

## GEOGRAPHIC VARIATION IN COLORATION AND MORPHOLOGY OF THE ACORN WOODPECKER<sup>1</sup>

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**Abstract.** Although geographic variation in coloration and morphology of Acorn Woodpeckers (*Melanerpes formicivorus*) is thought to be slight, a sedentary species restricted to a particular habitat across a broad geographic range may be expected to exhibit some geographic differentiation. I analyzed seven morphometric and five plumage coloration characters on 1,531 study skins from across the species' geographic range. Dividing the specimens examined into 25 population samples, I found highly significant geographic differences in most of the characters analyzed, including clinal patterns and discrete differences in both morphometric and plumage characters. Patterns of geographic differentiation in the two character sets were not significantly concordant. It is possible to identify seven geographic units within the species, each of which is diagnosable based on combinations of discrete and continuous character states.

**Key words:** *Acorn Woodpecker; coloration; morphometrics; geographic variation.*

**Resumen.** A pesar de que se ha pensado que la variación geográfica en el Carpintero Arlequín (*Melanerpes formicivorus*) es mínima, se puede esperar que una especie sedentaria y restringida a un hábitat particular que se distribuye sobre un área de distribución muy amplia, mostrará diferenciación en alguna escala geográfica. En este trabajo, se analizaron siete caracteres morfométricos y cinco de coloración del plumaje en 1,531 especímenes de toda el área geográfica de la especie. Se encontró variación geográfica significativa en la mayoría de los caracteres analizados, incluyendo patrones clinales y diferencias discretas entre poblaciones. Basándose en estos patrones, es posible identificar siete unidades geográficas en la especie, cada una diagnosticable con estados de caracteres discretos.

**Palabras clave:** *Carpintero Arlequín, morfometría, variación geográfica.*

### INTRODUCTION

Studies of geographic variation can provide important information regarding patterns of adaptation to different habitats, historical separation, and ecological isolation. A thorough understanding of patterns of geographic variation is hence a first step towards understanding evolutionary processes in natural populations (Zink and Remsen 1987). Studies of geographic variation, which until relatively recently consisted of simple descriptions of new subspecific taxa, have changed substantially and now involve numerical and statistical analyses without regard to prior named forms (e.g., Selander and Johnston 1967, Power 1970, Haffer and Fitzpatrick 1985).

The Acorn Woodpecker (*Melanerpes formicivorus*) is resident from southern Washington in the western United States south through Middle

America to Colombia (Short 1982, AOU 1983). Acorn Woodpeckers are largely restricted to montane forest, but occur in lowland forest in coastal California and parts of southern Mexico and Central America. Preferred habitats are oak forest and pine-oak forest, although they also occur in a wide variety of forests holding abundant dead tree trunks. Acorns appear to be an important element in their biology (Short 1982), although their occurrence in certain lowland forests suggest that acorns may not be critical.

Although several subspecies of Acorn Woodpeckers have been described, Short (1982) argued that geographic differences are very slight. This apparent lack of geographic differentiation is puzzling, because the sedentary nature of the species and its close ties to a particular habitat suggest that geographic differentiation and perhaps local adaptation might be expected. The purpose of this study was to test for geographic variation in a variety of characters describing size, shape, and coloration of Acorn Woodpeckers.

