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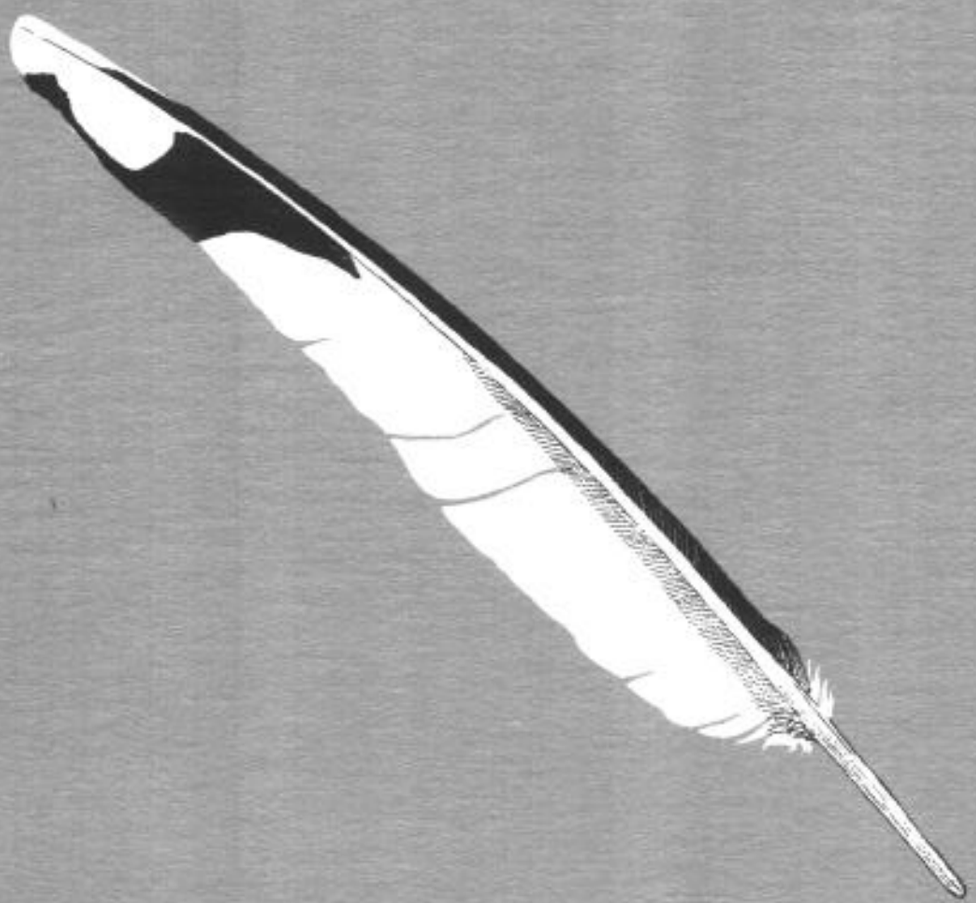

Speciation and Geographic Variation in Black-tailed Gnatcatchers

by

Jonathan L. Atwood

SPECIATION AND GEOGRAPHIC VARIATION IN BLACK-TAILED GNATCATCHERS

ORNITHOLOGICAL MONOGRAPHS

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INTRODUCTION

The gnatcatchers, genus *Polioptila,* represent a well defined yet poorly studied taxon of New World birds. Comprised of approximately 10 species (Paynter 1964, A.O.U. 1983), the genus has generally been classified near the gnatwrens *Microbates* and *Ramphocaenus* (Mayr 1946; Mayr and Amadon 1951; Paynter 1964), although differences in external morphology, nests, and eggs indicate that *Polioptila* might not be closely related to these genera (Rand and Traylor 1953; Paynter 1964; Kiff 1977). At higher taxonomic levels the position of *Polioptila* is even less certain, with most authors considering the genus to be a member of the Old World insect eaters (family Muscicapidae, subfamily Sylviinae; Ridgway 1904; Mayr and Amadon 1951; A.O.U. 1983). However, the results of DNA × DNA hybridization comparisons suggest that the gnatcatchers, along with the gnatwrens, Verdin (*Auriparus flaviceps*), true creepers (*Certhia, Salpornis*), and wrens, are not closely allied to the sylviine warblers but rather represent a monophyletic New World clade (Sibley and Ahlquist 1985). These authors (pers. comm.) place the gnatcatchers, gnatwrens, and Verdin in the subfamily Polioptilinae of the family Certhiidae, with other subfamilies of the Certhiidae being the Certhiinae (true creepers) and the Troglodytinae (wrens).

Regardless of its relationship to other groups of birds, *Polioptila* itself is a distinctive, easily recognized genus with little phenetic divergence among its component species. This morphological uniformity has led to some confusion with regard to species limits within the genus. As an extreme example of the taxonomic difficulties presented by *Polioptila,* Phillips et al. (1973) noted that museum specimens now considered to represent three distinct species (*P. plumbea, P. albiloris,* and *P. nigriceps*) had earlier been ascribed to a single subspecies by Griscom (1930).

Goals of the Study

In this study I consider a long-standing question concerning species limits within the "black-tailed" gnatcatchers that are presently referred to as *Polioptila melanura* (A.O.U. 1983). Although this systematic problem is addressed mainly on the basis of behavioral and ecological data, I also provide information on morphological character variation in three (as defined here) sibling species: *P. melanura, P. californica,* and *P. nigriceps* (Fig. 1). This study is intended primarily as a taxonomic revision; however, the results are presented in the context of other recent studies of geographic variation in birds and thereby contribute to the growing body of literature dealing with the evolutionary significance of intraspecific variability (Zink and Remsen 1986). Also, I compare the distributional and cladistic patterns of these three species of *Polioptila* with other genera occurring in the arid regions of western North America, and use these comparisons as the basis for discussing the possible history and mode of speciation in the "black-tailed" gnatcatchers (Cracraft 1982, 1983).

Nomenclatural History

The first formal reference to a gnatcatcher of the "black-tailed" group was the description by Baird (1854) of *Culicivora plumbea* from Arizona. The absence of a black cap in the type specimen, a male in basic plumage, was considered to be

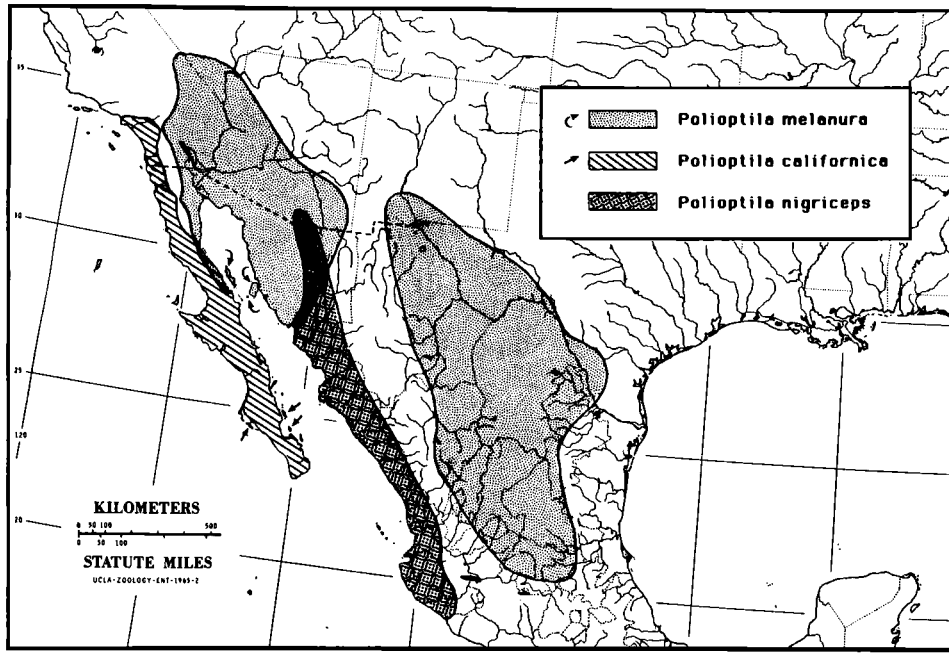


FIG. 1. Approximate geographic distributions of *Polioptila melanura, P. californica,* and *P. nigriceps.*

characteristic of the species. Subsequently, Lawrence (1855) described from Texas a specimen of a male gnatcatcher with a black cap and mostly black outer rectrices, believing it to be an example of the black-capped *Culicivora atricapilla* of Middle America [= present day White-lored Gnatcatcher, *Polioptila albiloris* (Ridgway 1904; A.O.U. 1983)]. Lawrence (1857) later recognized that his black-tailed gnatcatcher and *atricapilla* were actually different species. However, either being unaware of the existence of Baird's *plumbea* or of the similarity of *plumbea* to his putative species, Lawrence described this black-tailed, black-capped gnatcatcher from Texas as a new species, naming it *Polioptila melanura* following Sclater's (1855) change of the generic name of *Culicivora* to *Polioptila.* During these early years, *Polioptila plumbea* (Baird) was referred to by the English names Lead-colored Gnatcatcher or Arizona Gnatcatcher, and *Polioptila melanura* (Lawrence) as the Black-capped Gnatcatcher (Baird et al. 1875; Coues 1878).

Later, Brewster (1881) reported that the presence or absence of a black cap in these birds, rather than being a valid character separating *P. plumbea* and *P. melanura,* instead was merely dependent on age, season, and sex. Consequently, he considered *melanura* to be synonymous with the older name *plumbea.* However, Penard (1923) recognized that Pallas in 1769 had incorrectly assigned another species of gnatcatcher from Middle and South America (the present-day Tropical Gnatcatcher, *Polioptila plumbea*) to the genus *Todus.* Correct placement of this species (*Todus plumbea*) in the genus *Polioptila* thus resulted in a nomenclatural conflict with Baird's *Polioptila plumbea* and, because of priority, required that *Polioptila plumbea* (Baird) be changed to *Polioptila melanura* (Lawrence). During the early 1900s the previous English names for *Polioptila melanura* had been

replaced in general usage by the name Plumbeous Gnatcatcher (A.O.U. 1886; Ridgway 1904; Grinnell 1915; Bailey 1927).

Polioptila californica was also originally described as a distinct species (Brewster 1881), with the first associated English name being the California Black-capped Gnatcatcher. During the early 1900s, *P. californica* was generally known as the Black-tailed Gnatcatcher (A.O.U. 1886; Ridgway 1904; Willett 1912; Grinnell 1915; Bailey 1927).

The presently accepted view of species limits in "black-tailed" gnatcatchers was proposed by Grinnell (1926). Despite recognizing that the two forms could be easily distinguished vocally (Grinnell 1904), Grinnell believed that *P. melanura* and *P. californica* were nonetheless conspecific. The primary basis for this conclusion was the morphological similarity of populations in the Cape region of Baja California to populations in the Sonoran desert of southeastern California and Arizona. According to Grinnell (1926), "even though *californica* [of coastal southern California and northern Baja California] is to *melanura* of southeastern California and Arizona as a full species, variation geographically to the southward, through the [central Baja California population], to the Cape form, and intergradation thence with *melanura* through individual variation, warrants considering [*californica*] just the extreme in a continuous series of subspecies." The English names Grinnell gave to these forms were the Plumbeous Black-tailed Gnatcatcher for the nominate subspecies (including populations later described as *P. m. lucida*) and the California Black-tailed Gnatcatcher for *P. m. californica* (Grinnell 1926). These revisions were accepted in the 4th edition of the A.O.U. Check-list (A.O.U. 1931).

Recent field ornithologists in the United States and Mexico have generally ascribed the English name Black-tailed Gnatcatcher to all populations of gnatcatchers with outer rectrices that are mostly black (Peterson 1941; A.O.U. 1957). Some investigators have distinguished the "coastal" Black-tailed Gnatcatcher (*P. m. californica*) from populations of *P. m. lucida* occurring in the deserts of California (McCaskie and Pugh 1964; Atwood 1980). Rea (1983) and Unitt (1984) both alluded to the possibility of *P. melanura* and *P. californica* being distinct species on the basis of their vocal differences, but provided no in depth analysis of species limits. Curiously, the most recent contribution to the nomenclatural confusion surrounding these birds has come from the A.O.U. Check-list Committee itself, which reversed the more traditional associations of common and scientific names by applying the English name Plumbeous Gnatcatcher to *Polioptila (melanura) californica* and Black-tailed Gnatcatcher to *Polioptila melanura* (A.O.U. 1985).

Here, I use species names and limits in the "black-tailed" gnatcatchers as follows: (a) *Polioptila californica,* composed of the currently recognized (A.O.U. 1957) subspecies *P. melanura californica, P. melanura pontilis,* and *P. melanura margaritae,* and (b) *Polioptila melanura,* composed of the subspecies *P. melanura melanura, P. melanura lucida,* and *P. melanura curtata.* Support and discussion of these conclusions will be provided in subsequent sections.

The third species included in this study, the mostly white-tailed Black-capped Gnatcatcher (*Polioptila nigriceps*), also has had a rather confused nomenclatural history because of uncertainties regarding its relationship to the White-lored Gnatcatcher (*Polioptila albiloris*). I follow here the treatment used by the 6th edition

(1983) of the A.O.U. Check-list. Further information concerning the taxonomic history of *P. nigriceps* is found in Baird (1864), Brewster (1881, 1889), Ridgway (1904), van Rossem (1931b), Brodkorb (1944), Friedmann (1957), Phillips (1962), Paynter (1964), and Phillips et al. (1973).

MATERIALS AND METHODS

Field studies of *P. melanura, P. californica,* and *P. nigriceps* were conducted from 1979–1985. While tape recording vocalizations throughout the range of each species and obtaining additional specimens from localities that were poorly represented in museum collections, I visited 14 states of Mexico (Baja California, Baja California (Sur), Chihuahua, Coahuila, Colima, Durango, Guanajuato, Hidalgo, Jalisco, Nayarit, San Luis Potosí, Sinaloa, Sonora, Queretaro), and four of the United States (Arizona, California, Nevada, New Mexico).

Information regarding available specimens of *Polioptila melanura* (including populations here considered to be *Polioptila californica*) and *Polioptila nigriceps* was requested from major ornithological collections in the United States and Canada. Study skins from the following institutions were then borrowed or examined through visit: American Museum of Natural History; University of Arizona; Baylor University, Strecker Museum; California Academy of Sciences (CAS); University of California, Berkeley, Museum of Vertebrate Zoology (MVZ); University of California, Los Angeles, Dickey Collection (DC); California State University, Long Beach; California State University, San Jose; National Museum of Canada; Carnegie Museum; Cincinnati Museum; Cornell University; Delaware Museum of Natural History; Denver Museum of Natural History; Field Museum of Natural History; Harvard University, Museum of Comparative Zoology; University of Florida, Florida State Museum; University of Illinois; Los Angeles County Museum of Natural History; Louisiana State University, Museum of Zoology; University of Michigan, Museum of Zoology; Milwaukee Public Museum; Nevada State Museum; Occidental College, Moore Laboratory of Zoology; Yale University, Peabody Museum; San Bernardino County Museum of Natural History; San Diego Natural History Museum; Texas A&M University; Texas Natural History Collection; United States National Museum of Natural History; Welder Wildlife Foundation. Analyses of clutch sizes and nesting chronology were based on data provided by the following institutions: Western Foundation of Vertebrate Zoology; California Academy of Sciences; University of California, Berkeley, Museum of Vertebrate Zoology; University of Florida, Florida State Museum; Harvard University, Museum of Comparative Zoology; and Yale University, Peabody Museum. Newly collected specimens, prepared mainly as study skins but also including some skeletal material, are deposited at the Los Angeles County Museum of Natural History, the University of California, Los Angeles, and California State University, Long Beach.

A total of 851 study skins (509 males, 342 females) were used in the analysis of inter- and intraspecific variation; excessively worn or soiled specimens and specimens still in juvenal plumage were excluded from analysis. Geographic groupings of these specimens into 33 sample areas are shown in Figures 2 and 3, and the number of individuals representing each locality is summarized in Table 1. Because the three species are non-migratory, specimens collected throughout the year were assumed to represent primarily resident populations.

TABLE 1

SPECIMENS USED IN ANALYSES OF MORPHOLOGICAL AND VOCAL VARIATIONS

Area code	Sp.[a]	Sample area	Linear measurements		Color analysis		Vocal recordings
			Males	Females	Males	Females	Males
RI01	m	Riverside County, California	33	27	23	15	7
NE02	m	Needles (Colorado River), California	17	10	8	6	22
YU03	m	Yuma, Arizona	14	14	7	10	31
SF04	m	San Felipe, Baja California	12	11	8	6	26
BG05	m	Bahía San Luís Gonzaga, Baja California	8	7	8	5	19
AJ06	m	Ajo, Arizona	14	10	13	10	9
TU07	m	Tucson, Arizona	16	17	12	12	12
HE08	m	Hermosillo, Sonora	8	9	8	5	6
TI09	m	Isla Tiburón, Sonora	6	6	2	4	0
OB10	m	Ciudad Obregon, Sonora	15	6	12	4	11
CH11	m	Chihuahua, Chihuahua	7	7	6	3	5
PR12	m	Presidio County, Texas	20	11	18	4	0
SA13	m	Sabinas, Coahuila	11	5	8	4	7
SL14	m	Saltillo, Coahuila	8	6	7	2	9
DU15	m	Durango, Durango	18	10	13	8	17
HU16	m	El Huizache, San Luis Potosí	16	7	14	6	14
GU17	m	Guanajuato, Guanajuato	6	3	4	1	3
TE18	n	Tecoripa, Sonora	12	7	7	4	1
NA19	n	Navojoa, Sonora	30	20	20	10	19
CU20	n	Culiacan, Sinaloa	11	5	8	4	0
AC21	n	Acaponeta, Nayarit	22	10	6	4	2
CO22	n	Colima, Colima	9	3	7	2	2
LA23	c	Los Angeles County, California	55	42	47	39	24
SD24	c	San Diego County, California	22	21	19	14	12
ST25	c	San Telmo, Baja California	15	8	14	7	28
ER26	c	El Rosario, Baja California	17	7	14	7	22
BG27	c	Bahía San Luís Gonzaga, Baja California	12	5	4	5	26
PP28	c	Punta Prieta, Baja California	12	3	11	2	27
SI29	c	San Ignacio, Baja California (Sur)	17	11	8	6	31
MA30	c	Bahía Magdalena, Baja California (Sur)	14	9	6	5	17
LP31	c	La Paz, Baja California (Sur)	25	22	22	16	38
ES32	c	Isla Espíritu Santo, Baja California (Sur)	3	2	0	0	0
SJ33	c	Isla San José, Baja California (Sur)	4	1	0	0	0
Totals		(*P. melanura*)	229	166	171	105	198
Totals		(*P. nigriceps*)	84	45	48	24	24
Totals		(*P. californica*)	196	131	145	101	225
TOTALS		(All species)	509	342	364	230	447

[a] Species codes: m = *P. melanura*; n = *P. nigriceps*; c = *P. californica*.

MORPHOLOGICAL ANALYSES

Nineteen linear measurements of major body elements and feather lengths were taken from study skins to the nearest 0.1 mm using dial calipers. These measurements included: (a) bill length [BLEN]—the distance from the tip of the upper mandible to its unfeathered base; (b) bill width [BWID]—the distance from one tomium to the other taken at the position of the nostril; (c) bill depth [BDEP]—the distance from the culmen to the lower edges of the rami taken at the position of the nostril; (d) tarsus length—the diagonal of the tarsus taken from the posterior surface of the mid-point of the joint between the tibia and the metatarsus to the upper edge of the scute positioned opposite the origin of the hind toe; (e) middle

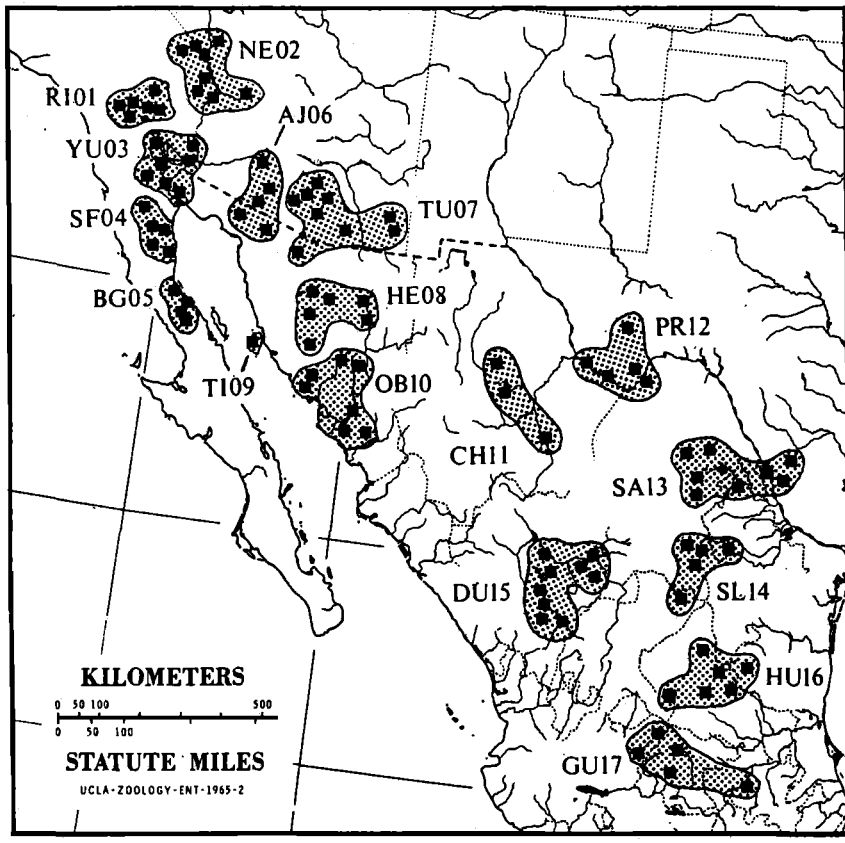


FIG. 2. Groupings of specimens of *Polioptila melanura* (indicated by squares) into samples for analysis. See Table 1 for sample sizes, and Appendix I for list of exact localities.

toe length—the distance from the upper edge of the scute opposite the insertion of the hind toe to the base of the claw on the dorsal surface of the toe (because of difficulties in consistently identifying the scutes that limited tarsal and middle toe measurements, these values, based on the same reference scute in each specimen, were summed for analysis to form the combined character TARTOE); (f) lengths of primaries 3–10 [P3LEN–P10LEN], calculated as the difference between total wing length (the chord of the unflattened, folded wing taken from the bend of the wing to the tip of the longest primary, P6LEN) and the distance from the tip of the longest primary to the tip of the particular primary being measured; (g) tail length [TLEN]—the distance from the point between the insertions of the central pair of rectrices to the tip of the longest rectrix; (h) relative length of rectrices 4–6 [R4PCT, R5PCT, R6PCT]—the difference between total tail length and the distance from the tip of the longest rectrix to the tip of the particular rectrix being measured divided by total tail length.

