cerro de Barolosa is 7 miles north and 10 miles west of Aguillilla, which is near the headwaters of the Río Nexpa. This suggests that Xántus used the term "Neshpa River" to include localities well above the headwaters of that river, although perhaps still in its drainage. If so, he must have traversed the range of *fraterculus*.

To me, it seems as though it would have been more trouble to "fake" this trip than to have taken it. Since the type specimen of *fraterculus* is extant, since it is recorded in the supposed collector's field register, and since the specimens presumably collected on the Río Nexpa by Xántus pertain to races found today in the Sierra de Coalcomán and the adjacent lowlands, I feel that Phillips' restriction of the type locality of *fraterculus* to the Nevado de Colima should be set aside and that the Río Nexpa, Sierra de Coalcomán, southern Michoacán, should be accepted as the type locality of *fraterculus* until positive evidence to the contrary is forthcoming.

As regards the *stricklandi* group, Malherbe (1845: 373) named *P[icus]*. (*Leuconotopicus*) *Stricklandi* without specifying a type locality other than "du Mexique." Moore (1946: 104) named *Dendrocopos stricklandi aztecus* from "Puerta [= Puerto] Lengua de Vaca, on the boundary line between the states of Michoacan and Mexico, 15 miles east of Zitácuaro, Michoacan, altitude about 9350 feet," at the same time restricting the type locality of the nominate race to the "Mt. Orizaba massif" of Veracruz. Actually, Puerto Lengua de Vaca is one mile by road east of the Michoacán-México boundary, and therefore within the state of México; *aztecus* has not yet been recorded from the state of Michoacán although Miller *et al.* (1957: 43) included that state in the range of the form.

D. s. aztecus appears to be a valid race on the basis of the great reduction in ventral streaking as opposed to the more heavily marked nominate race. In using this character one must compare specimens

collected at the same time of year, and preferably in fresh plumage, as wear accentuates the heaviness of the ventral streaking in the same fashion that it accentuates the ventral spotting of *arizonae*. Badly worn specimens are impossible to identify to race. However, there was a readily recognizable difference between the type series of *aztecus* (Moore Collection), collected in October, and four specimens from Veracruz (British Museum), three collected in November and one, collection date unspecified, in fresh plumage. Again, variation in this character is clinal and specimens from the Distrito Federal, Morelos, and eastern México are intermediate between samples collected in western México on the one hand and Puebla and Veracruz on the other. Arbitrarily, then, I would propose the following distributions within the *stricklandi* group:

I. *Dendrocopos stricklandi aztecus* Moore. High mountains from the México-Michoacán boundary east of Zitácuaro, Michoacán, east in the states of México and Morelos and the Distrito Federal.

II. *Dendrocopos stricklandi stricklandi* (Malherbe). High mountains in the states of Puebla and Veracruz.

SUMMARY

I studied Strickland's Woodpecker (*Dendrocopos stricklandi*) in Mexico from January through May, 1961, and in southeastern Arizona in June and July, 1961. As here considered, the species includes two groups. The *arizonae* group includes a series of populations characterized by dark brown pileum and nape, medium brown dorsum and rump, upper parts immaculate or nearly so, and underparts spotted and barred. This group ranges from southeastern Arizona and southwestern New Mexico south to the east-central part of the Mexican state of Michoacán, and it occurs between about 4,000 and 8,000 feet, occasionally higher.

The *stricklandi* group is characterized by dark, sooty brown coloration, heavily white-barred dorsum and rump, and streaked and barred underparts. It occupies high elevations, between 8,500 and 13,500 feet, in the Mexican states of México, Morelos, Puebla, and Veracruz, and in the Distrito Federal.

In the northwestern part of its range the *arizonae* group forages mainly in oaks, although its niche utilization may vary seasonally according to seasonal changes in the distribution of the insects on which it feeds. In the southeastern part of its range, populations of the *arizonae* group occur almost entirely in pine woodland. Although little is known of its foraging niche between the extremes of its distribution, vegetational surveys indicate that oaks become less prominent, and pines become more prominent, from northwest to southeast in the range of this group.

The *stricklandi* group occurs in woodlands and forests which are dom-

inated by conifers, especially by pines, with oaks and alders interspersed as less prominent elements.

In dimensions, there are four generally concordant northwest-southeast clines of decreasing size of bill, wing, tail, and tarsus in the *arizonae* group. Bill size continues to decrease sharply in the *stricklandi* group, but wing and tail lengths increase markedly, with abrupt reversal of the clines in those dimensions. Tarsal length shows less clinal variation than the other dimensions.

Clinal increase in relative bill length to the northwest is probably correlated with increasing dependence on foraging in oaks with their relatively deep-lying entomofauna. Increase in body size in the northwest may be in part correlated with increase in bill size, may reflect selection pressure exerted by climate in accordance with Bergmann's Rule, or may reflect nonhabitat specific increase in efficiency as a temporary adaptation to recently occupied parts of the range.

The relatively long wing and tail of *stricklandi* may reflect adaptation to flight in the less dense atmosphere of high altitudes. The very small bill of the *stricklandi* group may reflect dependence on conifers as primary foraging sites, reinforced by selection pressures exerted by climate in accordance with Allen's Rule. There is a further possibility that the very small bill of the *stricklandi* group may reflect a foraging method different from that used by *arizonae*.

Variants with traces of white dorsal markings are found throughout the range of the *arizonae* group and most specimens show at least some traces of this. In Jalisco and Michoacán, heavily barred variants occur, and these comprise 27.8 per cent of the 18 specimens collected from the southeasternmost population in 1961.

The *arizonae* and *stricklandi* groups are similar in coloration of the pileum and nape. They differ strongly and consistently in depth of color of the dorsum and rump and in ventral pattern. They differ less consistently, but to a considerable degree, in extent of the red on the head in adult males.

Some of the vocalizations of the two groups are similar.

Without the test of sympatry, the two groups are here regarded as conspecific, thus emphasizing allopatric distribution, similarities in dorsal pattern, in pileum and nape color, in vocalizations, and in ecology of the two groups where they approach geographically.

The recently named race *websteri* Phillips, originally described from Nayarit and western Jalisco, is recognized on the basis of size differences but is here given a more extensive range.

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