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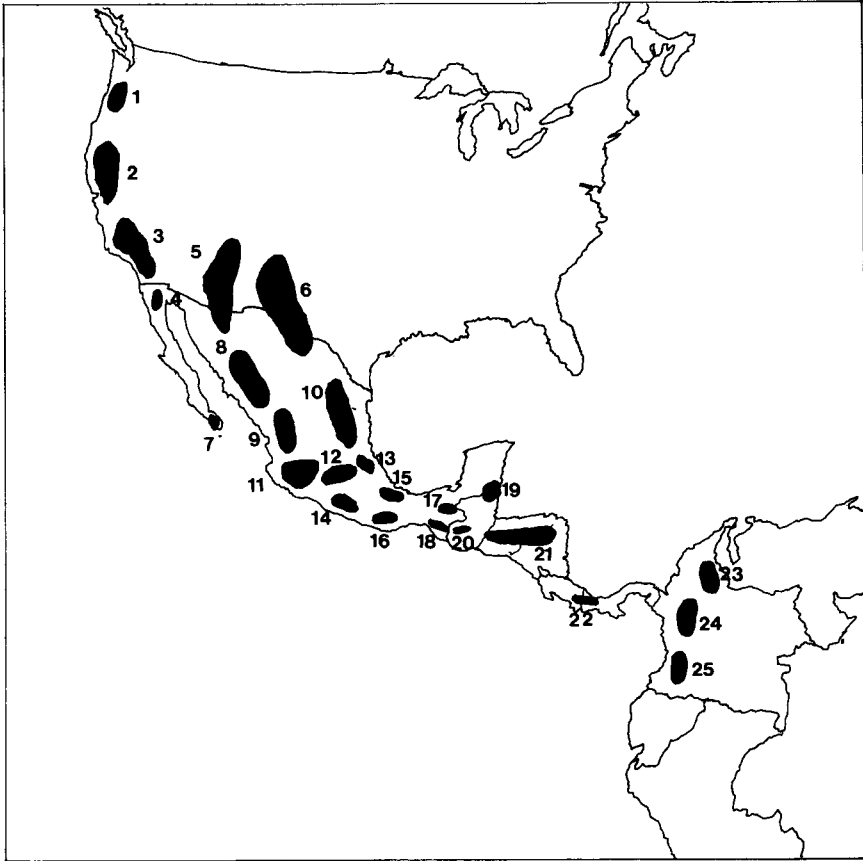


FIGURE 1. Map showing the 25 population samples used in analyses of geographic variation of Acorn Woodpeckers.

## METHODS

I examined 1,531 study skins of Acorn Woodpeckers in 16 museum collections in the United States, Mexico and Costa Rica (see Acknowledgments). I supplemented existing collections by collecting individuals at 15 localities in Mexico and one in Costa Rica between 1988 and 1990. From each specimen examined, I recorded the following information: locality, elevation above sea level, date of collection, iris color, sex, and age (after character descriptions in Koenig 1980). Only adults were included in the study. For statistical analysis, the specimens were grouped into 25 population samples, combining samples that were taken at geographically adjacent sites in continuous habitat (Fig. 1).

Four characters describing aspects of plumage coloration were as follows: (1) throat color

(THROAT), scored on a scale of increasing yellowness from one (white) to five (bright yellow) based on Field Museum of Natural History specimens FMNH 124531, 127147, 208826, 139257, and 207130; (2) pattern and intensity of breast streaking (BREAST), scored on a scale of increasingly heavy streaking from one (narrow black streaks on the chest) to four (heavy black band across the chest) based on specimens FMNH 127147, 139280, 139234 and 39896; (3) presence or absence of red feathers on the upper chest (RED); and (4) color of the iridescence on the back (BACK), which was scored as blue, green or intermediate. Seven measurements were taken from each specimen: (1) bill length (NT) from the anterior edge of the nostril, (2) total exposed culmen (TEC), (3) bill depth (BD) at the anterior edge of the nostril, (4) beak width (BW) at the

anterior edge of the nostril, (5) tarsus length (TAR), (6) wing chord (WC), and (7) tail length (TL), following Baldwin et al. (1931).

To minimize error, all measurements were taken with the same set of calipers, and repeatability (measurement error) was analyzed by measuring a series of 100 specimens twice and calculating Pearson product-moment correlations between the two sets of measurements. Redundancy of characters was assessed by calculating correlations among characters. Normality of character distributions was tested using the Shapiro-Wilk statistic (S.A.S. 1987), and appropriate transformations of scale were made to correct deviations from normality. Sexual dimorphism was tested by means of a two-factor analysis of variance (ANOVA) controlling for the effects of locality. A multivariate ANOVA (MANOVA) was used to test for the existence of geographic variation, and subsequently patterns in individual characters were analyzed using single-factor ANOVAs. Principal components analyses and cluster analyses (based on standardized Euclidean distances; results from other distance measures were similar) were used to understand the relationships of different populations in character space. Morphometric and coloration data were analyzed separately. Comparisons of distance matrix structure were accomplished using mantel test algorithms in NTSYS-pc, version 1.6 (Rohlf 1990).