Body mass of freshly collected specimens was recorded in the field to the nearest 0.1 g using a 10-g Pesola balance, and was converted to the cube-root of body mass [MASS] for analysis.

Twelve characteristics of coloration were examined. Those characters for which

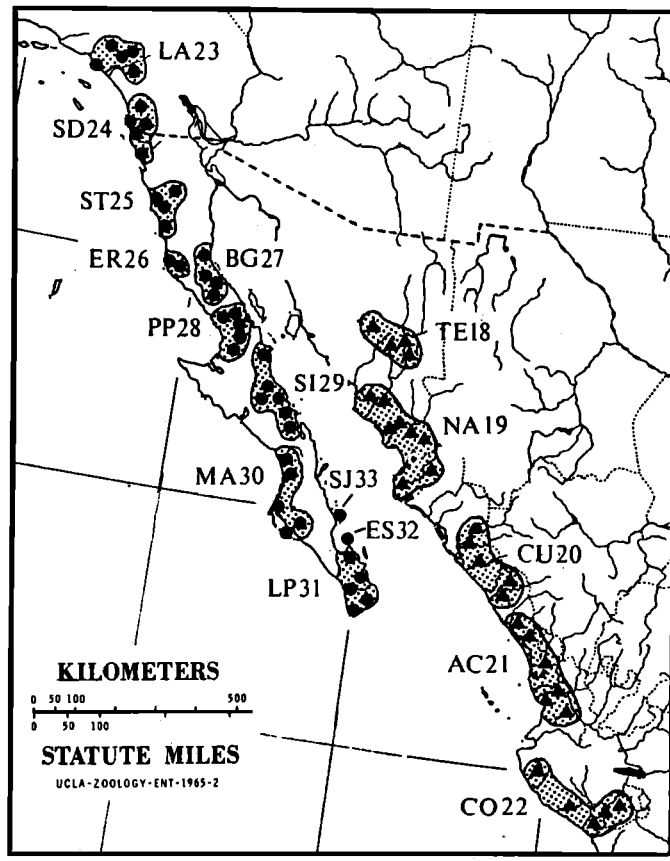


FIG. 3. Groupings of specimens of *Polioptila californica* (indicated by circles) and *P. nigriceps* (indicated by triangles). See Table 1 for sample sizes, and Appendix I for list of exact localities.

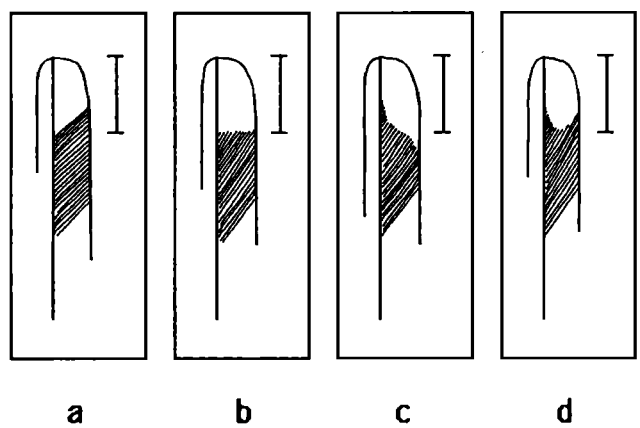


FIG. 4. Categories used in analysis of variation in tail spot shape. Vertical bar to the right of each diagrammed rectrix indicates the dimension used in measuring the lengths of differently shaped tail spots.

linear measurements were obtained using dial calipers included: (a) cap length [CAPLEN]—distance on alternate-plumaged males from the non-feathered base of the upper mandible to the posterior margin of the black cap and (b) relative length of tail spots on rectrices 5 and 6 [R5SPCT, R6SPCT]—distance proximally along the rachis from the feather tip (Fig. 4) divided by total tail length. Character states describing the coloration pattern of rectrices 5 and 6 were subjectively evaluated as follows: (a) tail spot shape on the inner vane [R5SSH, R6SSH], based on four categories (Fig. 4); and (b) extent of white on the outer vane [R5WEB, R6WEB] at a point approximately ⅓ of the total feather length from the feather tip, based on five categories (1 = 100 percent white; 2 = 75 percent; 3 = 50 percent; 4 = 25 percent; 5 = no white present). Additionally, the extent of white eye-ring feathering [EYERING] on specimens of alternate-plumaged males was estimated to the nearest 25 percent (no eye-ring = 0 percent; complete eye-ring = 100 percent).

Colorations of soft parts, including foot pad, tarsus, upper mandible, tip (distal ⅓) of lower mandible, base (proximal ⅔) of lower mandible, and iris were recorded from freshly collected specimens by direct comparison with standardized color swatches provided by Smithe (1975).

Variation in breast and back plumage coloration was analyzed using a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment. Flatness of the 100 percent line was maintained within limits of 1.0 percent, and flatness of the 0 percent line within 0.5 percent. The sample port was narrowed to a diameter of 11 mm to permit examination of limited areas of uniformly colored plumage; background of the contracted hole was painted with Krylon Spray Paint, Number 1602, Ultra Flat Black Enamel produced by Borden, Inc. Specimens with soiled, excessively worn or ruffled plumage were excluded. The 10 selected ordinate method of Hardy (1936) was used to calculate tristimulus values (*X, Y, Z*) from the spectrophotometer curves of percentage reflectance between 400 and 700 mμ. Dominant wavelength [BRSTW, BACKW], brightness [BRSTB, BACKB] and excitation purity [BRSTP, BACKP] were then determined from these values according to the procedures outlined by Judd (1933).

Biometric Analyses

Statistical routines were performed on the DEC MicroVAX II computer at Manomet Bird Observatory, using SAS (Version 5.16) procedures CANDISC, CLUSTER, CORR, DISCRIM, GLM, MEANS, NPAR1WAY, PRINCOMP, REG, TREE, UNIVARIATE, and VARCLUS. Redundancy among characters was analyzed through phenograms depicting the results of oblique component analysis of the correlation matrix of 28 morphological characters. Means, variances and coefficients of variation for each character were calculated for males and females of each sample area. Geographic variation within each character was examined using analysis of variance (ANOVA) for both sexes of each species; patterns of variation were summarized visually using pie diagrams to represent character means for each sample area. Pearson product-moment correlation coefficients, based on sample means, were calculated for males of *P. melanura* and *P. californica* to determine the relationship between body size (as expressed by MASS) and six measurements of body dimensions (BLEN, BWID, BDEP, TAR-

TOE, P6LEN, TLEN); the predictive value of MASS as an indicator of these six characters was further examined using linear regression.

Multivariate analysis of variance (MANOVA) was used to test whether the location of centroids representing each sample area, derived from 22 characters (BLEN, BWID, BDEP, TARTOE, P3–10LEN, TLEN, R4–6PCT, R5–6SSH, R5–6SPCT, R5–6WEB), were significantly different in multivariate space. For specimens in which three or fewer characters were missing, sample area means (calculated by sex) were substituted for the missing values in MANOVA and subsequent multivariate procedures. Specimens in which measurements of more than three characters were missing were excluded from the multivariate analyses.

Two distinct principal components analyses (PCAs), based on orthogonal, unrotated eigenvectors derived from the covariance matrix of the 22 characters listed above, were performed as a method of data reduction. To examine broad patterns of phenetic similarity among putative species groups, principal component (PC) scores were first obtained for all individuals (by sex); mean PC values for each sample area were then calculated based on these individual scores. Secondly, separate PCAs were performed for each species, with sample area means again being calculated for the first three PC ordinations using the scores obtained for individual specimens. Mean scores of PCs1–3 for each sample area were displayed visually using pie diagrams to depict the geography of intraspecific character variation, and the Sum of Squares Simultaneous Test Procedure (SS-STP) (Gabriel 1964; Gabriel and Sokal 1969) was used as a multiple comparison method to identify maximally nonsignificant subsets of these sample means.

Patterns of phenetic similarity between sample areas were also described through construction of phenograms based on average linkage (unweighted pair-group method using arithmetic averages, UPGMA) cluster analysis. UPGMA phenograms were similarly constructed using the results of canonical discriminant analysis (CDA), a method of dimension-reduction comparable to PCA but which summarizes between-class variation based on *a priori* identification of the groups (in this case, sample areas) being compared.

CDA was also used to compare the phenetic similarity of 20 specimens collected in a zone of sympatry (BG05, BG27), where hybrid individuals might most likely be found, with samples of *P. melanura* and *P. californica* obtained from adjacent regions of allopatric occurrence (YU03, SF04, ER26, PP28). Discriminant function analysis (DFA) was similarly used to examine these 20 specimens. Using a classification criterion calculated from the pooled covariance matrix of the allopatric reference specimens, DFA assigns each test individual (specimens from the zone of sympatry) to the class (specimens from allopatric regions) from which it has the smallest generalized squared distance. These assignments were then compared to identifications made prior to the analysis on the basis of non-morphological (vocal) characters.

Vocal Analyses

Approximately 20 h of magnetic tape recordings of calls of *Polioptila* were collected, representing a total of 447 individual males (Table 1). Recording equipment included a Sennheiser ME88 directional microphone and, at different times during the study, a Uher 4000 Report IC reel-to-reel recorder and a Sony TC D5M cassette recorder. Verbal descriptions of the behavioral context of each

vocalization were simultaneously recorded. To confirm uniformity of recording speed under battery powered field conditions, standard calibration tones from a tuning fork were frequently included during recording sessions. Magnetic tapes recorded during this study have been deposited in the Library of Natural Sounds, Cornell Laboratory of Ornithology. Sound spectrograms were prepared from these recordings using a Kay Elemetrics Model 7029A Sona-Graph (wide band setting; 80–8,000 Hz).

Vocalization playback experiments, similar to those developed by Lanyon (1963, 1967), were used to evaluate the possible importance of vocal differences in *Polioptila* as reproductive isolating mechanisms. Simultaneous playbacks of recordings of two species were presented to males during the breeding season from tape recorders located approximately 7–8 m apart. During the initial five-min exposure period the bird's response to a crudely mounted, male *P. californica* specimen positioned 1 m above each tape recorder was categorized as either (a) no evident response or (b) positive response, ranging from visual orientation toward the vocalization source, approach toward the vocalization source and/or countersinging directed toward the vocalization source, or actual physical contact with the specimen. One min of taped silence followed the first five-min exposure, after which the same sequence of recordings was repeated but with each species' vocalizations being switched to the opposite recorder. Again, the behavioral response of the test individual was categorized. To reduce the possibility of habituation caused by repeated exposures, each bird was tested with only one playback sequence.

RESULTS

Geographic and Ecological Distribution

The general distribution of *P. melanura, P. californica* and *P. nigriceps* shows that all three species are primarily allopatric or parapatric, although limited areas of sympatry exist between *P. melanura* and *P. californica* and between *P. melanura* and *P. nigriceps* (Fig. 1). The following discussion first provides an overview of each species' distribution. Secondly, ecological and behavioral observations are described from the areas where *P. melanura* and *P. californica* coexist.

Polioptila californica

Polioptila californica is nearly endemic to Baja California, with its range barely extending northward into the United States along the coast of southern California west of the Peninsular and Transverse Ranges (Fig. 1). It is common and widespread throughout the Baja California peninsula, except for (a) the area north of approximately 31°N latitude and east of the Sierra San Pedro Mártir, (b) the higher elevations of the Sierra Juárez, Sierra San Pedro Mártir, and Sierra de la Giganta characterized by pine-oak woodland and/or coniferous forest, and (c) certain islands in the Gulf of California (discussed below). North of Baja California the species' recent distribution has apparently always been somewhat patchy (Grinnell and Miller 1944), with this pattern being exaggerated by the extensive habitat destruction in coastal southern California that has occurred since World War II (Atwood 1980). Because its habitat in California is both restricted and declining, *P. californica* has been identified as a "Species of Special Concern" in the state

FIG. 5. *Polioptila californica* habitat in coastal southern California and Baja California north of 30°N latitude. Mexico, Baja California, San Telmo.

(Remsen 1978), and is currently considered a candidate for listing as a "Threatened Species" by the California Department of Fish and Game (J. Gustafson, pers. comm.).

Polioptila californica is found in a variety of major plant associations over its geographic range. North of latitude 30°N the species occurs primarily in coastal or inland sage scrub plant communities at elevations less than approximately 1,000 m (Fig. 5). Dominant plant species in these habitats include *Artemisia californica, Salvia* spp., *Eriogonum fasciculatum, Rhus integrifolia, Encelia californica, Opuntia* spp., and *Haplopappus* spp. (Munz and Keck 1959; Wiggins 1980). Most of these plants do not extend south of 30°N latitude, the approximate limit of the Mediterranean climatic zone (Wiggins 1980; Cody et al. 1983). South of 30°N latitude, *P. californica* is less restricted as to habitat or elevation, and occurs throughout all of the various subregions of the Sonoran desert which dominate the remainder of the Baja peninsula (Figs. 6, 7). Dominant plant species include, in various localities, *Agave* spp., *Yucca valida, Idria columnaris, Pachycormus discolor, Machaerocereus gummosus, Ambrosia* spp., *Atriplex* spp., *Lycium* spp., *Pachycereus pringlei, Lysiloma candida, Erythea brandegeei, Cyrtocarpa edulis, Acacia brandegeana, Cercidium microphyllum, Bursera hindsiana, Jatropha cinera, Opuntia* spp., and *Ferocactus* spp. In the open desert of the Magdalena Plains and Vizcaíno Peninsula, *P. californica* appears to be most abundant in relatively densely vegetated areas such as occur along washes, alluvial fans or other drainage systems. Farther south, in the Cape region, it is abundant in dense thorn scrub habitats.

Murphy (1983b) identified 24 islands in the Gulf of California with areas >0.5

FIG. 6. *Polioptila californica* habitat in the Vizcaino desert of central Baja California. Mexico, Baja California (Sur), 2 km N San Ignacio.

FIG. 7. *Polioptila californica* habitat in the Cape region of Baja California. Mexico, Baja California (Sur), 4 km N of Los Barriles.

km^2. Specimen records support the occurrence of *P. californica* on only two of these islands: Espíritu Santo and San José (Fig. 1). Additionally, specimens of *P. californica* were available from Isla Santa Margarita and Isla Magdalena on the Pacific coast of Baja California. These islands are presently separated from the peninsular mainland by narrow, shallow-water channels, and during recent geologic time were connected to the adjacent mainland.

Cody (1983) did not discriminate between Blue-gray Gnatcatchers (*P. caerulea*) and "black-tailed" gnatcatchers (including both *P. melanura* and *P. californica* as defined here) during his brief avifaunal surveys of many of the islands in the Gulf of California. Consequently, his summary of gnatcatcher distribution on these poorly studied islands is of uncertain value. Nonetheless, in the absence of better information, his observations are discussed here.

In addition to Espíritu Santo (including Partida Sur) and San José, Cody (1983) stated that "black-tailed" gnatcatchers were recorded on the following Gulf islands: Ángel de la Guarda (= *P. melanura,* see below), San Esteban (probably *P. melanura,* see below), Cerralvo, Carmen, Santa Cruz, Monserrate, Coronados, Danzante, San Francisco, and Santa Catalina. In contrast with these reports, on collecting trips Townsend (1923) and Banks (1963a, b) found only *P. caerulea* on Cerralvo, Carmen, Santa Catalina, Monserrate, Coronado, and Danzante; Banks (1963a) failed to find any gnatcatchers on Santa Cruz or San Francisco. The discrepancies in these data clearly indicate the need for additional specimen material from islands in this region, especially in light of the migratory behavior of *P. caerulea* and consequent high probability of this species occurring on virtually all of the Gulf islands.

Polioptila californica does not occur on any of the southern California Channel Islands (Diamond and Jones 1980), on Islas de Los Coronados, located 13 km W of Tijuana, Baja California (Jehl 1977), or on Isla Cedros, located 23 km NW of Punta Eugenia on the Vizcaíno Peninsula of Baja California (Grinnell 1928). In the Gulf of California, the species has been documented by specimens only from Espíritu Santo and San José, both considered by Murphy (1983b) to be "land-bridge" islands that were recently connected to the Baja peninsula during periods of lowered sea levels in the Pleistocene. Murphy (1983b) also described Carmen, Coronados, San Francisco, and Danzante as land-bridge islands, lending some credence to Cody's (1983) report of "black-tailed" gnatcatchers from these localities. Because I do not believe that either *P. californica* or *P. melanura* is a probable overwater colonist, and because Monserrate, Santa Catalina, Santa Cruz, and Cerralvo have not been connected to the Baja California peninsula in recent geologic time (Murphy 1983b), I am skeptical of Cody's (1983) listing of "black-tailed" gnatcatchers from these localities.

Polioptila melanura

Polioptila melanura is widely distributed throughout the arid lands of the southwestern United States and Mexico in two major, disjunct areas (Fig. 1). One of these regions, located west of the Continental Divide, follows the general boundaries of the Sonoran desert; the other, situated east of the Divide, the limits of the Chihuahuan desert. In northern Baja California, *P. melanura* is restricted to the area east of the Sierra Juárez and Sierra San Pedro Mártir; in the north central

FIG. 8. *Polioptila melanura* habitat in the Sonoran desert of southeastern California and northwestern Baja California. Mexico, Baja California, 16 km N of San Felipe.

portion of the peninsula, it occurs only in the immediate vicinity of the Gulf coast south to approximately 29°N latitude.

Ecologically, *P. melanura* occurs in a variety of major Sonoran desert plant communities. In the western part of its range (Figs. 8, 9) its typical habitat is dominated in different localities by plant species such as *Larrea tridentata, Franseria dumosa, Prosopsis juliflora, Cercidium* spp., *Olneya tesota, Fouquieria* spp., *Carnegiea gigantea, Ferocactus Wislizenii, Encelia farinosa, Lemaireocereus Thurberi, Lophocereus Schottii, Jatropha* spp., *Lysiloma divaricata, Acacia* spp., and *Bursera* spp. (Shreve and Wiggins 1964). In the eastern, Chihuahuan desert portion of the species' range (Figs. 10, 11), dominant plant species frequently include *Larrea tridentata, Flourensia cernua, Parthenium incanum, Jatropha dioica, Koeberlina spinsoa, Prosopsis* spp., *Lycium* spp., *Acacia* spp., *Lophocereus* spp., *Cassia* spp., *Celtis pallida, Agave* spp., *Atriplex* spp., *Allenrolfea* spp., *Mimosa* spp., and *Ephedra* spp. (Jaeger 1957; Morafka 1977).

I suspect that as a result of ecological barriers only limited gene flow presently occurs between the Sonoran and Chihuahuan desert populations of *P. melanura.* The closest point of present contact between these two major desert regions occurs across the Mogollon Plateau of extreme southeastern Arizona and southwestern New Mexico (Shreve and Wiggins 1964). In this area, described by Morafka (1977) as the Cochise Filter Barrier, "conditions are arid but not desert and the vegetation is a transition between desert and grassland" (Shreve and Wiggins 1964). Such conditions have probably existed to varying degrees since the Pliocene (6–4 MYBP), when the formation of present-day uplands coupled with declining temperatures caused the previously continuous expanse of desert or pre-desert scrub in this

FIG. 9. *Polioptila melanura* habitat in the Sonoran desert of southern Arizona and the northwestern Mexican mainland. Arizona, Pima Co., 3 km SE of Quijotoa.

FIG. 10. *Polioptila melanura* habitat in the Chihuahuan desert of Mexico. Mexico, Durango, 8 km W of San Juan del Río.

FIG. 11. *Polioptila melanura* habitat in the Chihuahuan desert of Mexico. Mexico, Guanajuato, 1.5 km WSW of Dolores Hidalgo.

area to be fragmented (Cooper and Silver 1964; Morafka 1977). *Polioptila melanura* occurs in very low densities in the patchy and limited areas of suitable habitat in this region, and I speculate that at the present time individuals only rarely disperse across the Continental Divide.

The distribution of *P. melanura* on islands in the Gulf of California is only slightly less confused than that described above for *P. californica.* Because the range of *P. melanura* on the peninsular mainland does not extend south of approximately 29°N latitude, presumably only those islands referred to as the "midriff" islands (Lindsay 1983; Murphy 1983b) would be potentially included in the species' range. Specimens of *P. melanura* are known from Tiburón and Angel de la Guarda. On the basis of vocal characters, T. L. George (pers. comm.) identified only *P. melanura* on Ángel de la Guarda; additionally, both George and Cody (1983) reported this species from San Esteban. Whereas Tiburón is a "land-bridge" island that probably was connected to the Sonoran mainland during lowered Pleistocene sea levels, both Ángel de la Guarda and San Esteban are considered "deep-water" islands that were unaffected in their isolation from the mainland by fluctuating sea levels (Murphy 1983b). Both Ángel de la Guarda and San Esteban are probably of comparatively recent origin, having been formed when their continental connections were severed by tectonic events approximately one million years ago; Ángel de la Guarda was formed from peninsular regions of Baja California, whereas San Esteban is thought to have broken away from the Sonoran side of the Gulf (Moore 1973; Bischoff and Henyey 1974; Murphy 1983b). None of the other midriff islands apparently support "black-tailed" gnatcatchers (Cody 1983), although more field work in this area is needed.

FIG. 12. *Polioptila nigriceps* habitat in the arid thorn scrub of the Mexican mainland's western coast. Mexico, Colima, 18 km S of Colima.

POLIOPTILA NIGRICEPS

The principal range of *P. nigriceps* extends along the arid coast of the Mexican mainland west of the Sierra Madre Occidentál from central Sonora south to Colima (Fig. 1). Phillips et al. (1973) described the first discovery of a breeding pair of this species in the United States, and subsequent observations have identified several localities in southeastern Arizona where small numbers of *P. nigriceps* have been sporadically observed in recent years (Davis and Russell 1984). North of approximately 28°N latitude the species might not be permanently resident (S. M. Russell, pers. comm.). *Polioptila nigriceps* is unrecorded from any of the islands in the Gulf of California.