## RESULTS

Repeatabilities for all seven morphometric characters exceeded 0.85. Redundancy of characters was generally low (correlation coefficients not exceeding 0.53), except between total exposed culmen and bill length, for which the correlation was 0.83. Because the repeatability of total exposed culmen was lower than that of bill length, this was eliminated from subsequent analyses. Five of the seven untransformed morphometric characters departed significantly from normality ( $P < 0.05$ ), but normality improved considerably after transformation to the natural logarithm, with only three characters departing slightly from normality. Significant sexual dimorphism, with males larger than females, existed in all characters except tail length, so sexes were treated separately in subsequent analyses.

The overall MANOVA test for geographic variation in morphometric characters indicated

highly significant differences among localities ( $P < 0.0001$ ). All six morphometric characters showed significant differences among localities (all  $P < 0.0001$ ). Patterns of variation are shown for each character in Figure 2.

All six morphometric characters indicated marked differentiation of the four population samples from Oregon, California, and northern Baja California from other population samples to the south and east (Fig. 2). Bill width and bill depth indicated some differentiation of the Colombian populations. Wing chord was considerably shorter in the population sample from southern Baja California than in other populations. Clinal variation was evident to varying degrees in all six characters.

Principal components analysis of the morphometric data emphasized these differences between populations. The first three components explained 76% of the variation in males and 74% of the variation in females. Figure 3 shows clearly the separation of the populations into two groups, especially in females: the populations of Oregon, California, and northern Baja California (numbers 1–4), and those from the remainder of the species' range. Within this last grouping, the association between Baja California's samples (7) with those of mainland Mexico is also evident, and the very small sized Central and South American populations (17–25) also group together. Close association among Arizona and northern Mexican populations evidences a high degree of continuity among the populations of mainland Mexico and intrapopulation clinal variation along the geographic range.

Although the plumage coloration characters are relatively subtle, strong geographic patterns were observed in all four characters (Fig. 4). The Colombian populations all had bright yellow throats, whereas the populations of Belize and northwestern Mexico had very white throats. Populations from Oaxaca south to Panama were characterized by the presence of red feathers on the chest, whereas populations farther north and south were polymorphic for the presence of these feathers. Streaking on the breast was darkest in the populations of the northwest, and became gradually lighter in the populations to the south, the only break being the exceptionally light streaking on the breasts of the populations of the tip of Baja California. In both sexes, some indication of north–south clines within both the coastal and interior groups was present. Females

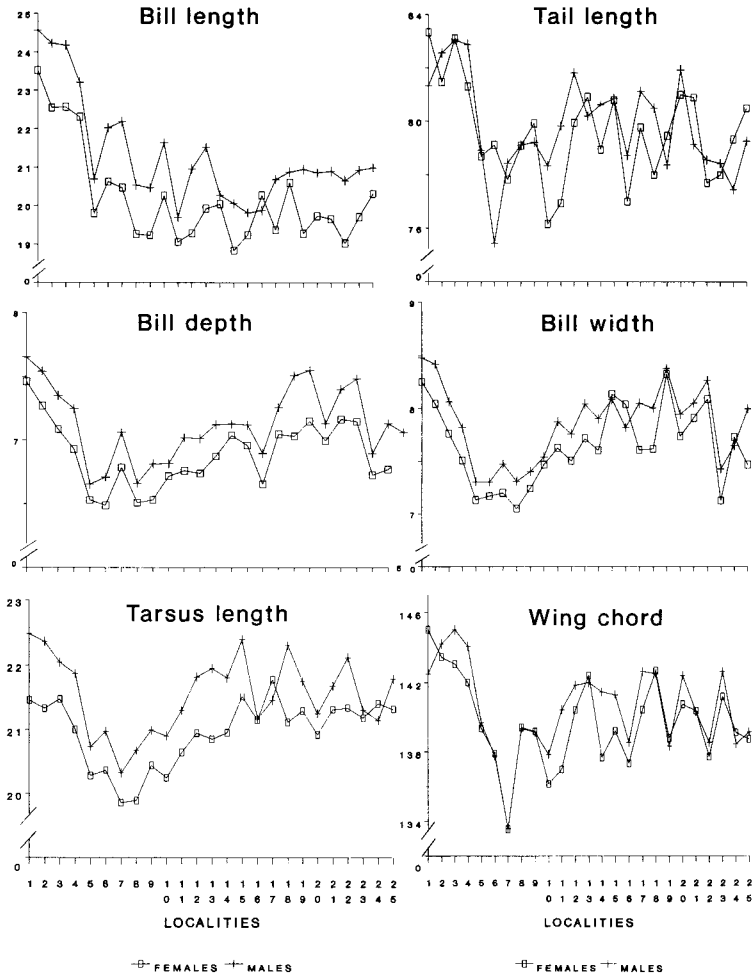


FIGURE 2. Geographic patterns of variation in six morphometric characters of Acorn Woodpeckers. Numbers correspond to regions shown in Figure 1.

from the Sierra de Miahuatlán of southern Oaxaca and from northern Chiapas had strongly green backs, although males are similar to those in other populations.

Cluster analyses revealed a variety of patterns, depending on the character set analyzed (Fig. 5). Analyses of morphometric data in both sexes revealed a cluster containing the populations of Oregon, California, and northern Baja California (1–4) apart from the remaining populations, and a cluster including the population of the southern tip of Baja California (7) and populations from mainland Mexico. Analyses of plumage coloration data showed a cluster containing the very

distinctive Colombian populations (23–25), those from Costa Rica-Panama (22) and of the southern tip of Baja California (7).

Mantel test comparisons of distance matrices showed significantly similar matrix structure between sexes and across character sets. When distance matrices from plumage and morphometric data sets were compared, significant common structure was found in both males and females ( $P < 0.001$ , in both cases). When distance matrices from males and females were compared, significant common structure was found in both morphometric and plumage data sets ( $P < 0.001$  in both comparisons).