Throughout most of its range *P. nigriceps* occurs primarily in vegetation described as Sinaloan thorn scrub or Sinaloan deciduous forest (Fig. 12), usually at elevations less than 800 m (S. M. Russell, pers. comm.). In central Sinaloa the dominant plant species of this vegetation type include *Trichlia trifolia, Zizyphus amole, Guazuma ulmfolia, Ceiba accuminata, Tabebuia rosea, Morisonia americana,* and *Caesalpinia eriostachys* (Raitt and Hardy 1979). At the northern limits of its range in central Sonora and the United States, *P. nigriceps* generally occurs in riparian associations dominated by *Prosopsis juliflora, Celtis reticulata, Sambucus mexicana, Senecio* spp., *Salix* spp., and *Acacia greggii* (Phillips et al. 1973).

AREAS OF SYMPATRY BETWEEN *POLIOPTILA MELANURA* AND *P. CALIFORNICA*

Three principal areas of sympatry were documented between *P. californica* and *P. melanura*: (a) near Palm Springs, Riverside County, California; (b) in the vicinity of Valle de Trinidad, Baja California; and (c) along the coastal Gulf strip

of north central Baja California. Because observations made in these areas form one of the principal lines of evidence supporting separation of *P. californica* and *P. melanura* as distinct species, details are provided below concerning their distribution, ecology, and behavior in localities where they coexist.

Palm Springs, Riverside Co., California

The sympatric occurrence of *P. californica* and *P. melanura* in the vicinity of Palm Springs is supported by three specimens of *P. californica* taken in this area in the early 1900s; past and recent specimens of *P. melanura* collected from the Palm Springs area are abundantly represented in museum collections. The first example of *P. californica* recorded from this region, a female collected 2 mi E of Palm Springs on 1 January 1904 (MVZ 39293), was thought by Grinnell (1904) to be "doubtless a straggler from the direction of Banning." Subsequent specimens (both labeled "Palm Springs") include a male collected on 19 April 1916 (DC 313A) and a female (labeled "breeding," but without additional notes) taken on 4 April 1918 (CAS 56641).

No recent records of *P. californica* have been obtained in the Palm Springs area, nor do I know of any recent observations of the species from the western side of San Gorgonio Pass where it was historically common (Atwood 1980). Some changes have occurred in the mesic vegetation of the desert washes found in the Palm Springs-San Gorgonio Pass area since World War II, and it is possible that plant associations once permitting occasional contact between *P. californica* and *P. melanura* no longer exist. No extensive contact zone has been documented in this region.

Valle de Trinidad, Baja California, Mexico

Valle de Trinidad was identified as an area of sympatry between *P. californica* and *P. melanura* by Grinnell (1928). As at Palm Springs, this locality is near a relatively low-elevation pass where habitat suitable for *P. californica* extends up from the west and makes contact with limited eastward extensions of typical *P. melanura* habitat. *Polioptila californica* is certainly the more common of the two species in the vicinity of Valle de Trinidad. I am aware of only one specimen record of *P. melanura* from this site (MVZ 50414). However, I tape-recorded a breeding pair of this species in desert wash vegetation 2 km NW of Ejido San Matías on 5–6 June 1982 (an area where *P. californica* was also recorded), and know of a reliable sight record of *P. melanura* made on 19 March 1983 approximately 6.5 mi NW of Valle de Trinidad (R. E. Webster, pers. comm.). *Polioptila californica* and *P. melanura* apparently have only minimal contact with one another in the Valle de Trinidad area. The former species occurs primarily in widespread sage scrub vegetation dominated by *Artemisia, Salvia,* and *Rhus,* whereas the latter is generally restricted to typical (but limited in extent) Sonoran desert wash vegetation dominated by *Prosopsis.*

Bahía San Luís Gonzaga (and Vicinity), Baja California, Mexico

The third known area of sympatry between *P. californica* and *P. melanura* is more extensive geographically than those at Palm Springs or Valle de Trinidad, and probably represents the only region where both forms come in contact regularly. This previously undescribed area extends north along the coastal Gulf strip

of north central Baja California from approximately latitude 29°N to the vicinity of Bahía San Luís Gonzaga and inland along the eastern base of the Sierra San Pedro Mártir as far north as Arroyo El Cajón. I visited several sites in this contact zone (Fig. 13).

Along the Gulf coast of Baja California between 31–29°N latitude, *P. californica* was generally encountered in relatively dense desert vegetation located along washes and major drainage systems, whereas *P. melanura* occurred in more open, arid plant communities. However, these ecological differences were subtle, and it was not uncommon to find pairs of *P. melanura* and *P. californica* holding adjacent or nearly adjacent territories. Interspecific territorial interactions between presumed breeding males, involving chases and agitated, species-specific vocalizations (described below), were observed twice.

At each of the sites in north central Baja California where *P. melanura* and *P. californica* coexisted, one of the two species was always substantially more common (Table 2). Contact localities such as near Las Encantadas or Arroyo El Cajón were characterized by open Sonoran desert vegetation dominated by *Larrea tridentata, Franseria dumosa, Prosopsis juliflora, Cercidium* spp., *Olneya tesota,* and *Fouquieria splendens*; at these sites *P. melanura* was more abundant than *P. californica.* Near El Crucero (Fig. 14) or Las Arrastras, where the vegetation was more typically that of the Vizcaíno desert of central Baja California (dominant plant species including *Agave* spp., *Yucca valida, Pachycormus discolor, Prosopsis juliflora, Machaerocereus gummosus, Ambrosia* spp., *Atriplex* spp., and *Lycium* spp.), *P. californica* was more numerous.

Of 92 pairs of "black-tailed" gnatcatchers observed in regions of sympatry near Valle de Trinidad and east of the Sierra San Pedro Mártir in north central Baja California, assortative mating occurred in all 60 pairs of *P. californica* and 32 pairs of *P. melanura.* Although I would not exclude the possibility that mixed pairs of *P. melanura* and *P. californica* might rarely occur where the two species come in contact with each other, I saw no such pairs during my field work, nor did I obtain morphological or behavioral evidence of recognizable hybrids (see below).

"San Felipe Canyon," San Diego Co., California

Unitt (1984) suggested a possible area of sympatry between *P. melanura* and *P. californica* in San Diego County, California, based on specimen records in 1893 of both species from a site labelled as "San Felipe Canyon." Unitt (1984) restricted this uncertain locality to either "the present San Felipe Valley or Sentenac Canyon." I have found *P. melanura* in the San Felipe Valley area, but know of only unconfirmed recent sight records of *P. californica.* If this is an additional area of sympatry between the two species, it is very limited in geographic extent, like the contact areas at Palm Springs and Valle de Trinidad.

In summary, *P. melanura* and *P. californica* are allopatric throughout most of their ranges. Only along the Gulf coast of Baja California between 31–29°N latitude do the two species show broad geographic overlap, and in this area ecological differences reduce opportunities for contact. Where *P. melanura* and *P. californica* are distributed syntopically, assortative mating occurs. No instances of mixed pairs of *P. melanura* and *P. californica* have been documented in the zone of sympatry.

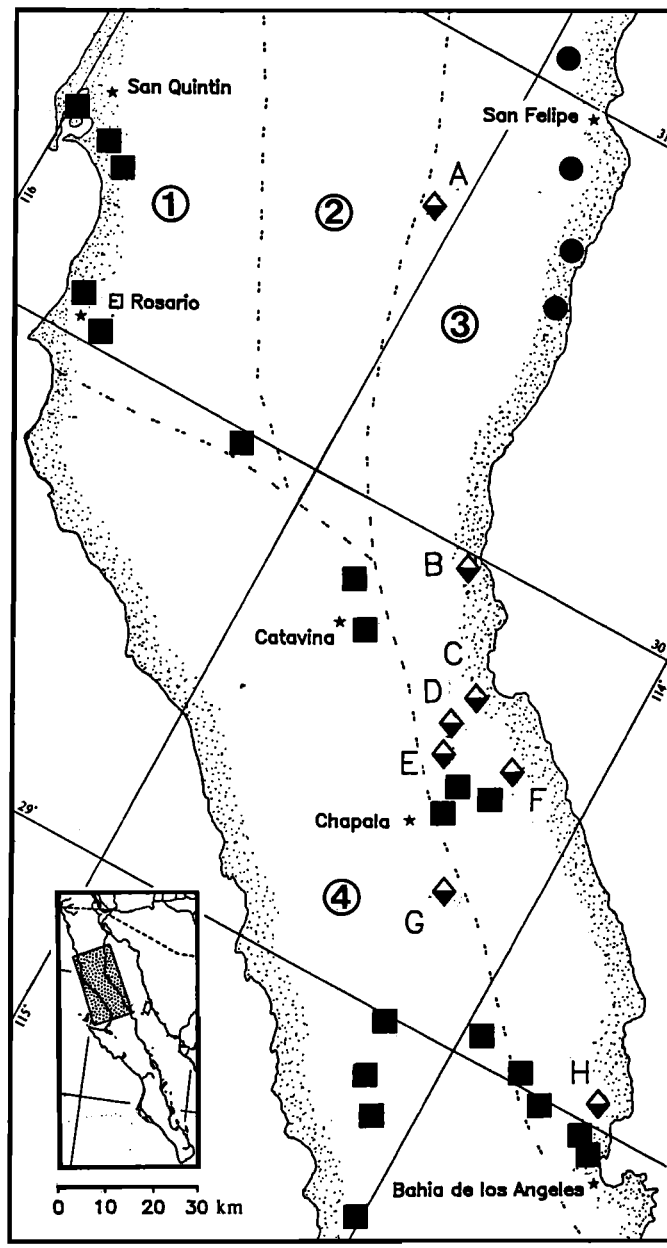


FIG. 13. Distribution of *Polioptila melanura* and *P. californica* in central Baja California. Solid squares = *P. californica*; solid circles = *P. melanura*; half-shaded diamonds = localities where *P. californica* and *P. melanura* are sympatric. Areas of documented sympatry include (A) Arroyo El Cajón; (B) Las Encantadas, 4.2 km NW; (C) Punta Finál, 8.3 km W; (D) Las Arrastras, 9.7 km NW; (E) Las Arrastras, 4.7 km NW; (F) Arroyo Calamajué, 18.3 km S of Ejido Hermenegildo Galiana; (G) El Crucero, 11.7 km NW; and (H) Bahía de los Angeles, 7.5 km N. Approximate distribution of major vegetation types indicated as follows: 1 = coastal sage scrub; 2 = chaparral and coniferous forest; 3 = Sonoran (Colorado) desert; 4 = Vizcaino desert.

TABLE 2

ABUNDANCE OF *Polioptila melanura* AND *P. californica* IN AREAS OF SYMPATRY

Locality	Number of pairs[a]		Dominant vegetation[b]
	P. melanura	*P. californica*	
Arroyo El Cajón	12	1	Sonoran
4 km NW Las Encantadas	13	4	Sonoran
10 km W Campo Punta Finál	2	1	Sonoran
10 km NW Las Arrastras	2	10	Vizcaino
10 km S Ejido Hermenegildo Galiana	1	2	Vizcaino
8 km NW El Crucero	1	10	Vizcaino
14 km NW El Crucero	1	3	Vizcaino
3 km N Bahía de los Angeles	0	6	Vizcaino
8 km N Bahía de los Angeles	2	14	Vizcaino

[a] Based on observations during random transects varying in length from 1–5 km and in duration from 1–4 h.
[b] See text for listing of dominant plant species.

BREEDING BIOLOGY

Although the field work associated with this study did not emphasize specific details of gnatcatcher breeding biology, incidental observations and information derived from museum egg collections indicate that in certain aspects consistent differences exist between *P. melanura* and *P. californica.* Mean clutch sizes from completed egg sets taken in southern California indicated that *P. melanura* lays significantly larger clutches ($\bar{X} = 4.21$, s.d. = 0.65; N = 33) than does *P. californica* ($\bar{X} = 3.84$, s.d. = 0.57; N = 61) (Wilcoxon 2-sample test, $P = 0.009$). Because all of these specimens were taken at approximately the same latitude, presumably

FIG. 14. Habitat in the region of sympatry between *Polioptila melanura* and *P. californica.* Mexico, Baja California, 8.3 km NW of El Crucero.

these differences are not merely the result of clinal variation in clutch size. Comparison of breeding chronology, based on southern California egg sets labeled as "fresh" or "slightly incubated" when collected, showed the mean date of nest initiation for *P. melanura* (6 April; s.d. = 13.84; N = 25) to be significantly earlier than that of *P. californica* (5 May; s.d. = 21.21; N = 47) (Wilcoxon 2-sample test, $P = 0.0001$). These differences in timing of breeding probably reflect the effects of climatic contrasts between the hot desert habitat of interior southern California and the more temperate coastal areas. I have no data concerning the relative breeding chronology of *P. melanura* and *P. californica* in areas where they occur sympatrically.

In southern California, mean nest height of *P. melanura* was significantly greater ($\bar{X} = 1.86$ m; s.d. = 1.03; N = 27) than that of *P. californica* ($\bar{X} = 1.04$ m; s.d. = 0.52; N = 35) (Mann-Whitney *U*-test, $P < 0.01$). These differences in nest placement probably reflect broad structural contrasts between the habitats of *P. melanura* (open desert wash vegetation, often including trees up to approximately 10 m in height) and *P. californica* (sage scrub vegetation, seldom exceeding 2 m in height). Study of a region where the two species are sympatric would reveal if nest height preferences differ when both occur in comparably structured habitats. Similarly, 75 percent of *P. melanura* nests in southern California (N = 24) were placed in *Prosopsis* or *Cercidium* whereas 73 percent of *P. californica* nests (N = 30) were in *Salvia* or *Opuntia*. The most frequently used nest sites were in both cases the dominant plants in the habitat of each gnatcatcher species; whether or not contrasts in nest site selection exist in areas of sympatry is unknown.

Polioptila melanura and *P. californica* appear to be similar in nest construction, incubation behavior, and care of the young (this study; Woods 1928). L. F. Kiff (pers. comm.) could discern no differences in egg shape, color, or size between the two species.

Vocal Differences and Reproductive Isolation

In the following discussion of gnatcatcher vocalizations, I first describe and compare the most frequently encountered calls of *P. melanura, P. californica,* and *P. nigriceps*. Vocal and contextual similarities were used as the basis for grouping these calls into distinct categories of assumed homology. Because most of these vocalization types appeared to be graded signals that were influenced by behavioral contexts difficult to define objectively, detailed quantitative analysis of vocal variation was deemed inappropriate. However, examples of spectrograms have been selected that demonstrate the extent of variation encountered for each call over the entire geographic range of each species. Based on a purely subjective analysis, I detected no evident patterns of intraspecific variation in any of the vocalization types.

Secondly, I also discuss the possible significance of interspecific vocal differences as reproductive isolating mechanisms, and describe the results of vocalization playback experiments conducted with each species.

Comparison of Major Vocalizations

Vocalization Type I
(*P. melanura*: *zeeee*)
(*P. californica*: *zeeer*; *feeur*)
(*P. nigriceps*: *feeur*)

This vocalization was frequently given by both sexes of all three species in a variety of contexts, including (a) male–female interactions, such as preceding, during, and following copulation, during nest construction, at incubation exchanges, or as a contact note between pair members; (b) agonistic encounters associated with territorial defense; and (c) agitated scolding elicited by the presence of predators or human disturbance. Minor sexual differences in the precise characteristics of these calls were found in each species; only vocalizations of males are presented here.

Type I vocalizations of *P. californica* were characterized by distinct frequency modulations; discrete, rapidly ascending and more slowly descending parallel bands of sound were generally evident in the spectrograms (Fig. 15, a–k). Audibly these calls resembled the "mewing" sound made by a small cat. The degree to which broad frequency noise occurred in the Type I vocalization of *P. californica*

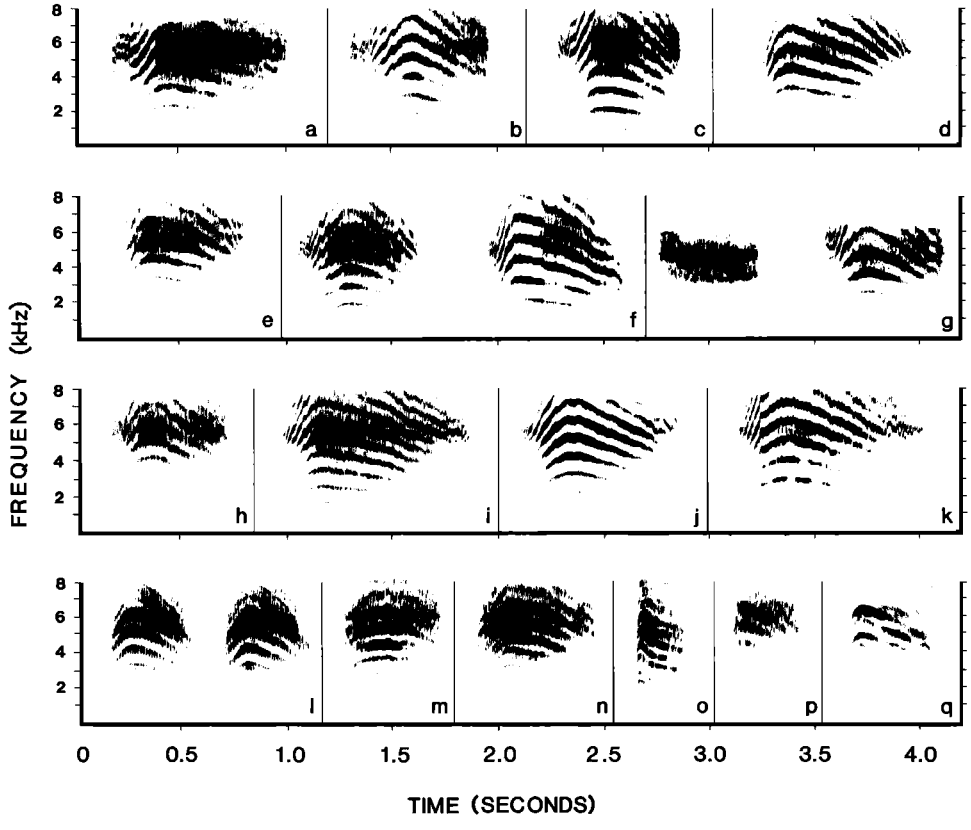


FIG. 15. Vocalization Type I in male *Polioptila californica* (a–k), *P. nigriceps* (l–n), *P. caerulea* (o), *P. plumbea* (p), and *P. albiloris* (q). Localities as follows: (a) California, San Diego Co., Lake Hodges; (b) California, San Diego Co., Camp Pendleton Marine Corps Base; (c) Mexico, Baja California, 11 km W Meling Ranch; (d) Mexico, Baja California, Arroyo El Cajón; (e) Mexico, Baja California, 4 km NW Las Encantadas; (f) Mexico, Baja California, 6 km NW Bahía de los Angeles; (g) Mexico, Baja California, 16 km NW El Crucero; (h) Mexico, Baja California, 9 km N Cataviña; (i) Mexico, Baja California (Sur), 30 km S Mulege; (j) Mexico, Baja California (Sur), 4 km N Los Barriles; (k) Mexico, Baja California (Sur), 5 km N La Paz; (l) Mexico, Sonora, 12.7 km W Alamos; (m) Mexico, Sinaloa, 8.3 km E Villa Unión; (n) Mexico, Colima, 16 km S Colima; (o) Mexico, Baja California (Sur), 4 km N Los Barriles; (p) Costa Rica, Parque Nacionál Cahuíta; (q) Mexico, Chiapas, Tonala.

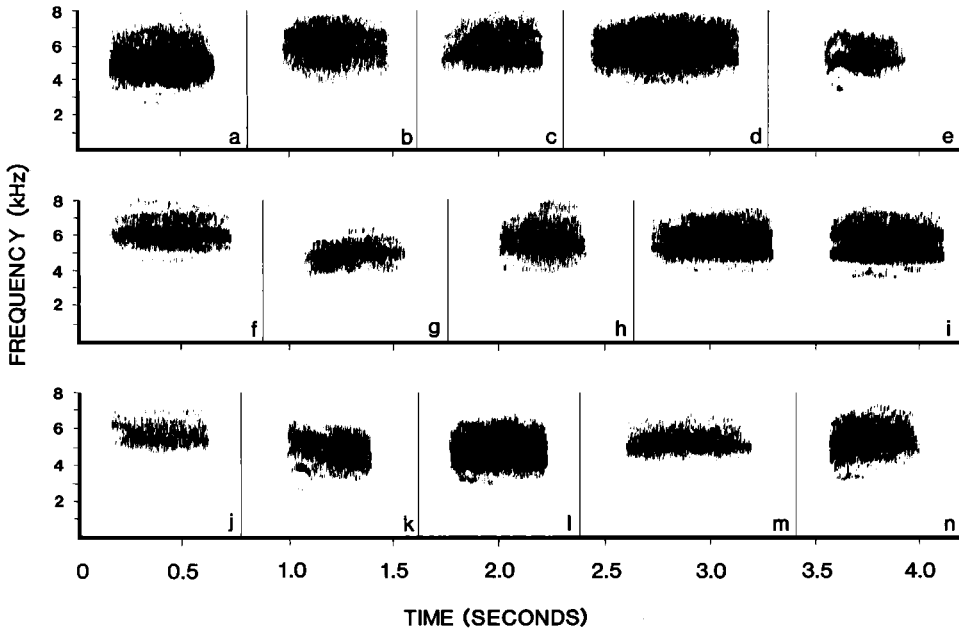


FIG. 16. Vocalization Type I in male *Polioptila melanura*. Localities as follows: (a) California, San Bernardino Co., 8 km W Ft. Piute; (b) Arizona, Mohave Co., Alamo Lake State Park; (c) Mexico, Baja California, Cantu Palms; (d) Mexico, Sonora, 42 km S Guaymas; (e) Mexico, Sonora, 8 km W Carbo; (f) Mexico, Baja California, 16 km N San Felipe; (g) Mexico, Baja California, 34 km N Puertocitos; (h) Mexico, Baja California, 10 km NW Las Arrastras; (i) Mexico, Baja California, 6 km NW Bahía de los Angeles; (j) Mexico, Baja California, 16 km NW El Crucero; (k) Mexico, Baja California, 4 km NW Las Encantadas; (l) Mexico, Coahuila, Lago Tulillo; (m) Mexico, San Luis Potosí, 20 km N El Huizache; (n) Mexico, Guanajuato, 1.5 km WSW Dolores Hidalgo.

varied substantially, probably due at least in part to differences in the behavioral context of the call. In cases where the bird appeared to be completely unagitated, Type I calls often had a clear, whistled quality (Fig. 15, j), whereas intense levels of agitation were characterized by harsh vocalizations with only minimal development of a distinct banding pattern or frequency modulation (Fig. 15, a, g). The most typical Type I vocalizations in *P. californica* were calls that began with a distinct "mewing" quality and then became increasingly harsh as the vocalization ended (Fig. 15, i).