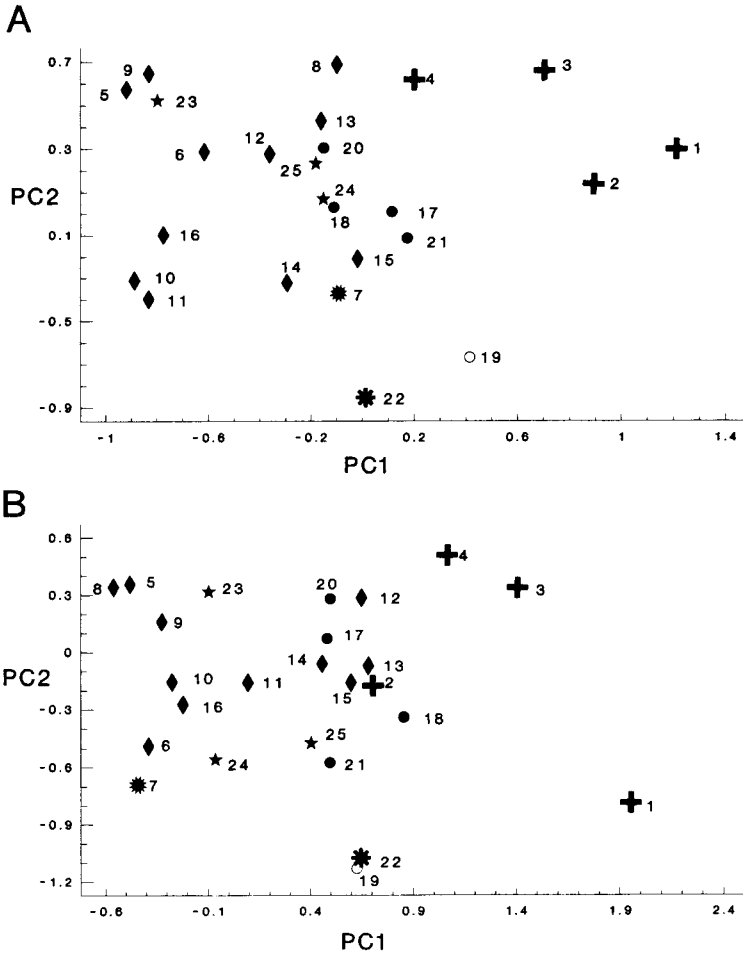


FIGURE 3. Population means in principal component space for (A) females, and (B) males from 25 populations of Acorn Woodpeckers. Numbers correspond to regions shown in Figure 1. Plus signs indicate the *bairdi* group; diamonds indicate the *formicivorus* group; the twelve point star indicates the *angustifrons* group; filled circles indicate the *lineatus* group; the open circle indicates the *albeolus* group; asterisks indicate the *striatipectis* group; and the points stars indicate the *flavigula* group.

## DISCUSSION

*Contra* the statements of Short (1982), strong geographic differentiation exists in Acorn Woodpeckers. Several characters show discrete differences among groups of populations; other characters show broad clinal variation across the species' range. Two additional characters showing discrete differences among populations but not analyzed quantitatively were as follows: (1) all nine individuals that I collected from the southern tip of Baja California had brown irides, whereas individuals from all other populations

have white or slightly pink irides; and (2) individuals from the populations of Colombia all have greatly reduced red coloration on the head—females lack red on the head completely, and males have only a very small patch compared to other populations.

Based on the geographic patterns outlined above, it is therefore possible to define seven geographic groups of populations of Acorn Woodpeckers, as follows.

*Formicivorus* group: Consisting of populations recognized as belonging to the subspecies *for-*

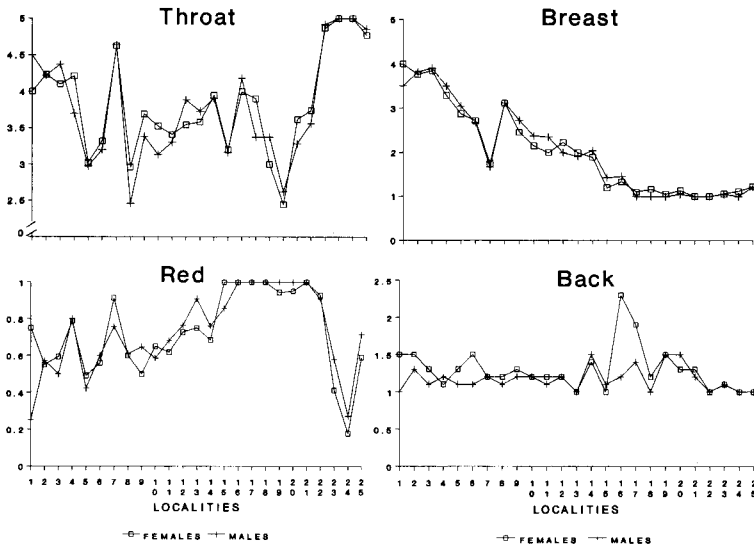


FIGURE 4. Geographic patterns of variation in four plumage characters of Acorn Woodpeckers. Numbers correspond to regions shown in Figure 1.

*micivorus* and the sometimes-recognized *aculeatus*, this group ranges from Arizona and New Mexico south through much of Mexico to the Isthmus of Tehuantepec, and is separated from other groups by the Mohave Desert and the lowlands of the Isthmus of Tehuantepec. Because this group tends to have intermediate values for most characters, this group is used as the basis for comparison for the remaining groups described below.

**Bairdi group:** Consisting of populations currently recognized as belonging to the subspecies *bairdi* and *martirensis*, this group ranges from Oregon south through California to northern Baja California, and is separated from other groups by the Mohave Desert to the east and the deserts of central Baja California. This group is clearly distinct from other groups on the basis of bill length, wing chord, and, to a lesser degree, breast streaking. The subspecies *martirensis* is slightly different from the populations of *bairdi* to the north, although many of the differences are part of broad geographic clines.

**Angustifrons group:** Consisting of a sole subspecies of the same name, this group is restricted to the pine-oak woodlands in the mountains of the southern tip of Baja California, and is separated from other groups by the Gulf of California and the deserts of central Baja California. This group is distinct from all others in having

brown, rather than white, irides, and in its exceptionally short wings.

**Lineatus group:** Consisting of a sole subspecies of the same name, this group is distributed from easternmost Oaxaca and Chiapas south to Nicaragua, and is separated from other groups by the lowlands of the Isthmus of Tehuantepec and the Nicaragua Depression. These populations are characterized by red feathers on the chest, a very lightly streaked breast, and a wide and deep bill.

**Albeolus group:** Consisting of a sole subspecies of the same name, this group is distributed in the lowlands from Belize and the north of Honduras. Fairly similar to the last mentioned group, this group differs in having extremely white throats, wide beaks and shorter wings.

**Striatipectus group:** Consisting of a sole subspecies of the same name, this group is distributed in the mountains of Costa Rica and Panama, and is separated from other groups by the Nicaragua Depression to the north, and an apparent distributional gap to the east in much of Panama. The group is easily characterized by the intensely yellow throat like the Colombian populations, the ubiquity of red feathers on the chest, and smaller differences in several morphometric characters.

**Flavigula group:** Consisting of a sole subspecies of the same name, this group is distributed in the Colombian Andes in three disjunct pop-