In delivery, Type I vocalizations of *P. californica* were generally presented as either single calls or as two or three nearly identical calls spaced at approximately 0.5-sec intervals. These sequential Type I calls were frequently given by males from exposed perches and apparently functioned, along with Type II vocalizations (see below), in territorial advertisement.

Type I calls of male *P. nigriceps* strongly resembled those of the Type I vocalizations of *P. californica* (Fig. 15, l–n). Furthermore, the Type I vocalizations of three other "white-tailed" gnatcatcher species that I have heard in North and Middle America (Blue-gray Gnatcatcher, *P. caerulea*—Fig. 15, o; White-lored Gnatcatcher, *P. albiloris*—Fig. 15, p; and Tropical Gnatcatcher, *P. plumbea*—Fig. 15, q) are similar to the calls of both *P. nigriceps* and the "black-tailed" *P. californica*.

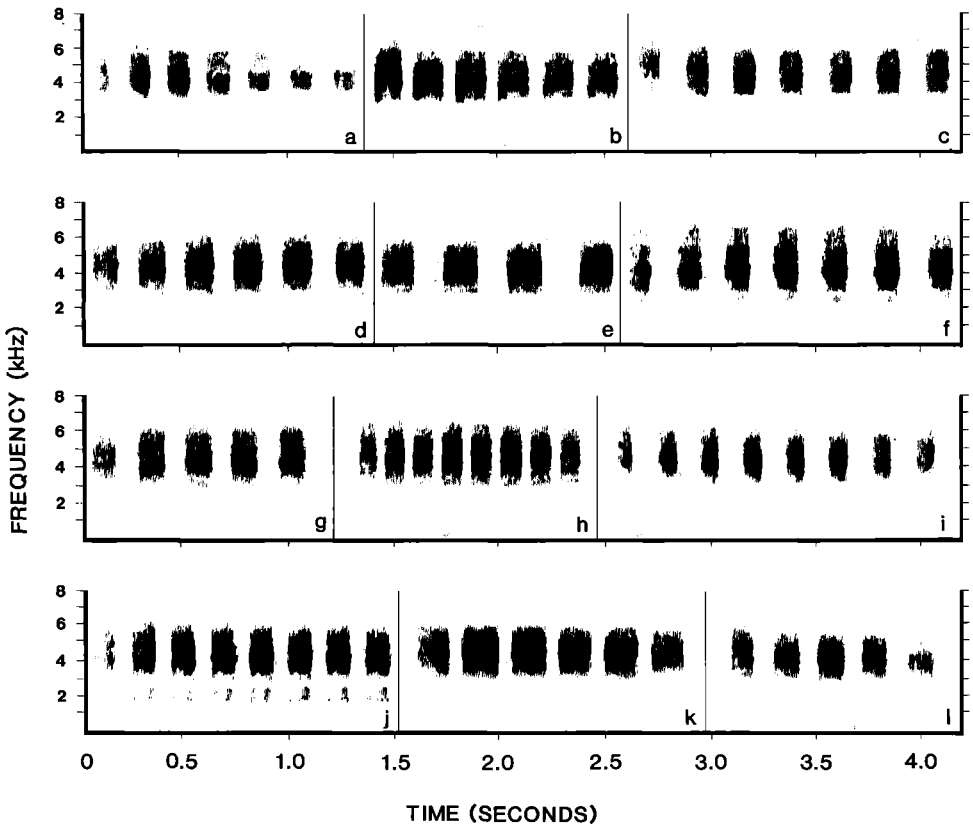


FIG. 17. Vocalization Type II in male *Polioptila melanura*. Localities as follows: (a) California, San Bernardino Co., 8 km W Ft. Piute; (b) Arizona, Mohave Co., Alamo Lake State Park; (c) Mexico, Sonora, 42 km S Guaymas; (d) Mexico, Baja California, Cañon Guadalupe; (e) Mexico, Baja California, 34 km N Puertocitos; (f) Mexico, Baja California, Arroyo El Cajón; (g) Mexico, Baja California, 10 km NW Las Arrastras; (h) Mexico, Baja California, 16 km NW El Crucero; (i) Mexico, Coahuila, Lago Tulillo; (j) Mexico, San Luis Potosí, 20 km N El Huizache; (k) Mexico, Coahuila, 37 km S Monclova; (l) Mexico, Guanajuato, 1.5 km WSW Dolores Hidalgo.

The discrete banding patterns typical of *P. californica* were largely nonexistent in the Type I vocalizations of male *P. melanura* (Fig. 16). Audibly, these calls generally lacked the "mewing" quality characteristic of *P. californica,* but instead consisted of harsh, broad frequency noise that only rarely (Fig. 16, e, k) showed limited tendencies toward the frequency modulation found in *P. californica.* Type I calls of *P. melanura* were similar to the harsh, non-"mewing" scold notes given by *P. californica* under agitated conditions (Fig. 15, g).

The delivery of Type I vocalizations by male *P. melanura* also differed sharply from that of *P. californica.* Only rarely were Type I calls given by *P. melanura* in a consecutive two or three-note sequence such as commonly occurred in *P. californica.* Whereas both species used Type I calls as part of their territorial advertisement, in *P. melanura* these vocalizations were almost always associated with other calls (especially vocalization Types III and IV, see below) that were nearly absent from the repertoire of *P. californica.*

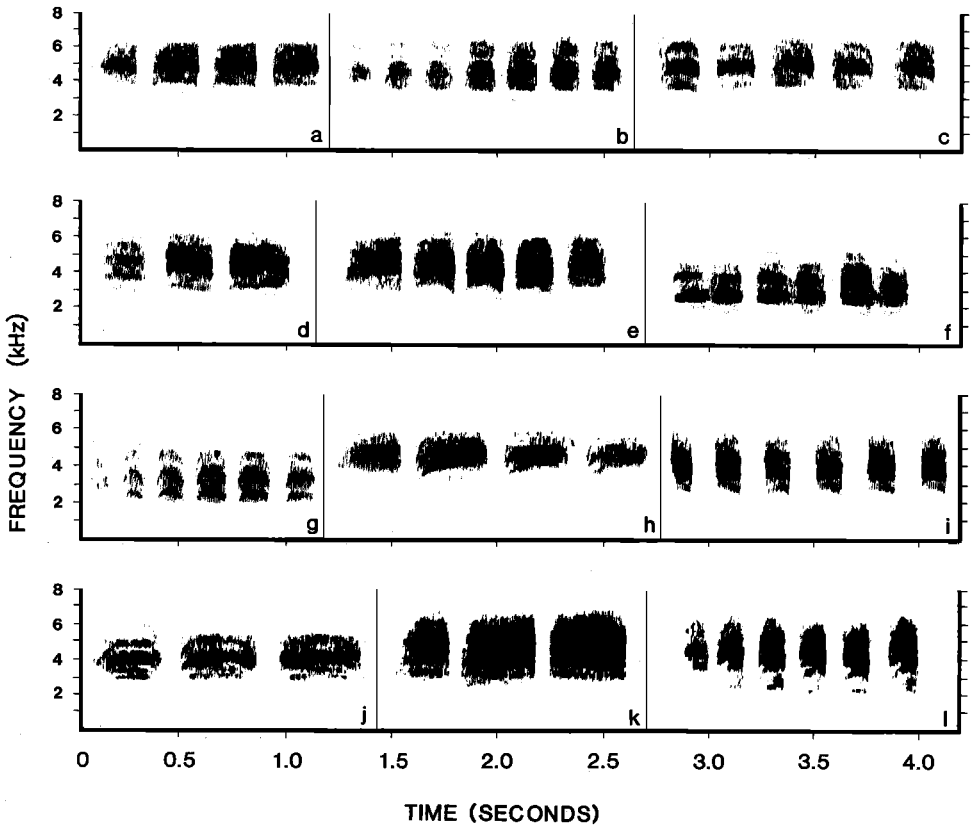


FIG. 18. Vocalization Type II in male *Polioptila californica*. Localities as follows: (a) California, San Diego Co., Lake Hodges; (b) Mexico, Baja California, 2 km W San Telmo; (c) Mexico, Baja California, 3 km E Ejido San Matías; (d) Mexico, Baja California, 30 km E El Rosario; (e) Mexico, Baja California, 16 km NW El Crucero; (f) Mexico, Baja California, 10 km NW Las Arrastras; (g) Mexico, Baja California, 12 km N Cataviña; (h) Mexico, Baja California, 6 km NW Bahía de los Angeles; (i) Mexico, Baja California, Arroyo El Cajón; (j) Mexico, Baja California (Sur), 30 km S Mulege; (k) Mexico, Baja California (Sur), 15 km SW Rosarito; (l) Mexico, Baja California (Sur), 4 km N Los Barilles.

Vocalization Type II
(*P. melanura*: *jee-jee-jee-jee-jee*)
(*P. californica*: *jzer-jzer-jzer*; *zew-zew-zew-zew*)

Vocalization Type II (Fig. 17, a–l) was by far the most frequent form of territorial advertisement used by *P. melanura*; it was often delivered monotonously from exposed perches for extended periods of time. Type II vocalizations were also given, usually in a rapid, modified form, as one of the common vocal components used during close pair interactions such as copulation. Only males gave typical Type II vocalizations.

In most cases Type II vocalizations of *P. melanura* consisted of 5–10 identical, evenly-spaced notes with abrupt beginnings and endings (Fig. 17, b–l). Most of the harsh, wide band noise comprising these notes was in the 4–6 kHz range. In contrast to the Type II vocalizations of *P. californica* described below, only rarely (Fig. 17, a) were Type II calls of *P. melanura* characterized by discrete concen-

trations of sound within this general frequency range. Type II calls of individual *P. melanura* varied considerably, possibly as a result of differing behavioral contexts. Numerous and closely spaced syllables of shorter duration were associated with Type II vocalizations given under high degrees of agitation (Fig. 17, h).

Although Type II calls of male *P. californica* (Fig. 18, a–l) generally resembled those of *P. melanura,* this vocalization type differed between the two species in several respects. Most importantly, the overall incidence with which Type II vocalizations were used by *P. californica* was substantially less than in *P. melanura.* Whereas Type II vocalizations were the dominant form of territorial advertisement given by *P. melanura, P. californica* more frequently used repeated sequences of two or three-note sequences of calls assumed to be homologous with the Type I vocalization of *P. melanura.* Compared to the extensive samples of Type II calls that were easily obtained from *P. melanura,* relatively few recordings of this vocalization type were collected from *P. californica.*

Also in contrast with *P. melanura,* spectrograms of Type II calls of *P. californica* generally displayed some localization of sound energy into variably distinct bands (Fig. 18, c, g). There was a tendency toward frequency modulation within each note of the Type II vocalization of *P. californica.* Although seldom discernable audibly as a distinct "mewing" sound because of the short duration of each element, this character was nonetheless reminiscent of the Type I call of the species. Type II vocalizations of *P. californica* were often characterized by less abrupt beginnings and endings (Fig. 18, j) than comparable calls of *P. melanura.* Finally, most non-agitated Type II calls in *P. melanura* consisted of approximately 5–10 identical elements delivered over a 1–2-sec interval. Type II vocalizations of *P. californica* usually included six or fewer syllables, each of which tended to be of longer duration than those of *P. melanura.*

Vocalization Type III
(*P. melanura*: *jit-jit-jit-jit*)

Vocalization Type III was one of the most frequently encountered calls of *P. melanura* (Fig. 19, a–d). It was often given during territorial advertisement, as a regular component of countersinging bouts with neighboring territorial males, and in scolding contexts. Each note of the call consisted of a very brief, wide band pulse of noise concentrated in the 4–7 kHz range. The individual notes comprising Type III calls of *P. melanura* were frequently delivered in rapid succession at intervals of approximately 0.2 sec, although isolated Type III calls were sometimes interspersed with other vocalization types. The number of repeated individual elements varied dramatically, but in most cases was <10.

Type III calls apparently also exist within the repertoire of *P. californica,* but are given rarely. In my only recording of this vocalization type (Fig. 19, e), the overall form appeared similar to Type III calls given by *P. melanura.* Slightly higher frequencies might characterize this vocalization in *P. californica,* but additional recordings would be necessary for confirmation.

Vocalization Type IV
(*P. melanura*: *ti-ti-ti-ti-ti*)

These intense, very high frequency (most sound energy distributed in the 7–8 kHz range) vocalizations (Fig. 19, f–dd) were primarily given by *P. melanura*

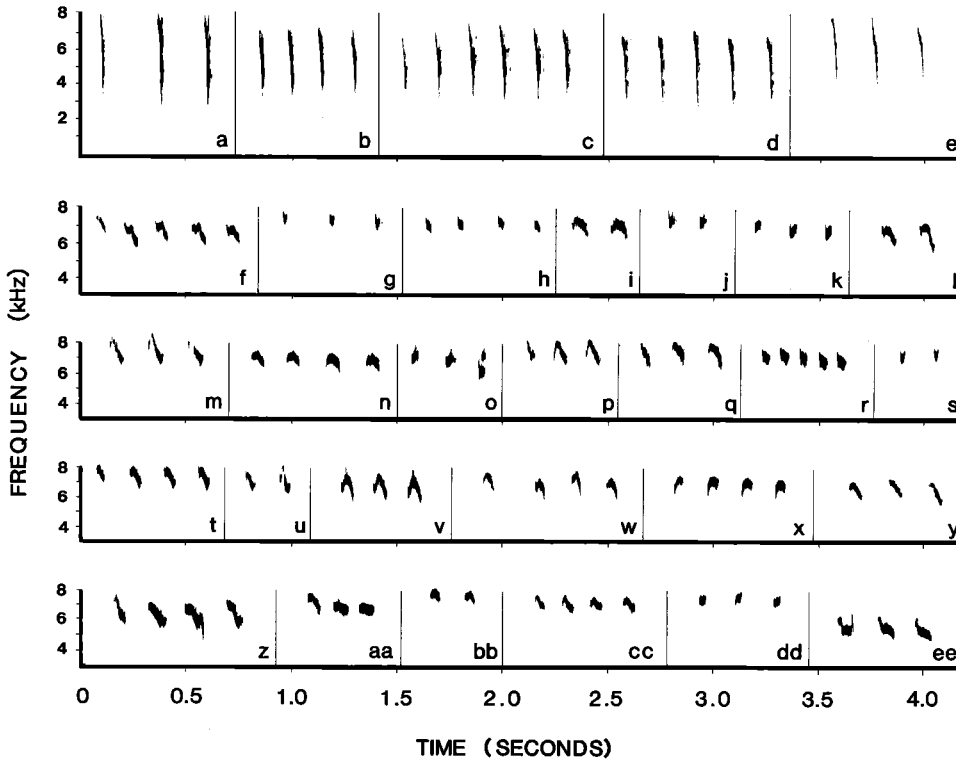


FIG. 19. Vocalization Types III (a–e) and IV (f–ee) in male *Polioptila melanura* (a–d, f–dd) and *P. californica* (e, ee). Localities as follows: (a) Mexico, San Luis Potosí, 20 km N El Huizache; (b) Mexico, Coahuila, Lago Tulillo; (c) Mexico, Baja California, Cantu Palms; (d) Mexico, Baja California, 6 km NW Bahía de los Angeles; (e) Mexico, Baja California, 6 km NW Bahía de los Angeles; (f) Mexico, Durango, 7 km W San Juan del Río; (g) Mexico, Durango, 7 km W San Juan del Río; (h) Mexico, Durango, 3 km N Rodeo; (i) Mexico, Coahuila, Lago Tulillo; (j) Mexico, San Luis Potosí, 10 km S Matehuala; (k) Mexico, Chihuahua, 25 km NE Ciudad Camargo; (l) Mexico, Durango, 3 km S Chocolate; (m) Mexico, Coahuila, 37 km S Monclova; (n) Mexico, Coahuila, 37 km S Monclova; (o) Mexico, Coahuila, 37 km S Monclova; (p) Arizona, Mohave Co., 40 km SE Yucca; (q) Arizona, Pima Co., 17 km S Why; (r) Arizona, Pima Co., 17 km S Why; (s) Arizona, Pima Co., 17 km S Why; (t) Arizona, Mohave Co., 40 km SE Yucca; (u) Arizona, Mohave Co., Alamo Lake State Park; (v) California, San Bernardino Co., 8 km W Fort Piute; (w) Mexico, Sonora, 8 km W Carbo; (x) Mexico, Sonora, 8 km W Carbo; (y) Mexico, Baja California, 16 km N San Felipe; (z) Mexico, Baja California, 3 km E Ejido San Matías; (aa) Mexico, Baja California, 34 km N Puertocitos; (bb) Mexico, Baja California, 10 km NW Las Arrastras; (cc) Mexico, Baja California, 6 km NW Bahía de los Angeles; (dd) Mexico, Baja California, 6 km NW Bahía de los Angeles; (ee) Mexico, Baja California, Agua Amarga.

in scolding contexts, and often were interspersed with Type III calls. Differences in the precise form of Type IV vocalizations might reflect individual or contextual variation. To my hearing, even those calls that differed substantially when viewed as spectrograms (Fig. 19, g, w) were audibly indistinguishable from one another.

As with Type III vocalizations, *P. californica* rarely gives a Type IV call (Fig. 19, ee) that is similar in form to those of *P. melanura* (Fig. 19, f, z). Type IV notes given by *P. californica* occurred at lower frequencies (5–6 kHz) than virtually all of the examples from *P. melanura*; however, this vocalization was so rarely encountered in *P. californica* that a more detailed comparison was impossible.

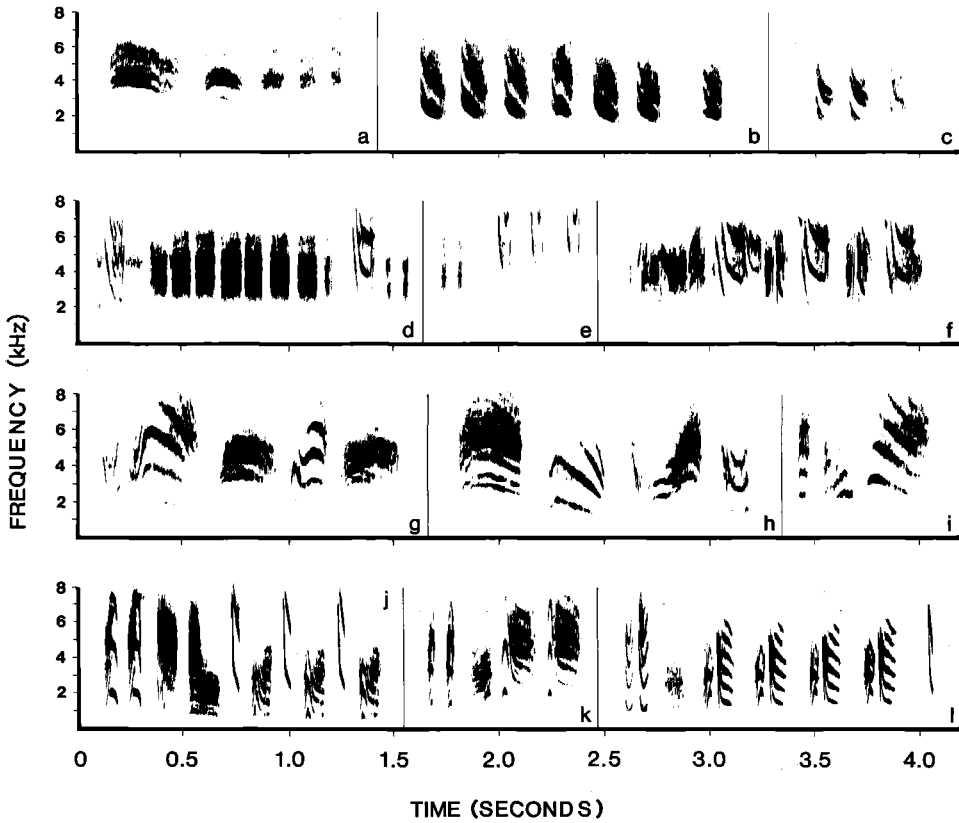


FIG. 20. Vocalization Types V (a–c) and VI (d–l) in male *Polioptila melanura* (a, d–f), *P. californica* (c, g–i) and *P. nigriceps* (b, j–l). Localities as follows: (a) California, San Diego Co., Anza Borrego State Park; (b) Mexico, Sonora, 12.7 km W Alamos; (c) Mexico, Baja California (Sur), 15 km SW Rosarito; (d) Mexico, Coahuila, 37 km S Monclova; (e) Mexico, San Luis Potosí, 20 km N El Huizache; (f) Mexico, Baja California, Arroyo El Cajón; (g–i) Mexico, Baja California (Sur), 15 km SW Rosarito; (j–l) Mexico, Sonora, 12.7 km W Alamos.

Vocalization Type V
(*P. melanura*: *jzeer-jzee-jze-jze-jze*)
(*P. californica*: *chew-chew*)
(*P. nigriceps*: *chew-chew*)

These vocalizations (Fig. 20, a–c) were used as alarm calls in each of the three species. Recordings were obtained during attacks by Sharp-shinned Hawks (*Accipiter striatus*), human inspection of active nests, approach of predators toward juveniles, and holding mist-netted individuals in the hand. I suspect that additional alarm calls exist in the repertoire of each species, especially several soft chip notes that are not discussed here.

Type V vocalizations of *P. nigriceps* (Fig. 20, b) and *P. californica* (Fig. 20, c) were virtually indistinguishable. Interspecific playback of these calls elicited rapid escape responses by both species. Although I do not have an available recording to use in spectrogram analysis, alarm calls I have heard from *P. caerulea* were reminiscent of those given by *P. nigriceps* and *P. californica*. By contrast, the Type

V vocalization of *P. melanura* is substantially different (Fig. 20, a). This call is interesting not only because of its dissimilarity to the apparently homologous calls of *P. californica* and *P. nigriceps,* but also because it is one of the few vocalizations of *P. melanura* that displays the frequency modulation associated with other calls of *P. californica* and *P. nigriceps.*

Vocalization Type VI
(warbled notes, all three species)

These vocalizations were given by males of each of the three species during territorial chases and conflicts. The spectrograms shown here (Fig. 20, d–l) reflect only short segments of what were usually lengthy, complex and non-repetitive sequences of calls. Type VI vocalizations were commonly heard and recorded during limited field work with *P. nigriceps* (Fig. 20, j–l). In contrast, *P. melanura* (Fig. 20, d–f) and *P. californica* (Fig. 20, g–i) seemed to use such vocalizations much less frequently.

The variety of Type VI vocalizations used by each species makes interspecific comparisons difficult. *Polioptila nigriceps* appeared to be the most different of the three species, both in the exact form of its calls as well as in the overall diversity of warbled and whistled vocalizations included in its repertoire (very few of the recorded Type VI calls of *P. nigriceps* are presented here). Type II vocalizations occurred as regular components of the Type VI calls of *P. melanura* (Fig. 20, d), but were apparently absent from *P. californica.* Type VI calls of *P. melanura* lacked the "mewing" notes repeatedly found in the *P. californica* series. Type VI calls of *P. californica* regularly incorporated Type I vocalizations (such as the initial note shown in Fig. 20, h); Type I calls appeared to be less frequently included in Type VI sequences of *P. melanura.*

Vocal Playback Experiments

Numerous studies of avian speciation, especially those involving sibling species, have used vocal differences as indicators of species limits and phylogenetic relationships (e.g., Payne 1986). The vocalizations of *P. californica* and *P. melanura,* although sharing certain resemblances, are nonetheless highly distinctive when compared to one another. To evaluate the possible importance of these differences as potential reproductive isolating mechanisms in *Polioptila,* playback experiments were performed similar to those developed by Lanyon (1963, 1967). The results of these tests, using playback sequences that included examples of vocalization Types I, II, III and IV (see above), are presented in Table 3.

Individual males of *P. melanura,* which were simultaneously presented with vocal recordings of *P. melanura* and either *P. californica* or *P. nigriceps,* responded to their own species' calls with strongly territorial, aggressive behavior (countersinging, close approach, or actual physical contact) while ignoring the vocalizations of the other species (Table 3). Following the initial 5-min exposure the recordings were switched, with each species' vocalizations being thereby associated with the opposite visual stimulus. After this switch occurred, the agonistic behavior of the test individuals was in all cases redirected to the model that "gave" vocalizations of *P. melanura* (Table 3).

Individuals of *P. californica,* which were simultaneously exposed to conspecific

TABLE 3

SPECIES RECOGNITION BASED ON VOCAL DIFFERENCES DURING PLAYBACK TESTS

Species	Playback combinations[a]					
	californica-melanura		*californica-nigriceps*		*melanura-nigriceps*	
P. melanura (A)[b]	0	7 (7)	—		5	0 (5)
P. melanura (B)	0	7 (7)	—		5	0 (5)
P. californica (A)	11	2 (13)	3	3 (6)	0	3 (8)
P. californica (B)	9	2 (13)	2	3 (6)	0	8 (8)
P. nigriceps (A)	0	3 (7)	2	8 (10)	0	5 (5)
P. nigriceps (B)	0	1 (7)	0	10 (10)	0	5 (5)

[a] For each species, values represent the number of tests in which aggressive territorial behavior was elicited by the playback of vocalizations of the indicated species; total number of trials indicated in parentheses. For example, in 13 presentations of recorded *californica* and *melanura* vocalizations to *P. californica* during exposure period B, *californica* responded positively toward its own calls in 9 cases and positively toward the calls of *melanura* in 2 cases; in 2 of the 13 trials no positive response was noted. See text for further discussion.

[b] Results during initial 5 min of playback exposure indicated by (A). Results from the second 5-min exposure period, in which association between playback recordings and visual stimuli were reversed from the initial arrangement, are indicated by (B).

recordings and those of *P. melanura,* similarly behaved aggressively only toward the model associated with their own species' calls, and largely ignored those of *P. melanura* (Table 3). *P. californica* showed little difference in response to its own vocalizations vs those of *P. nigriceps,* underscoring the pronounced resemblance of the Type I calls of each species (Fig. 15). When simultaneously presented with calls of *P. melanura* and *P. nigriceps, P. californica* responded aggressively toward the model associated with the recordings of *P. nigriceps* (Table 3).

Playback of conspecific calls similarly elicited aggressive responses from *P. nigriceps,* while the vocalizations of both *P. melanura* and *P. californica* were largely ignored (Table 3). Simultaneous presentation of *P. californica* and *P. melanura* recordings were generally ignored by *P. nigriceps*; in the few instances where positive responses were observed, these were directed toward models associated with vocalizations of *P. melanura.*

Experimental testing of vocal discrimination by *P. californica* and *P. melanura* thus suggests that differences in vocalizations might serve as an important isolating mechanism between the two species of "black-tailed" gnatcatchers. However, because subtle plumage differences also exist between *P. californica* and *P. melanura* (see below), I cannot exclude the possibility that morphological contrasts might also function in species recognition.

MORPHOLOGICAL VARIATION

SECONDARY SEXUAL VARIATION

Sexual dimorphism in a total of six measurements of body size and eight measurements of coloration was examined using nonparametric pairwise comparisons of males and females from various sample areas. In all three species, males were generally 1–4 percent larger than females (Table 4) in BLEN, P6LEN, and TLEN. However, only in measurements of P6LEN were significant differences ($P < 0.05$) noted for most of the sample area comparisons involving each species. In all three species no evidence was found for consistent sexual dimorphism in measurements of BWID, BDEP or TARTOE (Table 4).

Size dimorphism in small birds is generally thought to reflect the results of Darwinian sexual selection, with larger males theoretically being better able to

TABLE 4

SECONDARY SEXUAL DIMORPHISM IN LINEAR MEASUREMENTS

Character[a]	Species	N[b]	Samples[c]		Mean percent difference[d]		Number significant comparisons[e]	
			m > f	f > m	m > f	f > m	m > f	f > m
BLEN	*P. californica*	8	8	0	3.01	—	2	0
	P. melanura	13	13	0	1.78	—	0	0
	P. nigriceps	4	4	0	2.02	—	0	0
BWID	*P. californica*	8	4	4	1.90	2.95	0	0
	P. melanura	16	11	5	4.14	3.09	0	0
	P. nigriceps	3	1	2	5.28	0.92	0	0
BDEP	*P. californica*	8	4	4	4.95	1.49	0	0
	P. melanura	17	8	9	2.08	1.47	0	0
	P. nigriceps	3	2	1	2.67	5.13	0	0
TARTOE	*P. californica*	8	6	2	1.40	0.42	1	0
	P. melanura	15	8	8	1.97	0.97	3	0
	P. nigriceps	4	2	2	1.69	2.61	0	0
P6LEN	*P. californica*	8	8	0	2.82	—	4	0
	P. melanura	14	14	0	3.05	—	11	0
	P. nigriceps	4	4	0	3.61	—	3	0
TLEN	*P. californica*	8	8	0	1.80	—	1	0
	P. melanura	12	12	0	2.19	—	3	0
	P. nigriceps	4	4	0	1.70	—	0	0

[a] Character abbreviations as defined in Methods.
[b] Total number of sample areas used in comparisons. Areas represented by <4 specimens of either sex for a given character were excluded from analysis.
[c] Number of sample areas where males were larger than females (m > f) or females larger than males (f > m).
[d] Percent difference between sexes for each sample area expressed as percent of the larger sex; i.e., (Larger Mean minus Smaller Mean) divided by Larger Mean.
[e] Wilcoxon 2-sample test; $P < 0.05$.

acquire and defend territories and mates (Amadon 1959). Johnson (1980) suggested that the proportionately longer wings and tails of male *Empidonax* flycatchers, relative to their body weight, functioned to increase flight efficiency. This interpretation of adaptive value might also be true for size dimorphism in *Polioptila,* but additional data on female body weights are needed to confirm that the longer wing and tail measurements of male gnatcatchers do indeed result in reduced wing loading relative to females.

In measurements of coloration for each species (Table 5), values for BRSTW, BACKW, BRSTP and BACKP were generally higher in females than in males, although only for BACKP were most (all) of the comparisons significant ($P < 0.05$). These differences reflect the more brownish coloration, especially on the back, of females in each of the three species. No consistent sexual differences were found in the characters BRSTB or BACKB. Values for R6SPCT and R5SPCT were generally greater in males than in females, although most comparisons failed to detect statistically significant differences (Table 5).

The possibility of differences between species in the relative degree of sexual dimorphism was tested using ANOVA for each of the characters that showed consistent contrasts between males and females (BLEN, P6LEN, TLEN, BRSTW, BRSTP, BACKW, BACKP, R6SPCT, R5SPCT). Only in measurements of R6SPCT and R5SPCT were significant ($P < 0.05$) interspecific differences observed. In both of these characters *P. nigriceps* was much less sexually dimorphic

TABLE 5

SECONDARY SEXUAL DIMORPHISM IN COLOR ANALYSES

Character[a]	Species	N[b]	Samples[c]		Mean percent difference[d]		Number significant comparisons[e]	
			m > f	f > m	m > f	f > m	m > f	f > m
BRSTW	*P. californica*	8	1	7	0.18	0.19	0	0
	P. melanura	11	3	8	0.12	0.20	0	2
	P. nigriceps	2	1	1	0.07	0.07	0	0
BRSTB	*P. californica*	8	6	2	5.60	5.09	0	1
	P. melanura	11	3	8	8.91	3.63	0	0
	P. nigriceps	2	1	1	13.14	1.46	0	0
BRSTP	*P. californica*	8	2	6	5.22	23.19	0	1
	P. melanura	11	1	10	6.71	14.32	0	2
	P. nigriceps	3	1	1	2.69	19.03	0	0
BACKW	*P. californica*	8	0	8	—	3.94	0	2
	P. melanura	8	0	8	—	3.70	0	2
	P. nigriceps	2	0	2	—	2.72	0	0
BACKB	*P. californica*	8	6	2	6.73	1.74	0	0
	P. melanura	9	4	5	4.17	3.10	0	0
	P. nigriceps	2	2	0	8.49	—	1	0
BACKP	*P. californica*	8	0	8	—	71.04	0	5
	P. melanura	9	0	9	—	71.25	0	9
	P. nigriceps	2	0	2	—	81.56	0	2
R6SPCT	*P. californica*	8	7	1	25.61	6.01	1	0
	P. melanura	13	9	4	10.51	4.68	1	0
	P. nigriceps	4	3	1	5.75	4.46	1	0
R5SPCT	*P. californica*	8	8	0	39.58	—	2	0
	P. melanura	14	12	2	20.97	4.92	2	0
	P. nigriceps	4	1	3	2.22	1.82	0	0

[a] Character abbreviations as defined in Methods.

[b] Total number of sample areas used in comparisons. Areas represented by <4 specimens of either sex for a given character were excluded from analysis.

[c] Number of sample areas where males were larger than females (m > f) or females larger than males (f > m).

[d] Percent difference between sexes for each sample area expressed as percent of the larger sex; i.e., (Larger Mean minus Smaller Mean) divided by Larger Mean.

[e] Wilcoxon 2-sample test; $P < 0.05$.

than either *P. californica* or *P. melanura* (Table 5); *P. californica* was significantly more sexually dimorphic than *P. melanura* (R6SPCT, $P = 0.019$; R5SPCT, $P = 0.035$; Wilcoxon 2-sample test).

RELATIVE VARIABILITY

Several studies have examined the relative variability of different morphological characters in passerine birds (Rothstein 1973; Grant 1979a, b; Johnson 1980; Power 1983; Zink 1986), and have used this type of information to address important evolutionary questions. Are certain morphological characters less variable than others and, if so, do characters with low variability reflect high fitness levels in which phenotypic variation is constrained through stabilizing selection (Simpson 1944; Bird et al. 1981; Via and Lande 1985)? Is the extent of character variability found within sibling species attenuated to the degree that relative variation is reduced among sibling species (Johnson 1980)? Do species that are morphologically uniform over extensive geographic areas exhibit lower degrees of variability than species characterized by pronounced geographic variation (Zink

TABLE 6

VARIABILITY AND GEOGRAPHIC HETEROGENEITY IN 30 MORPHOLOGICAL CHARACTERS OF *Polioptila melanura*[a]

Character	Males				Females			
	SS	*F*	CV[b]	CV[c]	SS	*F*	CV[b]	CV[c]
BLEN	13.8	3.69**	.053	.054	9.8	2.89**	.058	.053
BWID	5.5	7.12**	.086	.083	3.8	4.82**	.099	.095
BDEP	3.5	4.25**	.102	.096	2.3	3.14**	.106	.104
TARTOE	27.8	2.96**	.031	.030	11.9	1.45	.032	.030
P10LEN	170.5	4.94**	.054	.051	54.5	1.42	.064	.051
P9LEN	182.9	7.22**	.031	.030	70.0	4.41**	.028	.025
P8LEN	176.1	8.06**	.025	.026	96.0	6.34**	.025	.023
P7LEN	195.4	9.37**	.024	.025	113.9	6.77**	.025	.024
P6LEN	192.7	8.70**	.025	.025	114.4	7.38**	.024	.024
P5LEN	186.6	8.25**	.026	.026	111.7	7.36**	.024	.023
P4LEN	177.9	7.34**	.027	.027	103.8	6.63**	.025	.024
P3LEN	182.2	7.97**	.027	.027	108.1	6.94**	.026	.025
TLEN	504.3	14.71**	.029	.062	286.0	8.53**	.032	.032
R6PCT	0.0	0.63	.031	.027	0.0	0.40	.032	.030
R5PCT	0.0	0.68	.022	.019	0.0	1.29	.023	.022
R4PCT	0.0	1.32	.017	.014	0.0	1.75	.016	.014
BRSTW	216.5	5.01**	.003	.003	117.5	2.28**	.003	.003
BRSTB	2,815.7	13.44**	.135	.126	1,630.1	8.83**	.127	.124
BRSTP	265.1	2.36**	.318	.307	289.2	4.15**	.213	.207
BACKW	691.3	1.44	.013	.009	259.8	4.09**	.005	.003
BACKB	83.9	15.97**	.092	.094	75.8	14.93**	.092	.075
BACKP	201.1	1.76	.667	.609	379.4	2.34*	.298	.307
R6SPCT	0.3	11.51**	.252	.245	0.1	5.77**	.270	.281
R5SPCT	0.1	8.05**	.378	.387	0.0	4.51**	.362	.378
R6SSH	101.3	4.15**	.762	.567	121.1	3.36**	.836	.762
R5SSH	212.7	3.73**	.773	.608	84.9	2.62**	.657	.644
R6WEB	0.5	1.30	.157	.047	0.3	1.47	.117	.051
R5WEB	82.5	7.82**	.224	.220	37.8	3.73**	.250	.252
MASS	0.0	2.90**	.022	.029	—	—	—	—
CAPLEN	34.0	1.58	.087	.077	—	—	—	—

[a] ANOVA, by species and sex, showing Sum of Squares (SS) and *F* values (** = $P < 0.01$; * = $P < 0.05$) for each character. Sample areas represented by <5 specimens (see Table 1) were excluded from analysis. Character abbreviations as defined in Methods.
[b] Coefficient of variation, for all individuals (by species and sex).
[c] Coefficient of variation, mean per sample area.

1986)? Is there an adaptive "explanation" for patterns of variability among characters (Rothstein 1973; Grant 1979a; Power 1983; Zink 1986)?

Character variability in three species of *Polioptila* is summarized in Tables 6, 7, and 8. In both sexes of all three species mean coefficients of variation (CVs) per sample area were less than 10 percent for all "non-color" characters (BLEN, BWID, BDEP, TARTOE, P10LEN–P3LEN, TLEN, R6PCT, R5PCT, R4PCT, MASS); similar magnitudes have been reported for CVs from other species of passerine birds, including both sibling and non-sibling species groups and species characterized by both minimal and pronounced degrees of geographic differentiation (see reviews in Johnson 1980; Zink 1986). As appears to be generally true of other species (Zink 1986), bill and leg-foot characters were more variable in *Polioptila* than were wing or tail characters; in all three species, BLEN was less variable than BWID or BDEP.

Among BLEN, BWID, BDEP, TARTOE, P10LEN–P3LEN, TLEN, R6PCT, R5PCT, and R4PCT, only BLEN of males showed significant interspecific dif-

TABLE 7

VARIABILITY AND GEOGRAPHIC HETEROGENEITY IN 30 MORPHOLOGICAL CHARACTERS OF *Polioptila californica*[a]

Character	Males				Females			
	SS	*F*	CV[b]	CV[c]	SS	*F*	CV[b]	CV[c]
BLEN	2.0	1.00	.050	.047	3.0	2.23	.053	.060
BWID	2.5	5.27**	.091	.084	0.1	0.45	.089	.101
BDEP	0.9	2.35*	.087	.085	0.2	0.69	.096	.102
TARTOE	12.5	2.17*	.032	.030	11.2	2.49*	.036	.032
P10LEN	24.8	1.23	.058	.055	22.5	1.31	.069	.061
P9LEN	16.7	1.17	.034	.033	25.6	4.31**	.028	.029
P8LEN	25.4	3.09**	.023	.022	25.6	4.45**	.025	.023
P7LEN	20.9	2.63**	.022	.021	25.3	4.57**	.023	.022
P6LEN	22.4	2.70**	.022	.022	24.9	4.53**	.023	.023
P5LEN	30.1	3.40**	.023	.023	29.4	5.12**	.024	.024
P4LEN	33.5	3.26**	.025	.025	23.4	4.15**	.024	.024
P3LEN	29.3	2.97**	.025	.026	18.3	3.01*	.026	.034
TLEN	132.0	8.45**	.029	.029	48.3	4.39**	.031	.032
R6PCT	0.0	2.18*	.032	.028	0.0	3.63*	.028	.027
R5PCT	0.0	0.54	.018	.017	0.0	2.36*	.022	.020
R4PCT	0.0	1.12	.015	.013	0.0	2.24	.015	.013
BRSTW	221.8	6.57**	.004	.003	65.5	3.79**	.003	.002
BRSTB	1,808.8	27.38**	.138	.132	1,578.8	25.92**	.137	.135
BRSTP	406.2	6.46**	.314	.314	392.5	5.19**	.003	.294
BACKW	628.9	0.61	.025	.017	42.4	1.24	.005	.004
BACKB	18.9	5.60**	.119	.113	13.6	3.94**	.121	.089
BACKP	50.5	1.03	.520	.442	89.4	1.33	.269	.281
R6SPCT	0.2	27.84**	.347	.347	0.1	24.06**	.547	.579
R5SPCT	0.1	33.29**	.374	.383	0.0	22.01**	.711	.747
R6SSH	10.4	0.71	.308	.303	6.2	0.57	.357	.340
R5SSH	12.6	0.60	.348	.300	38.2	1.65	.438	.420
R6WEB	69.4	27.41**	.255	.295	52.6	28.66**	.242	.300
R5WEB	23.4	8.66**	.125	.124	13.9	10.21**	.111	.115
MASS	0.1	3.21**	.027	.024	—	—	—	—
CAPLEN	14.9	1.54	.071	.063	—	—	—	—

[a] ANOVA, by species and sex, showing Sum of Squares (SS) and *F* values (** = $P < 0.01$; * = $P < 0.05$) for each character. Sample areas represented by <5 specimens (see Table 1) were excluded from analysis. Character abbreviations as defined in Methods.

[b] Coefficient of variation, for all individuals (by species and sex).

[c] Coefficient of variation, mean per sample area.

ferences in relative variability based on mean CVs per sample area (Kruskal-Wallis test, $P = 0.003$). Only for TARTOE of *P. nigriceps* did variability differ significantly between the sexes, with mean CVs being less in males than in females (Wilcoxon 2-sample test, $P = 0.037$).

CVs of coloration characters (BRSTW, BRSTB, BRSTP, BACKW, BACKB, BACKP, R6SPCT, R5SPCT, R6SSH, R5SSH, R6WEB, R5WEB, CAPLEN) varied from less than 1 percent (BRSTW in all three species) to 61 percent (BACKP in *P. melanura*) (Tables 6, 7, 8). In general, CVs for plumage brightness and purity were high in both sexes of all three species, whereas BRSTW and BACKW were characterized by low CVs. Johnson (1980) found similar results for these characters in his spectrophotometric analysis of *Empidonax* flycatchers.

Significant interspecific differences in variability were found only in those coloration characters describing the extent of white on rectrices 6 and 5 (R6SPCT, R5SPCT, R6SSH, R5SSH, R6WEB, R5WEB) (Kruskal-Wallis test, $P < 0.01$). These characters were less variable in *P. nigriceps* than in either of the "black-

TABLE 8

VARIABILITY AND GEOGRAPHIC HETEROGENEITY IN 22 MORPHOLOGICAL CHARACTERS OF *Polioptila nigriceps*[a]

Character	Males				Females			
	SS	*F*	CV[b]	CV[c]	SS	*F*	CV[b]	CV[c]
BLEN	2.1	0.88	.069	.068	1.2	1.30	.063	.060
BWID	1.2	4.74*	.087	.081	0.3	3.36*	.070	.059
BDEP	1.2	5.11**	.100	.102	0.1	0.73	.103	.092
TARTOE	15.4	6.08**	.030	.028	9.15	4.00*	.040	.041
P10LEN	20.6	2.91*	.048	.046	11.4	1.14	.083	.077
P9LEN	26.4	4.69**	.029	.027	11.4	2.49	.038	.039
P8LEN	28.9	5.06**	.026	.023	8.3	3.21	.025	.028
P7LEN	33.8	5.74**	.025	.023	9.6	5.35*	.020	.022
P6LEN	33.8	5.74**	.025	.023	12.0	7.22**	.019	.020
P5LEN	35.9	5.72**	.026	.026	16.4	7.33**	.023	.023
P4LEN	41.7	5.98**	.028	.027	24.5	9.29**	.025	.026
P3LEN	43.0	5.78**	.030	.034	11.8	2.24	.037	.035
TLEN	150.6	10.81**	.036	.036	25.9	4.40*	.033	.029
R6PCT	0.0	0.66	.039	.035	0.0	0.25	.039	.041
R5PCT	0.0	1.47	.026	.020	0.0	0.02	.021	.020
R4PCT	0.0	2.15	.012	.011	0.0	0.43	.014	.015
BRSTW	15.7	0.54	.004	.003	—	—	—	—
BRSTB	25.8	0.34	.162	.167	—	—	—	—
BRSTP	16.6	0.51	.366	.347	—	—	—	—
R6SPCT	0.0	3.12*	.054	.050	—	—	—	—
R5SPCT	0.0	1.41	.122	.120	—	—	—	—
R6SSH	0.4	2.24	.206	.109	—	—	—	—
R5SSH	0.2	0.45	.333	.160	—	—	—	—
R5WEB	0.0	0.43	.112	.036	—	—	—	—
CAPLEN	56.8	6.43**	.108	.108	—	—	—	—

[a] ANOVA, by species and sex, showing Sum of Squares (SS) and *F* values (** = $P < 0.01$; * = $P < 0.05$) for each character. Sample areas represented by <5 specimens (see Table 1) were excluded from analysis. Character abbreviations as defined in Methods.