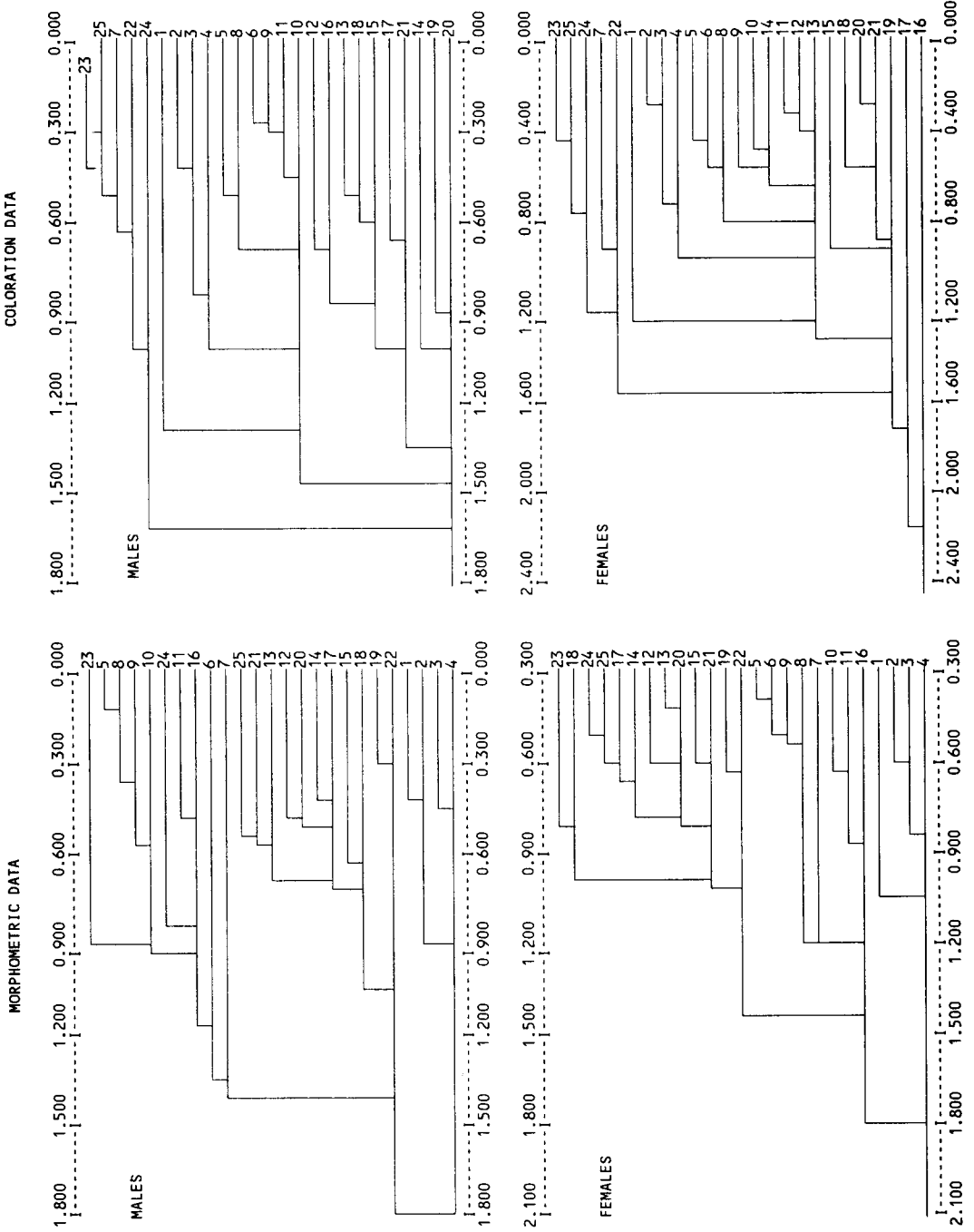


FIGURE 5. Results of cluster analyses of plumage coloration and morphometric data from 25 populations of Acorn Woodpeckers. Numbers correspond to regions shown in Figure 1.