[b] Coefficient of variation, for all individuals (by species and sex).

[c] Coefficient of variation, mean per sample area.

tailed" species, and CVs in *P. melanura* were lower than those obtained for *P. californica.* Considering the difficulties involved in obtaining accurate measurements from museum specimens, CVs for CAPLEN were surprisingly low, ranging from 6 percent in *P. californica* to 11 percent in *P. nigriceps.* In *P. melanura,* analysis of sexual differences in relative variability for characters BRSTW, BRSTB, BRSTP, BACKW, BACKB, BACKP, R6SPCT, R5SPCT, R6SSH, R5SSH, R6WEB, and R5WEB indicated that females are less variable than males in BRSTP, BACKW, and BACKP; no sexual differences in variability were noted in other characters. Among these characters for *P. californica,* only in R6SPCT and R5SPCT were there significant sexual differences in relative variability, with females being more variable than males (Wilcoxon 2-sample test; R6SPCT: $P = 0.008$; R5SPCT: $P = 0.003$). Because of small sample sizes of female *P. nigriceps,* analysis of sexual differences in variability was not performed for this species.

In Table 9, I present by sample area CVs for selected morphological characters (BLEN, TARTOE, P6LEN, TLEN) of *P. melanura* and *P. californica.* In none of these characters for either species were there evident ecological patterns associated with these values. For example, samples of *P. melanura* from the Chihuahuan desert had CVs for BLEN ranging from 4.75 percent (GU17) to 7.86 percent (CH11); Sonoran desert samples were comparably variable, with values ranging

TABLE 9

GEOGRAPHIC DIFFERENCES IN RELATIVE VARIABILITY IN *Polioptila melanura* AND *P. californica*

Area	Species	Characters[a]			
		BLEN	TARTOE	P6LEN	TLEN
RI01	*P. melanura*	3.42	3.15	2.22	2.57
NE02	*P. melanura*	6.37	2.69	1.80	2.94
YU03	*P. melanura*	4.03	2.10	2.15	2.75
SF04	*P. melanura*	5.05	3.16	2.26	2.63
BG05	*P. melanura*	5.89	3.51	1.24	1.14
AJ06	*P. melanura*	6.32	2.71	3.10	3.53
TU07	*P. melanura*	5.26	3.03	2.17	2.36
HE08	*P. melanura*	5.64	3.61	3.22	3.52
OB10	*P. melanura*	4.58	2.42	2.80	2.89
CH11	*P. melanura*	7.86	2.29	4.61	3.78
PR12	*P. melanura*	5.90	3.23	2.62	2.22
SA13	*P. melanura*	5.64	3.83	2.72	2.06
SL14	*P. melanura*	4.94	4.71	2.50	2.87
DU15	*P. melanura*	5.35	3.08	2.64	3.52
HU16	*P. melanura*	6.09	3.49	1.70	3.14
GU17	*P. melanura*	4.75	1.98	2.92	2.64
LA23	*P. californica*	5.64	3.40	2.23	2.78
SD24	*P. californica*	5.07	3.77	2.31	2.26
ST25	*P. californica*	2.74	2.98	2.51	3.04
ER26	*P. californica*	5.19	2.78	2.28	3.61
BG27	*P. californica*	4.85	2.30	2.01	2.57
PP28	*P. californica*	4.21	2.91	2.91	3.31
SI29	*P. californica*	5.69	1.81	1.97	2.88
MA30	*P. californica*	3.45	3.86	2.17	2.64
LP31	*P. californica*	4.78	3.18	1.75	2.72

[a] Character abbreviations as defined in Methods.

from 3.42 percent (RI01) to 6.37 percent (NE02). The CV for P6LEN of *P. californica* was significantly correlated ($P < 0.05$) with latitude and longitude, suggesting a clinal decrease in variability of P6LEN south (and east, by virtue of geographical orientation) along the Baja California peninsula (Table 10). No other significant correlations were found between CVs for BLEN, TARTOE, P6LEN or TLEN, and latitude or longitude, suggesting no simple geographical pattern in character variability.

Grant (1979a) suggested that the absence of presumed competition with congeneric species might allow increased levels of variability in insular populations. However, Zink (1986) found that samples of the Fox Sparrow (*Passerella iliaca*) that occurred syntopically with the closely related Song Sparrow (*Melospiza melodia*) were more variable than populations where presumed competition was not a factor, and suggested that competition with Song Sparrows might "cause" Fox Sparrows to exhibit increased variability, thereby enabling them to exploit a wider niche.

In the present study, character variability was compared between sympatric samples of *P. melanura* and *P. californica* (BG05, BG27) and sample areas where each species occurs allopatrically (Table 9). In neither species was there an evident increase or decrease in variability of BLEN or TARTOE for samples collected from the region of overlap. However, CVs for P6LEN (1.24 percent) and TLEN

TABLE 10

CORRELATION COEFFICIENTS BETWEEN COEFFICIENTS OF VARIATION FOR 4 MORPHOLOGICAL VARIABLES AND LATITUDE AND LONGITUDE

	Character CVs[a]			
	BLEN	TARTOE	P6LEN	TLEN
Polioptila melanura				
Latitude	.081	−.289	−.284	.035
Longitude	−.171	−.415	−.361	.134
Polioptila californica				
Latitude	.096	.236	.976*	−.235
Longitude	.093	.274	.967*	−.228
Polioptila nigriceps				
Latitude	−.212	−.486	.625	.784
Longitude	−.320	−.336	.730	.708

[a] Character abbreviations as defined in Methods. Pearson product-moment correlation coefficients calculated between coefficients of variation for each sample area vs latitude and longitude. Significant correlations ($P < 0.05$) indicated by an asterisk*.

(1.14 percent) from BG05 represented the lowest values for each of these characters recorded among 16 samples of *P. melanura*; *P. californica* specimens from the contact zone showed no clear decrease in variability, although CVs for both P6LEN (2.01 percent) and TLEN (2.57 percent) were slightly lower than those from most other sample areas for the species (Table 9). Possibly *P. melanura* and *P. californica* are less variable where they coexist; unfortunately, sample sizes from this area of sympatry are small, and further speculation seems unwarranted at present.

CHARACTER CORRELATIONS AND REDUNDANCY

Assessment of information redundancy in each of the three species, using oblique component cluster analysis based on the matrix of correlation coefficients among 28 variables, indicated only one major grouping of highly intercorrelated characters, that being the measurements of primaries 3–9 (P3–9LEN). All three species showed this pattern of character redundancy; only the phenogram for *P. melanura* is presented here (Fig. 21). Moderately correlated character groupings, again found in all three species, included R6–5SPCT and R6–4PCT. Remaining characters showed only slight degrees of intercorrelation, thus suggesting relatively high levels of independent information content.

UNIVARIATE CHARACTER ANALYSES

Geographic heterogeneity among characters.—The results of ANOVA for each of 30 morphological characters in *P. melanura* and *P. californica,* and for 22 characters in *P. nigriceps,* are presented in Tables 6, 7, and 8. In males of all three species, significant *F*-values were obtained for most measurements of bill, leg, wing, and tail characters, indicating that geographic differences in these characters exist across the various sample areas representing each species. Exceptions to this generalization included BLEN in *P. californica* and *P. nigriceps,* and measurements of tail shape (R6PCT, R5PCT, R4PCT) in all three species; ANOVA failed to detect significant geographic differences among the sample areas included in analyses of these characters. Similar results were found for females.

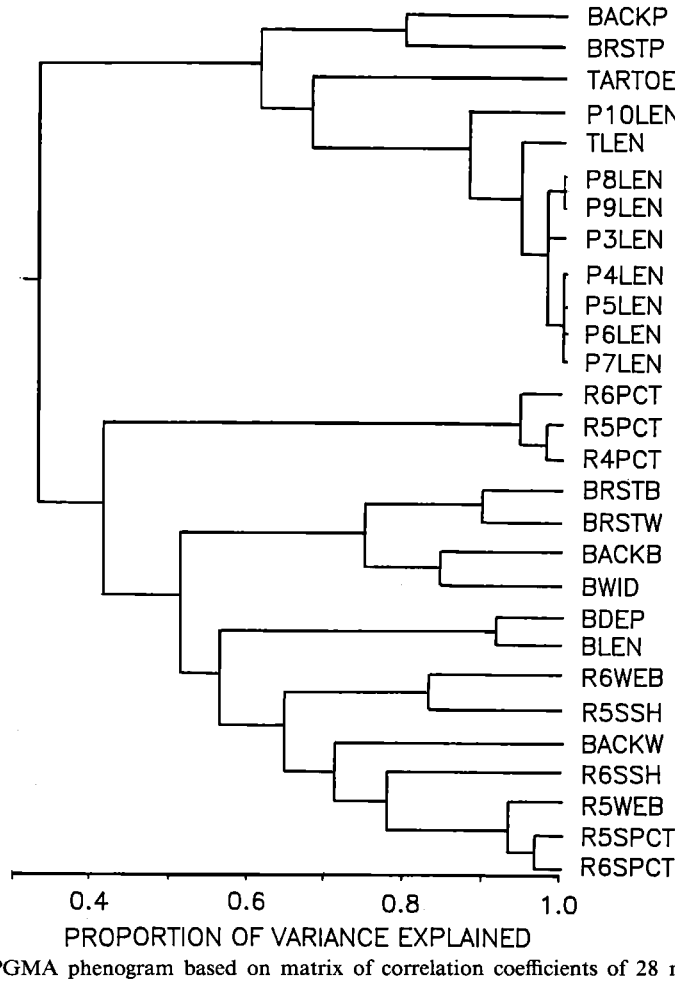


FIG. 21. UPGMA phenogram based on matrix of correlation coefficients of 28 morphological characters in *Polioptila melanura* (males). Character abbreviations as defined in Methods.

Significant *F*-values were also obtained in both sexes of *P. melanura* and *P. californica* for most characters of plumage coloration or pattern, again indicating geographic heterogeneity among the sample areas examined. In *P. nigriceps* only R6SPCT and CAPLEN varied significantly among sample areas. "Coloration" characters that were geographically invariant (at least among the sample areas included here) in male *P. melanura* and *P. californica* included BACKW, BACKP and CAPLEN; in *P. melanura,* R6WEB did not vary across sample areas, nor did R6SSH or R5SSH in *P. californica.*

Geographic patterns of character variation.—Univariate analyses revealed consistent patterns of intraspecific geographic variation among 30 morphological characters; sharp interspecific differences were also repeatedly observed. In *P. melanura,* Chihuahuan and Sonoran desert populations frequently contrasted sharply with one another, but generally little pattern of character variation was found within these major portions of the species' range. Both *P. californica* and *P. nigriceps* showed north-south clinal variation in many characters; samples of

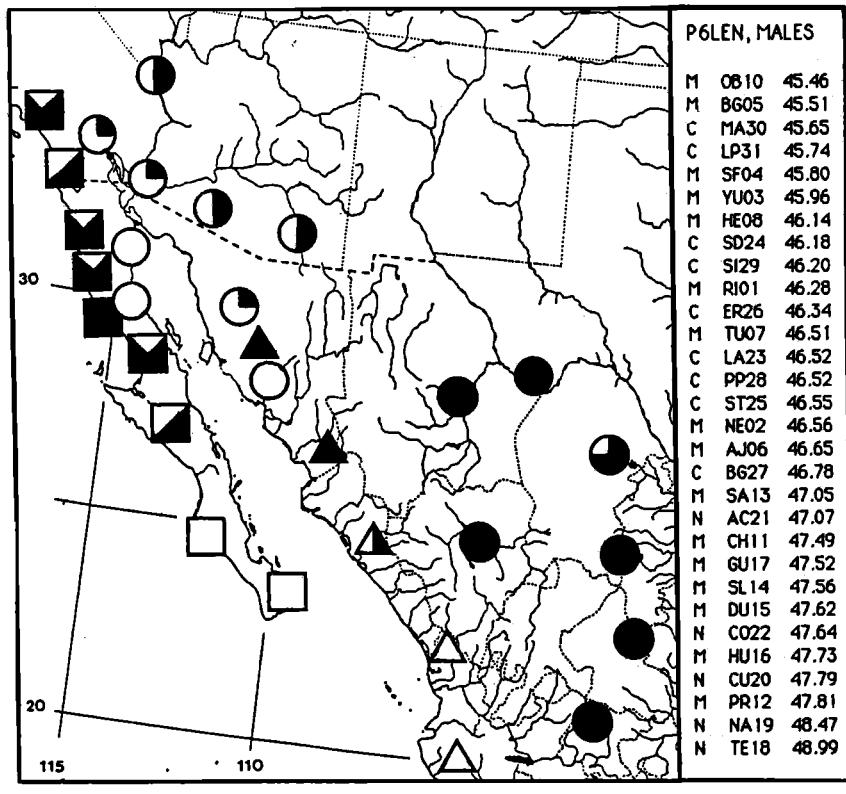


FIG. 22. Variation in P6LEN (wing length) in three species of *Polioptila* (males). Species symbols as follows: Circles = *Polioptila melanura*; squares = *P. californica*; triangles = *P. nigriceps*. For *P. melanura* and *P. californica*, open symbols represent lowest one-fifth of the range of means, solid symbols the largest one-fifth; intermediate values are indicated by progressively shaded symbols. In *P. nigriceps*, open symbols represent the smallest one-third of the range of means, solid symbols the largest one-third. Means are listed in increasing order of magnitude adjacent to the alphanumeric code for each sample locality; species codes (M = *P. melanura*, C = *P. californica*, N = *P. nigriceps*) are provided to the left of each sample area code.

P. californica from the Cape region of Baja California (MA30, LP31) frequently differed from populations north of approximately 27°N latitude.

Island populations of *P. melanura* (TI09) and *P. californica* (ES32, SJ33) from the Gulf of California were excluded from the following univariate and multivariate analyses of geographic variation, primarily because mean values from these localities were based on extremely small sample sizes (Table 1). Also, in many characters the mean values from these populations were either extremely large or extremely small, and inclusion of these samples tended to obscure patterns of variation among less divergent sample areas, because of the plotting technique used in the following sections. Without additional specimen material from these islands I prefer not to discuss these populations in detail, although I recognize their evolutionary and taxonomic interest. Certainly future work could be profitably directed toward thorough morphological descriptions of island gnatcatcher populations from the Gulf of California.

Sexual differences in variation.—No pronounced differences between the sexes

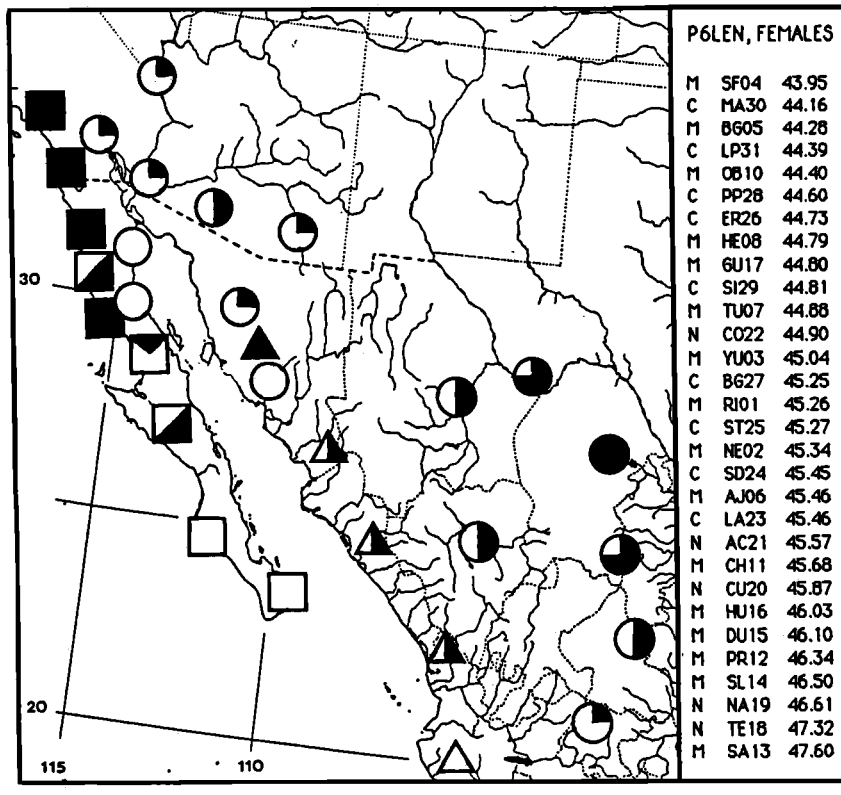


FIG. 23. Variation in P6LEN (wing length) in three species of *Polioptila* (females). See legend to Figure 22.

were exhibited by any of the three species in the broad patterns of their geographical variation. As an example of this uniformity, found in virtually all characters, plots for wing length (P6LEN) of males (Fig. 22) and females (Fig. 23) are presented. Both sexes of *P. melanura* showed similar patterns of geographic variation in this character, with most Chihuahuan desert samples being longer-winged than most samples from the Sonoran desert. The sample of short-winged females from GU17, contrasting with the generally larger means in other Chihuahuan desert populations as well as with the sample of males from GU17, is probably an artifact of the extremely small (N = 3) sample size upon which the area mean for females was based. Both sexes of *P. nigriceps* were characterized by a north-south cline of decreasing P6LEN. In *P. californica* I see no clear pattern of geographic variation in P6LEN north of approximately 28°N latitude for either sex; populations of this species in the Cape region of Baja California (MA30, LP31) were short-winged in both males and females.

Variation in size.—Variation in overall body size, as indicated by the cube root of body mass (MASS), is shown for males of *P. melanura* and *P. californica* (Fig. 24). Females were not analyzed for this character because sample sizes were small and many specimens were in breeding condition when collected; small samples of males were also excluded. In *P. melanura,* heavier individuals occurred in the three Chihuahuan desert localities. Sonoran desert samples of *P. melanura* were

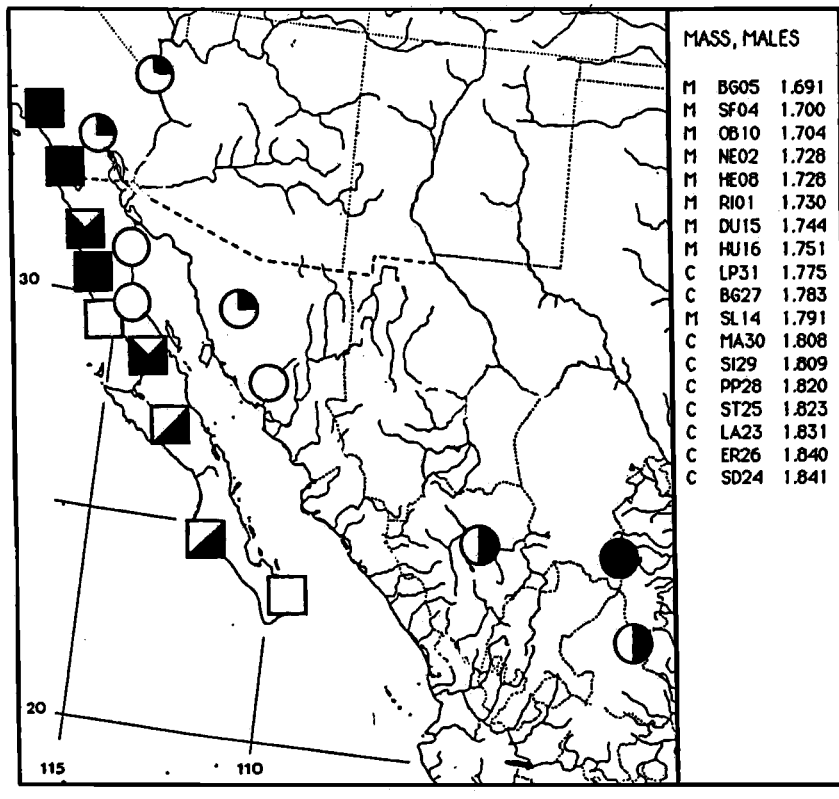


FIG. 24. Variation in MASS in *Polioptila melanura* and *P. californica* (males). See legend to Figure 22.

characterized by relatively small means for MASS, especially in northeastern Baja California (SF04, BG05). A north-south cline of decreasing MASS was evident in populations of *P. californica*, with the exception of small values for this character in the sample taken from the zone of sympatry with *P. melanura* (BG27).

Little interspecific overlap in MASS was found between *P. melanura* and *P. californica*. Samples of *P. californica* were heavier than all except the largest Chihuahuan desert sample (SL14) of *P. melanura* (Fig. 24).

To assess the degree to which variation in other morphological measurements might be "explained" by overall body size, I calculated correlation coefficients between MASS and 6 measurements of bill, leg, wing, and tail (BLEN, BWID,

TABLE 11

CORRELATION COEFFICIENTS BETWEEN CUBE-ROOT MASS AND 6 MORPHOLOGICAL CHARACTERS[a]

Species	BLEN	BWID	BDEP	TARTOE	P6LEN	TLEN	R5PCT
P. melanura	0.74*	0.45	0.71*	0.91*	0.92*	0.95*	−0.29
P. californica	0.05	0.26	0.21	0.23	0.22	0.43	−0.50

[a] Character abbreviations as defined in Methods. Underlined values indicate that the character was significantly associated with MASS in a linear regression model ($P < 0.01$). Statistically significant correlations ($P < 0.01$) indicated by an asterisk *.

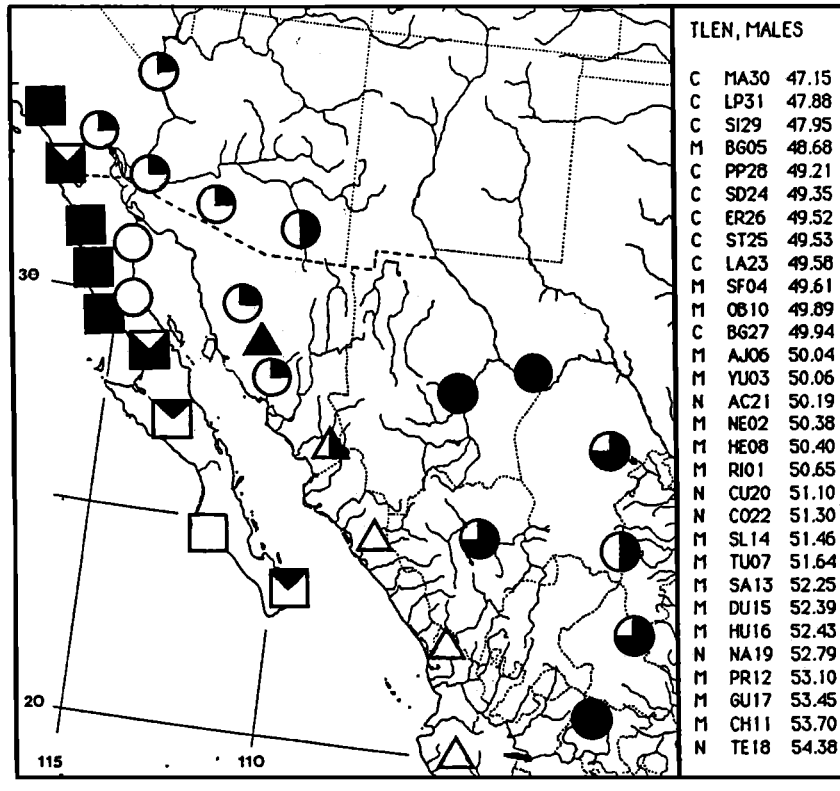


FIG. 25. Variation in TLEN in three species of *Polioptila* (males). See legend to Figure 22.

BDEP, TARTOE, TLEN, R5PCT); additionally, linear regression was used to assess the value of MASS as a predictor of these characters (Table 11). In *P. melanura,* BLEN, BDEP, TARTOE, P6LEN, and TLEN were all significantly correlated with MASS (Pearson product-moment correlation coefficient; $P < 0.05$); R5PCT, an expression of tail shape as opposed to tail length, and BWID failed to include a significant "size" component in their variation. By contrast, in *P. californica* none of these characters were significantly correlated with MASS, suggesting that in this species variation in these morphological characters is decoupled from size variation, at least to the extent that "size" is truly portrayed by cube-root of body mass.

Variation in body dimensions.—In nearly all measurements of basic body dimensions, each species showed relatively clear and repetitive patterns of geographic variation. As an example of these recurring patterns, pie diagrams for TLEN are plotted in Figure 25; geographic variation in other characters is summarized in Tables 12 (*P. melanura*) and 13 (*P. californica*).

In *P. melanura,* sample areas from the Chihuahuan desert were uniformly large in mean TLEN (Fig. 25); this character was generally small in Sonoran desert populations, especially in northeastern Baja California (SF04, BG05). Samples of *P. nigriceps* demonstrated a decreasing north-south pattern of clinal variation in this character. Similar clinal variation was evident in *P. californica,* with more or less uniformly long-tailed populations occurring north of approximately 27°N

TABLE 12

GEOGRAPHIC PATTERNS OF CHARACTER VARIATION IN *Polioptila melanura*

Character[a]	Region[b]	Size distribution of sample means[c]								
		I	>	II	>	III	>	IV	>	V
MASS	Sonora	—		—		—		3		3
	Chihuahua	1		—		2		—		—
BLEN	Sonora	—		—		1		3		4
	Chihuahua	1		1		2		3		—
BWID	Sonora	—		1		2		4		2
	Chihuahua	2		—		2		1		1
BDEP	Sonora	—		2		4		2		1
	Chihuahua	2		3		1		1		—
TARTOE	Sonora	—		—		4		2		3
	Chihuahua	5		1		1		—		—
P6LEN	Sonora	—		—		3		3		3
	Chihuahua	6		1		—		—		—
TLEN	Sonora	—		—		1		6		2
	Chihuahua	3		3		1		—		—
R5PCT	Sonora	2		4		2		1		—
	Chihuahua	1		1		4		—		1
BRSTW	Sonora	—		1		3		2		3
	Chihuahua	2		2		3		—		—
BRSTB	Sonora	1		2		1		4		1
	Chihuahua	—		—		—		3		4
BRSTP	Sonora	3		3		1		2		—
	Chihuahua	—		2		—		2		3
R5SPCT	Sonora	3		4		2		—		—
	Chihuahua	—		—		—		1		6
R5WEB	Sonora	2		1		6		—		—
	Chihuahua	—		—		—		—		7
CAPLEN	Sonora	6		2		—		—		—
	Chihuahua	1		3		1		—		1
EYERING	Sonora	6		2		—		—		—
	Chihuahua	1		3		1		—		1

[a] Character abbreviations as defined in Methods.

[b] Regions composed of the following sample areas: Sonora = RI01, NE02, YU03, SF04, BG05, AJ06, TU07, HE08, OB10; Chihuahua = CH11, PR12, SA13, SL14, DU15, HU16, GU17.

[c] Number of samples falling in each of 5 equal size groupings based on total range of character means per species. I = largest of the range of sample area means, V = smallest one-fifth. II, III, and IV represent progressively smaller, intermediate values.

latitude and generally short-tailed populations in the Cape region of Baja California (MA30, LP31).

Interspecifically, most samples of *P. californica* were shorter in TLEN than most samples of *P. melanura*; *P. nigriceps* and *P. melanura* overlapped broadly in this character (Fig. 25). In BLEN, 15 of 16 sample areas of *P. melanura* were smaller than samples of *P. californica,* and all *P. californica* samples had smaller mean BLEN values than *P. nigriceps.* Interspecific differences in BDEP and TARTOE paralleled those of BLEN. Broad overlap of area means occurred for BWID and P6LEN among the three species.

Variation in tail shape.—I see no clear patterns of geographic variation in R5PCT in any of the three species (Fig. 26); ANOVA indicated that this character was geographically homogeneous among sample areas of each species (Tables 6, 7, 8). Interspecifically, most sample areas of *P. californica* had smaller mean values

TABLE 13

GEOGRAPHIC PATTERNS OF CHARACTER VARIATION IN *Polioptila californica*

Character[a]	Region[b]	Size distribution of sample means[c] I	>	II	>	III	>	IV	>	V
MASS	Northern Baja	3		1		—		—		—
	Central Baja	—		1		1		—		1
	Cape region	—		—		1		—		1
BLEN	Northern Baja	1		—		1		1		1
	Central Baja	—		—		1		—		2
	Cape region	—		—		1		1		—
BWID	Northern Baja	1		2		—		1		—
	Central Baja	—		—		—		—		3
	Cape region	1		—		—		—		1
BDEP	Northern Baja	2		—		2		—		—
	Central Baja	—		—		2		—		1
	Cape region	—		—		—		1		1
TARTOE	Northern Baja	1		1		1		1		—
	Central Baja	—		—		1		—		2
	Cape region	—		1		—		—		1
P6LEN	Northern Baja	—		3		1		—		—
	Central Baja	1		1		1		—		—
	Cape region	—		—		—		—		2
TLEN	Northern Baja	3		1		—		—		—
	Central Baja	1		1		—		1		—
	Cape region	—		—		—		1		1
R5PCT	Northern Baja	—		—		—		2		2
	Central Baja	—		—		2		1		—
	Cape region	1		—		—		1		—
BRSTW	Northern Baja	1		2		1		—		—
	Central Baja	—		2		—		—		1
	Cape region	—		1		—		1		—
BRSTB	Northern Baja	—		—		1		—		3
	Central Baja	—		—		—		3		—
	Cape region	1		1		—		—		—
BRSTP	Northern Baja	—		2		1		—		1
	Central Baja	—		1		—		1		1
	Cape region	—		1		—		1		—
R5SPCT	Northern Baja	—		—		—		3		1
	Central Baja	—		1		2		—		—
	Cape region	1		1		—		—		—
R5WEB	Northern Baja	—		—		—		—		4
	Central Baja	—		1		1		1		—
	Cape region	1		—		1		—		—
CAPLEN	Northern Baja	—		—		—		1		3
	Central Baja	—		—		2		—		1
	Cape region	2		—		—		—		—
EYERING	Northern Baja	—		—		—		1		3
	Central Baja	—		—		2		—		1
	Cape region	2		—		—		—		—

[a] Character abbreviations as defined in Methods.

[b] Regions composed of the following sample areas: Northern Baja = LA23, SD24, ST25, ER26; Central Baja = BG27, PP28, SI29; Cape region = MA30, LP31.

[c] Number of samples falling in each of 5 equal size groupings based on total range of character means per species. I = largest of the range of sample area means, V = smallest one-fifth. II, III, and IV represent progressively smaller, intermediate values.

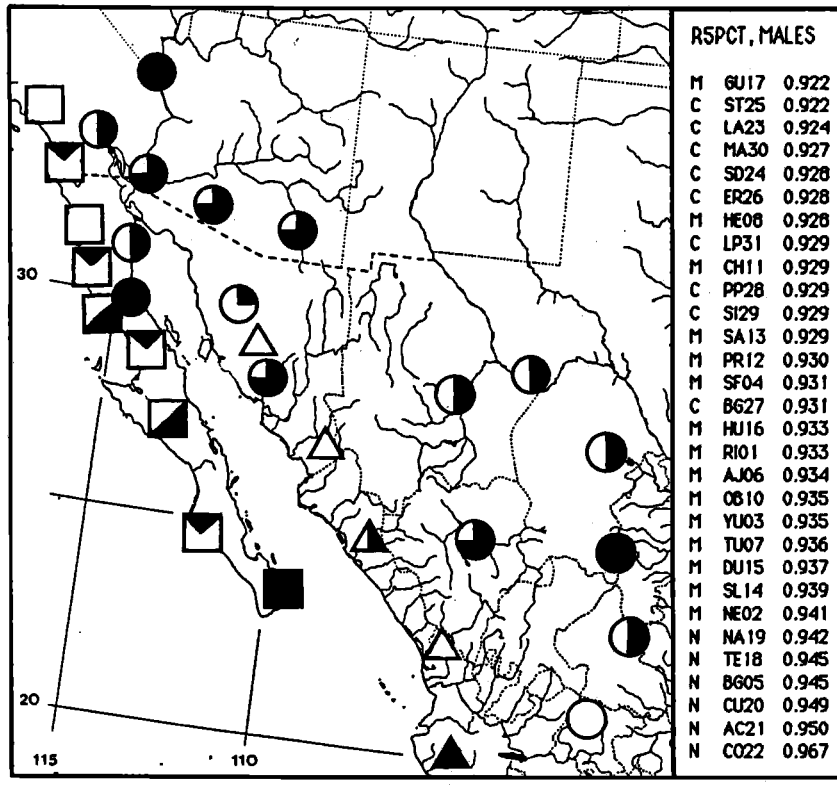


FIG. 26. Variation in R5PCT in three species of *Polioptila* (males). See legend to Figure 22.

for R5PCT (i.e., more strongly graduated tails) than most samples of *P. melanura.* Of the three species, *P. nigriceps* had the largest values for R5PCT (least graduated tails), with all 6 sample area means of this species exceeding those from *P. melanura.*

Variation in plumage coloration.—No clear geographic patterns of intraspecific variation were evident in spectrophotometric measurements of plumage wavelength (BRSTW, BACKW) or purity (BRSTP, BACKP) in any of the three species (Tables 12, 13). In BRSTB, specimens of *P. melanura* from the Sonoran desert sample localities, especially in northeastern Baja California (SF04, BG05), were generally characterized by larger means (i.e., whiter plumage) than most samples from the Chihuahuan desert (Fig. 27). Within the Sonoran desert sample areas of *P. melanura* there appeared to be a north-south clinal variation of increasing BRSTB values (i.e., increasingly paler plumage); the sample of *P. melanura* from the area of sympatry with *P. californica* (BG05) was noticeably white-breasted. BRSTB did not appear to vary clinally in populations of *P. melanura* from the Chihuahuan desert. In *P. californica,* BRSTB was characterized by low mean values (darker coloration) in the northern sample areas and higher means (whiter plumage) farther south; some indication of a relatively sharp step can be seen in this cline near approximately 30°N latitude. Northern samples of *P. nigriceps* generally had higher mean values for BRSTB when compared to samples from farther south.

Considerable overlap in BRSTB existed among the three species, especially

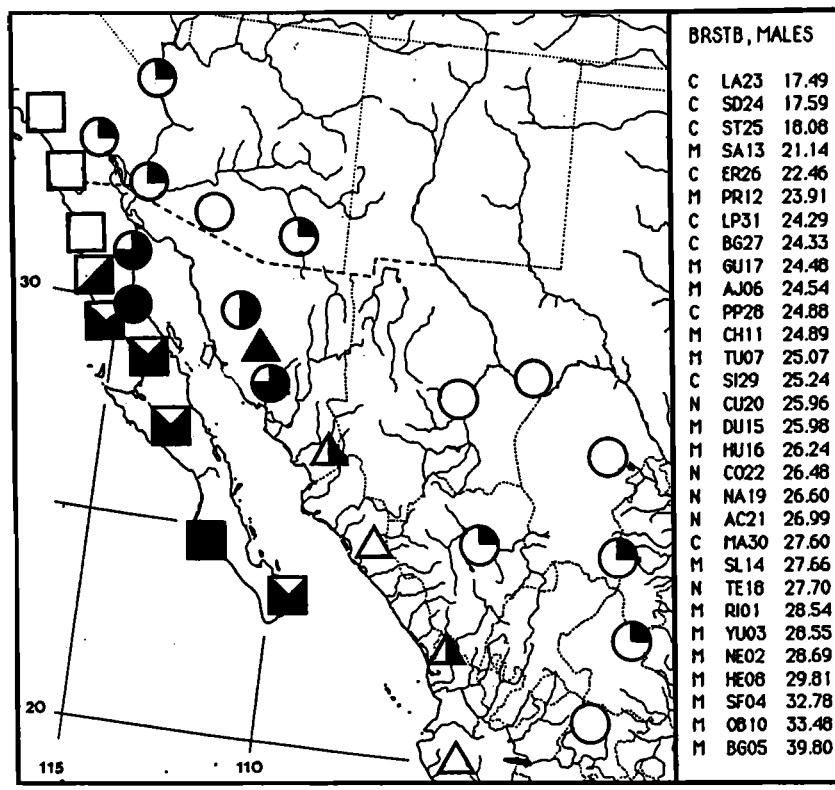


FIG. 27. Variation in BRSTB in three species of *Polioptila* (males). See legend to Figure 22.

between central and southern Baja California populations of *P. californica* and Chihuahuan desert populations of *P. melanura* (Fig. 27). Most Sonoran desert populations of *P. melanura* had higher values of BRSTB than most samples of *P. californica,* although some overlap occurred in sample area means. From the area of sympatry in northeastern Baja California (BG05, BG27), mean values of BRSTB in *P. californica* and *P. melanura* differed sharply; in this region I found the two species to be visually separable under most field conditions on the basis of overall plumage brightness.

Variation in three characters of tail coloration, all expressions of the amount of white present, was examined in rectrices 5 and 6. These characters included (a) tail spot length, expressed as percent of total tail length (R6SPCT, R5SPCT), (b) the amount of white present on the outer vane (R6WEB, R5WEB), and (c) tail spot shape (R6SSH, R5SSH). Patterns of variation in these characters between rectrices 5 and 6 were identical; only characteristics of rectrix 5 are discussed here.

In R5SPCT, specimens of *P. melanura* from the Chihuahuan desert localities were characterized by smaller values (i.e., shorter tail spots relative to total tail length) than samples from Sonoran desert localities (Fig. 28). Both *P. californica* and *P. nigriceps* exhibited clinal variation in R5SPCT, with smaller values for this character found in northern populations and larger sample means in the south. All three species exhibited patterns of geographic variation in R5WEB that were identical to those shown by R5SPCT (Tables 12, 13).

Interspecifically, sample means of R5SPCT and R5WEB for *P. californica* over-

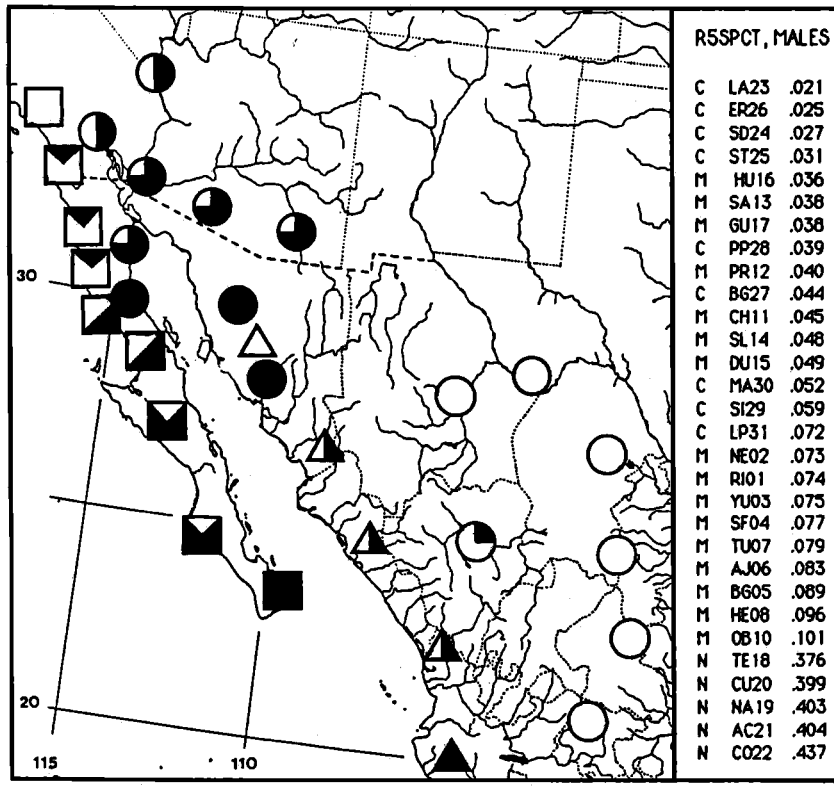


FIG. 28. Variation in R5SPCT in three species of *Polioptila* (males). See legend to Figure 22.

lapped considerably with samples of *P. melanura* from the Chihuahuan desert; no overlap in these characters was found between *P. californica* and Sonoran desert populations of *P. melanura* (Fig. 28). The mostly white-tailed *P. nigriceps* had much larger values for R5SPCT and R5WEB than either *P. melanura* or *P. californica.*

Shape of the tail spots on rectrices 5 and 6 (R6SSH, R5SSH) varied both inter- and intraspecifically (Fig. 29). Sonoran desert populations of *P. melanura* were characterized primarily by tail spot shape "A," whereas samples of this species from Chihuahuan desert localities had spot types "A" and "B." In *P. californica,* tail spot shape "A" was nearly absent from sample areas north of 29°N latitude (LA23, SD24, ST25, ER26); instead, these populations were characterized mostly by types "C" and "D." In central and southern Baja California (SI29, LP31) tail spot types "C" and "D" continued to be the dominant forms, although approximately 20 percent of the specimens from these areas had spot type "A." Tail spot shape of *P. nigriceps* was uniformly categorized as "A" throughout the species' range.

Similar patterns of variation were found in the extent and positioning of the white eye-ring feathering on alternate-plumaged males (Tables 12, 13). In *P. melanura,* most samples were characterized by complete white eye-rings. Samples of *P. melanura* from the Chihuahuan desert showed, in comparison with Sonoran desert populations, a greater tendency for the white feathering to be restricted or

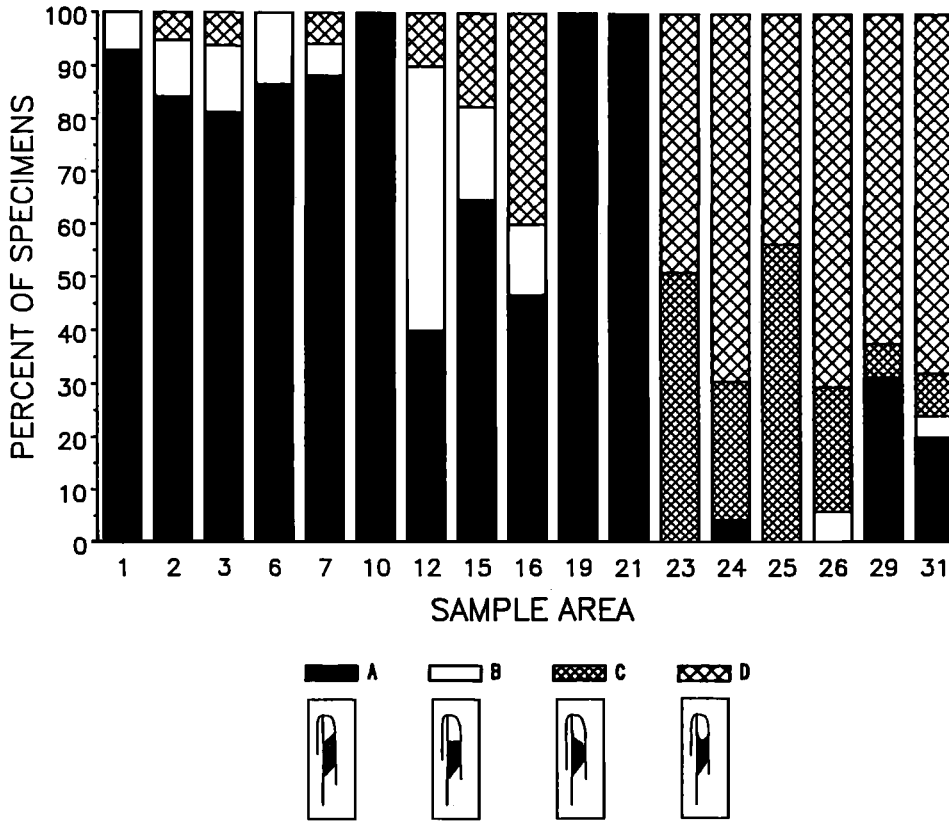


FIG. 29. Variation in R6SSH in three species of *Polioptila* (males). Shape of white spot on inner vane of rectrix is indicated in legend figures A, B, C, and D. Each sample area indicated by numeric code (see Table 1); only samples represented by >15 specimens are included.

even lacking above the eye. Most alternate-plumaged male *P. californica* had incomplete eye-rings with white being largely restricted to an area below the eye; however, a clinal pattern of geographic variation in this character was evident, and increasingly complete eye-rings occurred in populations south of central Baja California. Similar to *P. californica,* complete white eye-rings were rare in alternate-plumaged male *P. nigriceps,* with white feathering being restricted primarily to an area below the eye.