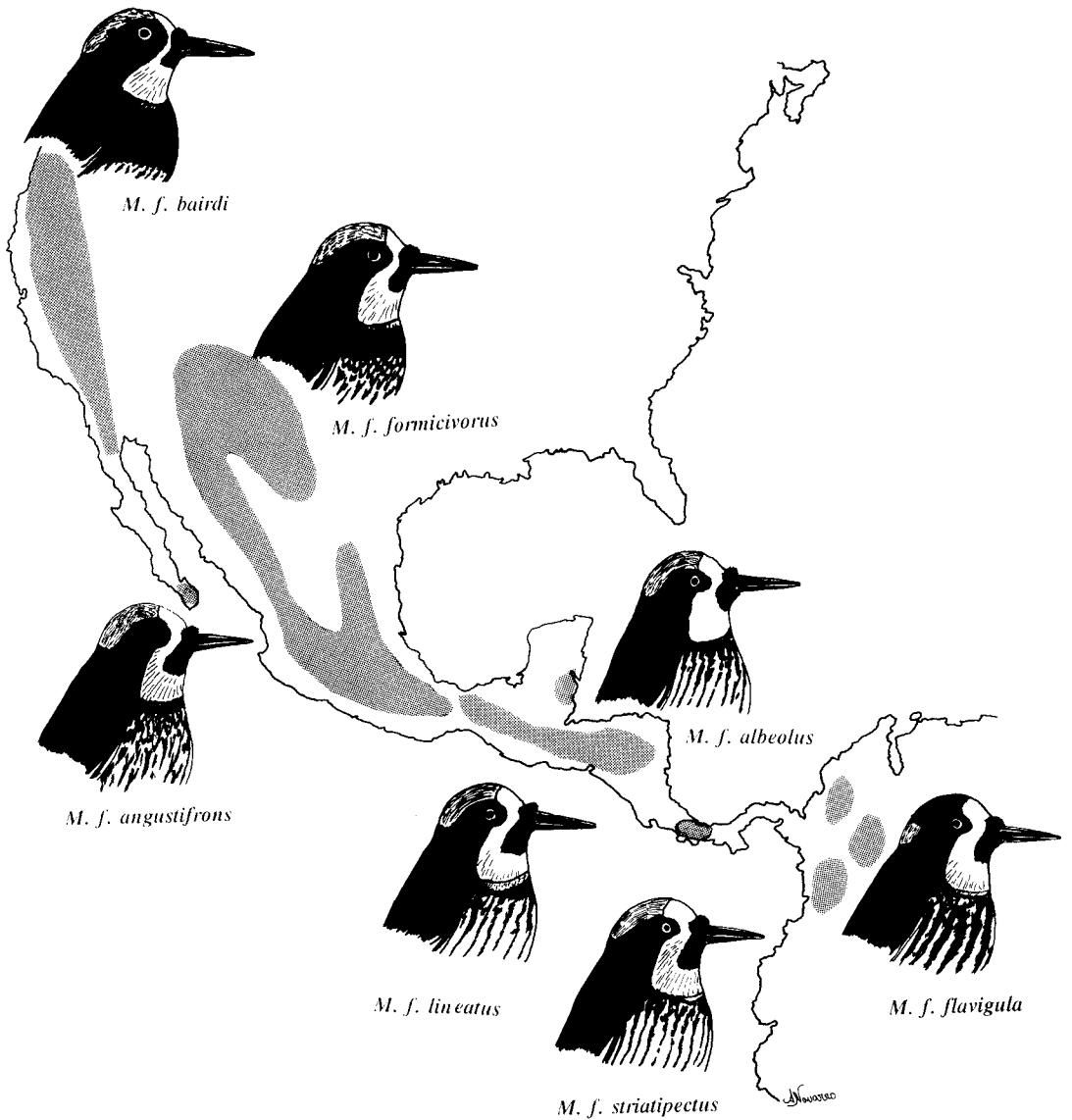


FIGURE 6. Map of the major subspecific groupings of Acorn Woodpecker populations showing male plumage patterns.

ulations. It is clearly distinct from others in the extreme reduction of red coloration on the head (see below), as well as in the bright yellow coloration of the throat.

The *angustifrons* group of southern Baja California is interesting in that it shows no obvious affinity to populations to the north in California and Oregon (*bairdi* group). Most bird populations in the region (e.g., *Aphelocoma coerulescens*) are thought to have been derived from pop-

ulations to the north in California. However, disjunct populations of other avian species at the southern tip of Baja California, such as *Columba fasciata*, *Hylocharis xantusii*, *Sitta carolinensis*, *Pipilo erythrophthalmus*, *P. fuscus*, *Aimophila ruficeps*, and *Junco phaeonotus*, all show some indication of close affinities to mainland populations (Davis 1959). Hence, it is possible that the isolated *angustifrons* group was derived from populations on the mainland, rather than from



California to the north. A possible alternative explanation, however, is that this population has changed so much in isolation that its affinities to the populations to the north are not discernable. Studies of molecular characters currently in progress should resolve this question.

The *flavigula* group in Colombia presents a rare opportunity to understand the directionality of plumage evolution. Juveniles of both sexes in Colombia have a completely red crown and nape (like a northern adult male), exactly as do juveniles of northern populations. In northern populations, this red crown would then be reduced in females but not in males. In adults of the Colombian populations, however, the red coloration is drastically reduced in both the female and the male, with only a small patch of red remaining on the nape in males. Hence, even though the red coloration is all but lost in adult plumages in Colombia, a fully red-crowned stage exists in the ontogeny of the group, strongly suggesting that the reduction of red coloration in the *flavigula* group is a secondary loss, and that the original state in the species as a whole was a fully red crown. A general tendency for such secondary changes in red plumage patches involved in sexual dichromatism appears to exist in isolated or peripheral woodpecker populations; other examples include populations of *Colaptes auratus*, *Picoides stricklandii*, *Melanerpes uropygialis*, and *Picus auricularis* (Short 1982).

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