Although often difficult or impossible to see in museum specimens, the extent of the white eye-ring in alternate-plumaged male gnatcatchers was surprisingly evident during field observations, suggesting that it might serve an important signalling function to the birds themselves. In general, the partial white eye-rings of *P. californica* (excluding populations from the Cape region of Baja California) and *P. nigriceps* were only apparent under careful inspection, whereas the complete eye-ring of *P. melanura* (especially the Sonoran desert populations) was obvious even from considerable distances.

Variation in soft parts coloration.—Descriptions of soft parts coloration, based on comparison of freshly collected specimens with standardized color swatches provided in Smithe (1975), were available from 119 specimens (80 males, 39

TABLE 14

FACTOR LOADINGS ON PRINCIPAL COMPONENTS 1–3, CALCULATED OVER ALL SPECIES COMBINED[a]

Character[b]	PC1		PC2		PC3	
	Males	Females	Males	Females	Males	Females
BLEN	.044	.029	−.003	.031	.411	.228
BWID	.012	.008	.001	.014	.049	.038
BDEP	−.004	−.001	.014	.023	.057	.036
TARTOE	.034	.062	.102	.140	.502	.276
P10LEN	.197	.243	.186	.198	−.047	−.796
P9LEN	.289	.281	.073	.074	−.145	−.072
P8LEN	.304	.293	.097	.111	.049	.028
P7LEN	.313	.309	.103	.130	.089	.099
P6LEN	.320	.309	.105	.119	.106	.111
P5LEN	.321	.308	.108	.121	.099	.106
P4LEN	.328	.304	.114	.121	.079	.065
P3LEN	.308	.312	.134	.144	.129	.071
TLEN	.447	.468	−.031	−.121	−.431	.123
R4PCT	.001	.000	−.001	−.001	.001	.000
R5PCT	.001	.000	−.002	−.001	.001	−.001
R6PCT	.000	−.001	.000	.001	−.003	−.005
R6SSH	−.161	−.141	.547	.516	.336	−.078
R5SSH	−.175	−.201	.659	.658	−.299	.299
R6SPCT	.015	.014	−.029	−.026	.038	.031
R5SPCT	.014	.013	−.023	−.019	.041	.030
R6WEB	−.057	−.056	.159	.195	.091	−.029
R5WEB	−.126	−.116	.340	.292	−.310	−.271
Proportion of variance	.483	.421	.214	.231	.076	.077

[a] PCA based on total sample (by sex) of all three species. Percent of total variance (over all species) explained by first 3 PC axes = 77.3% (males), 72.9% (females).

[b] Character abbreviations as defined in Methods.

females) from the following sample areas: RI01, SF04, BG05, HE08, OB10, CH11, SA14, DU15, HU16, NA19, AC21, ER26, BG27, PP28, MA30, and LP31. Of six soft part characters, five showed no intra- or interspecific variability, at least within the limitations of subjective color analysis possible under field conditions. Iris coloration was uniformly perceived as Natal Brown (Color 219A), upper mandible coloration as Blackish Neutral Gray (Color 82), distal tip of the lower mandible as Blackish Neutral Gray, tarsus as intermediate between Blackish Neutral Gray and Dark Neutral Gray (Color 83), and foot pad as Glaucous (Colors 79 or 80).

The only soft part that showed evident variation in color was the proximal base of the lower mandible. In specimens of both male (N = 17) and female (N = 11) *P. melanura* collected in the Chihuahuan desert, the lower mandible was uniformly Blackish Neutral Gray from base to tip. In the Sonoran desert populations of this species, as well as in *P. californica* and *P. nigriceps,* I consistently perceived the base of the lower mandible as being distinctly lighter colored (Medium Neutral Gray, Color 84) relative to the Blackish Neutral Gray tip.

MULTIVARIATE ANALYSES

Inter- and intraspecific variation.—To examine patterns of variation between and within species, principal components analysis (PCA) and canonical discrim-

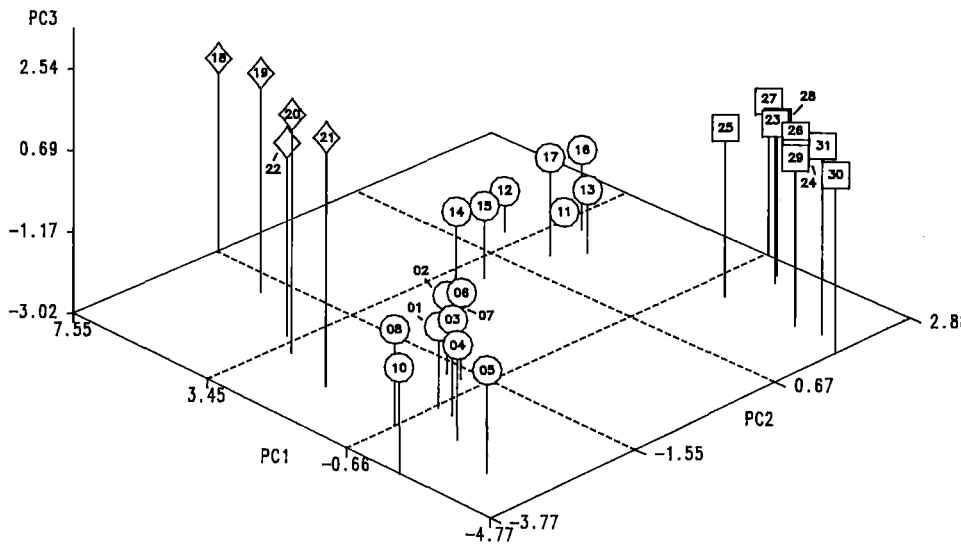


FIG. 30. Three-dimensional projection showing results of principal components analysis performed over all species (males only) using 22 morphological characters. Locality mean scores are plotted on PC axes 1–3. Diamonds = *Polioptila nigriceps*; circles = *P. melanura*; squares = *P. californica*. Numbers in each symbol indicate sample areas (see Table 1).

inant analysis (CDA) were used as methods of data reduction. In these techniques, the information content of 22 morphological characters (BLEN, BWID, BDEP, TARTOE, P3–10LEN, TLEN, R4–6PCT, R5–6SSH, R5–6SPCT, R5–6WEB) is simultaneously expressed in terms of single linear combinations of the original variables. The results of CDA were similar to those of PCA and are not described here.

Principal components analysis: interspecific variation.—Table 14 presents factor loadings on the first three principal components (PCs1–3), calculated for each sex over the entire data set (all three species combined). Comparable results were obtained for both males and females. PC1 accounted for 48.3 percent of the total variance in males and 42.1 percent in females; wing (P3–10LEN) and tail (TLEN) measurements were highly correlated with PC1 in both sexes. Separation of area means along PC2 were largely determined by R5–6SSH and, to a lesser extent, R5WEB, in both males and females. PC3 was correlated with BLEN, TLEN, and R5WEB in males, and P10LEN in females.

Mean scores by sample area on PCs1–3 are presented visually in Figure 30 (males) and 31 (females). Inspection of these 3-dimensional plots indicates four major clusters of samples in multivariate space: *P. californica, P. nigriceps,* Chihuahuan desert populations of *P. melanura,* and Sonoran desert populations of *P. melanura.* The plots of males and females were generally similar. Because of the relatively small sample sizes on which many area means of females were based, further analysis of minor differences between the sexes in the multivariate structure of variation was not pursued.

Cluster analysis.—Whereas broad patterns of variation between these species are evident from visual inspection of the PCA plots, distortions inherent in the plotting procedure prevent detailed analysis of similarities and differences among

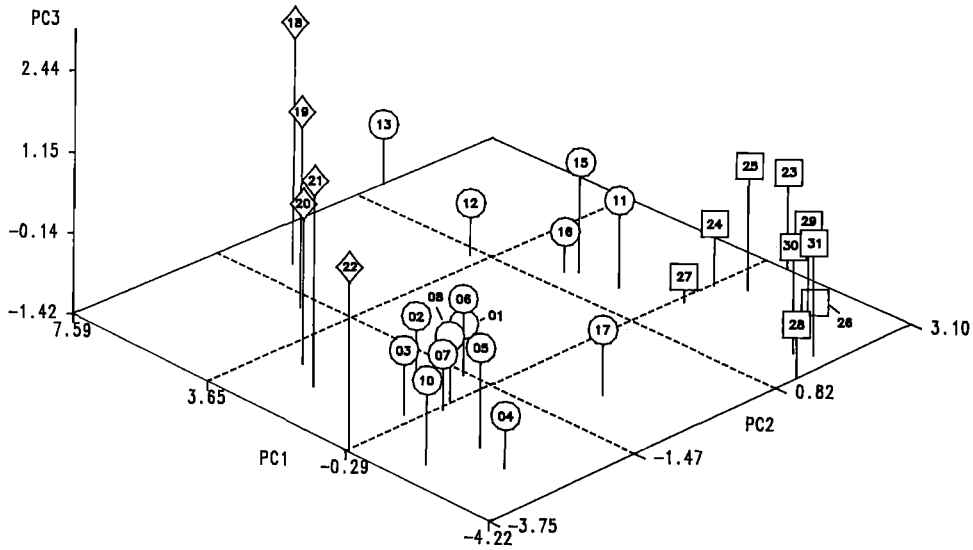


FIG. 31. Three-dimensional projection showing results of principal components analysis performed over all species (females only) using 22 morphological characters. See legend to Figure 30.

sample areas. Therefore, to examine intraspecific patterns of phenetic variation further, I constructed UPGMA phenograms for males and females.

Three major clusters are evident in the phenogram for males (Fig. 32). One unit included samples of *P. nigriceps*; within this cluster, TE18 and NA19 segregated together, and CU20, AC21, and CO22 formed a similar subgroup. The second major unit included all samples of *P. californica,* with populations from the Cape region of Baja California (SI29, MA30, LP31) forming a separate cluster from the northern sample areas (LA23, SD24, ST25, ER26, BG27, PP28). The third major unit was composed of all samples of *P. melanura,* with a pronounced separation between Chihuahuan (CH11, PR12, SA13, SL14, DU15, HU16, GU17) and Sonoran (RI01, NE02, YU03, SF04, BG05, AJ06, TU07, HE08) populations.

The phenogram for females (Fig. 33) was less well defined in its geographic patterns, probably mostly as a result of inaccuracies caused by including several areas that were represented by very small sample sizes. Clustering of the samples of males and females was identical in *P. nigriceps.* The sample of *P. melanura* from SA13, based on only five specimens, segregated from the remainder of the "black-tailed" group. Samples of *P. californica* were grouped with most of the Chihuahuan desert populations of *P. melanura* (CH11, PR12, DU15, HU16); within this unit, *P. californica* and *P. melanura* were clearly segregated. Sonoran desert populations of *P. melanura* were clustered together, along with GU17 (based on only three specimens) from the Chihuahuan desert.

Principal components analysis: intraspecific variation.—Geographic heterogeneity in 22-dimensional character space was tested for each species using multivariate analysis of variance (MANOVA). The sample area centroids for males of each species differed significantly from one another ($P < 0.0001$, Wilks' Lambda test criterion; *P. melanura*: $F = 2.32$; *P. nigriceps*: $F = 2.43$; *P. californica*: $F = 2.58$). In females, significant F values were obtained for *P. melanura* ($F = 1.99$)

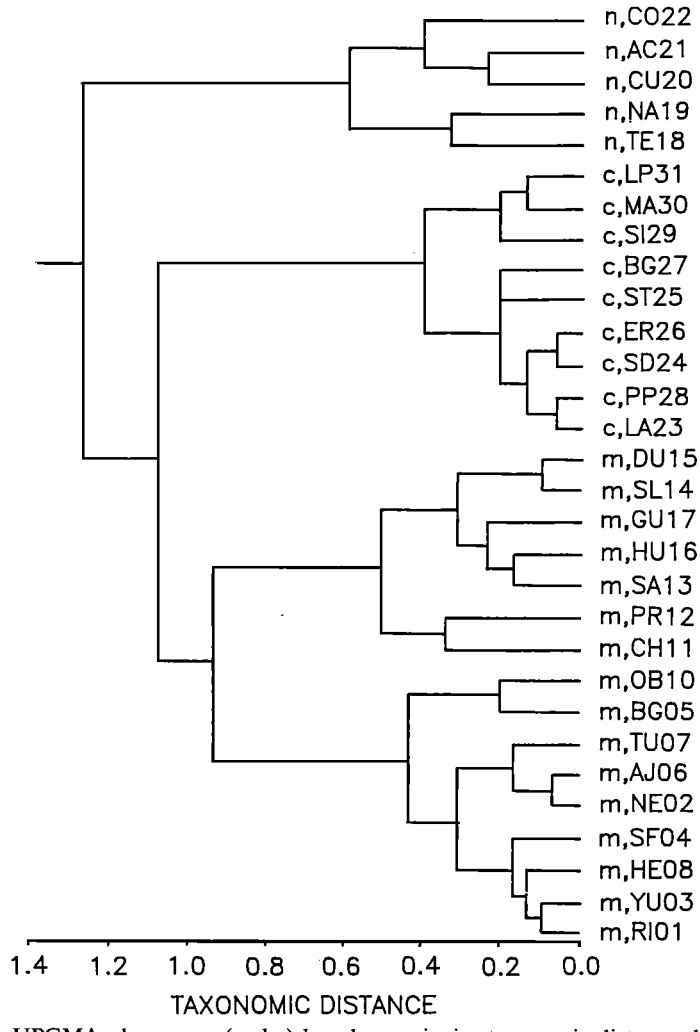


FIG. 32. UPGMA phenogram (males) based on pairwise taxonomic distances between sample areas, derived from locality means of 22 morphological characters. Species codes (m = *P. melanura*, c = *P. californica*, n = *P. nigriceps*) are provided to the left of each sample area code.

and *P. californica* ($F = 1.92$); the distribution of centroids in multivariate space were not significantly different in female *P. nigriceps* ($F = 1.23$, $P = 0.329$).

To examine these patterns of intraspecific phenetic variation further, PCAs were also performed for each species (males only, Table 15). For *P. melanura,* the first three PCs accounted for 79.8 percent of the total variance, with PC1 accounting for 57.8 percent. In *P. californica,* 68.8 percent of the variance was accounted for by PCs1–3, including 44.9 percent by PC1. PCs1–3 accounted for 89.0 percent of the variance in *P. nigriceps,* of which 71.7 percent was associated with PC1. High factor loadings were obtained for all three species for TLEN and wing length measurements (P3–10LEN) on PC1; R5SSH was highly correlated with PC2 in *P. melanura* and *P. californica,* whereas in *P. nigriceps* this axis was influenced mostly by TLEN. In all three species PC3 included high loadings for

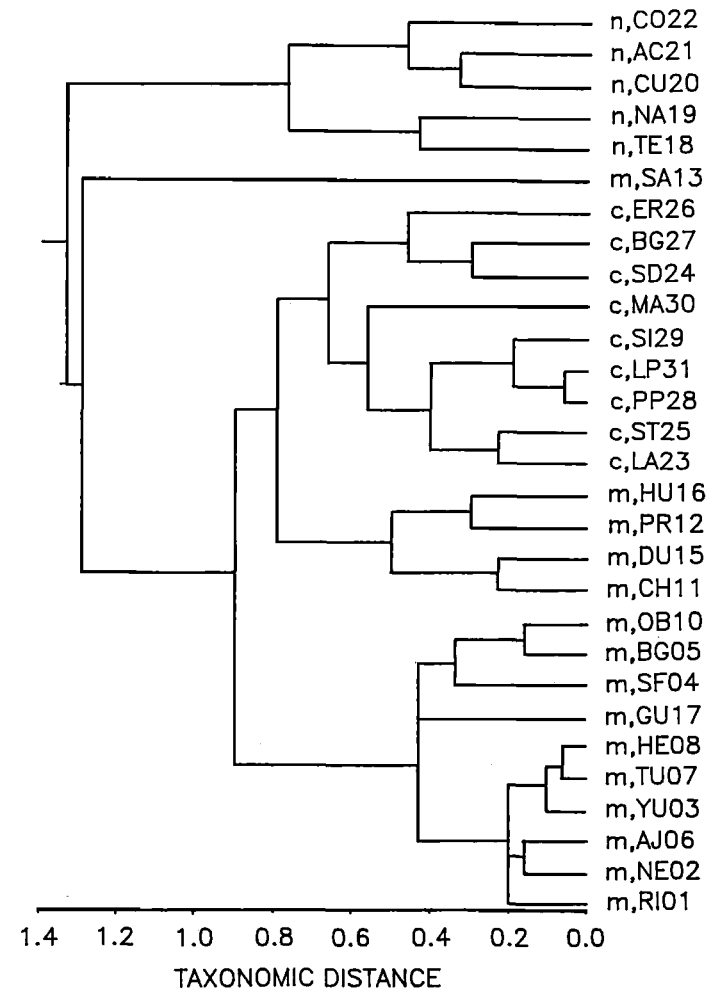


FIG. 33. UPGMA phenogram (females) based on pairwise taxonomic distances between sample areas, derived from locality means of 22 morphological characters. Species codes (m = *P. melanura*, c = *P. californica*, n = *P. nigriceps*) are provided to the left of each sample area code.

P10LEN and TLEN; other important variables accounting for separations along PC3 included R6SSH (*P. melanura*) and TARTOE (*P. nigriceps*).

ANOVA results for each species, based on the mean PC scores for each sample area, are presented in Table 16. Significant *F*-values were obtained for all species across sample areas for PC1, indicating geographic heterogeneity in the morphological characteristics summarized by this axis. Sample means for PC2 varied significantly across sample areas only in *P. melanura*, although the *F*-value for these scores in *P. nigriceps* was nearly significant ($F = 2.50$, $P = 0.051$). Significant geographic variation in the combination of characters represented by PC3 was found in *P. melanura* and *P. nigriceps*; the *F*-value across sample areas of *P. californica* was relatively high, although not significant ($F = 1.84$, $P = 0.073$).

Mean PC scores for each species were plotted using pie diagrams, and maximally nonsignificant subsets of area means were determined using the Sum of Squares

TABLE 15

FACTOR LOADINGS ON PRINCIPAL COMPONENTS 1–3, CALCULATED FOR EACH SPECIES[a]

	P. melanura			*P. californica*			*P. nigriceps*		
Character[b]	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
BLEN	.023	.023	.133	.001	−.011	.016	−.061	−.115	.323
BWID	.011	.001	−.025	−.002	−.003	.009	.000	.001	−.064
BDEP	.001	.001	.051	−.004	.006	.003	−.026	−.029	.084
TARTOE	.056	−.026	.108	.026	−.012	.077	.026	−.207	.488
P10LEN	.264	−.120	−.595	.278	−.037	.876	.244	.361	−.530
P9LEN	.308	−.132	−.179	.319	.081	.228	.271	.317	−.126
P8LEN	.312	−.090	−.041	.317	.045	−.057	.306	.203	.006
P7LEN	.325	−.089	.014	.323	.028	−.075	.312	.088	.178
P6LEN	.329	−.089	.029	.330	.036	−.112	.325	.084	.226
P5LEN	.325	−.082	.013	.342	.037	−.123	.335	.073	.250
P4LEN	.328	−.076	−.005	.363	.048	−.132	.349	.081	.142
P3LEN	.315	−.038	.015	.333	.046	−.121	.351	.054	.218
TLEN	.398	.096	.414	.374	−.144	−.277	.456	−.800	−.368
R4PCT	.000	−.001	−.001	.000	.000	.000	.000	.001	−.003
R5PCT	.000	−.001	−.001	.000	.000	.001	−.001	.002	−.004
R6PCT	.000	−.001	−.001	.000	.001	.002	.000	.002	.000
R6SSH	.114	.189	.570	.006	.378	.099	.000	.000	.000
R5SSH	.162	.931	−.272	−.049	.905	−.042	−.001	.007	.023
R6SPCT	−.001	−.007	−.008	−.004	.002	.007	−.001	.001	.003
R5SPCT	−.003	−.008	−.002	−.002	.000	.003	−.001	.001	.008
R6WEB	.004	.022	−.005	.054	−.011	−.115	.000	.000	.000
R5WEB	.098	.132	.089	.037	.015	−.067	.003	.005	.021
Proportion of variance	.578	.157	.064	.449	.136	.103	.717	.122	.051

[a] PCAs, calculated by species, males only. Percent of total variance explained by first 3 PC axes: *P. melanura* = 79.8%; *P. californica* = 68.8%; *P. nigriceps* = 89.0%.
[b] Character abbreviations as defined in Methods.

Simultaneous Test Procedure (SS-STP). These plots summarize geographic variation across many characters, and thus portray "dominant themes" of morphological variation (Zink 1986).

Four homogeneous subsets of mean scores for PC1 were obtained in *P. melanura*; two subsets were identified in both *P. californica* and *P. nigriceps* (Fig. 34). In all three species these results reflected geographic patterns of character variation that were observed through univariate analysis (Tables 12, 13). As in the univariate plots of TLEN (Fig. 25) and P6LEN (Figs. 22, 23), both characters correlated importantly with the variation described by PC1. Plots of PC1 values for each sample area showed a major separation in *P. melanura* between Chi-

TABLE 16

GEOGRAPHIC HETEROGENEITY IN PRINCIPAL COMPONENT (PC) SCORES

	F-values[a]		
Species	PC1	PC2	PC3
P. melanura	10.90**	2.02*	2.74**
P. nigriceps	6.55**	2.50	4.93*
P. californica	3.77**	0.83	1.84

[a] *F*-values calculated (one-way ANOVA) for males of each species. ** = $P < 0.01$; * = $P < 0.05$.

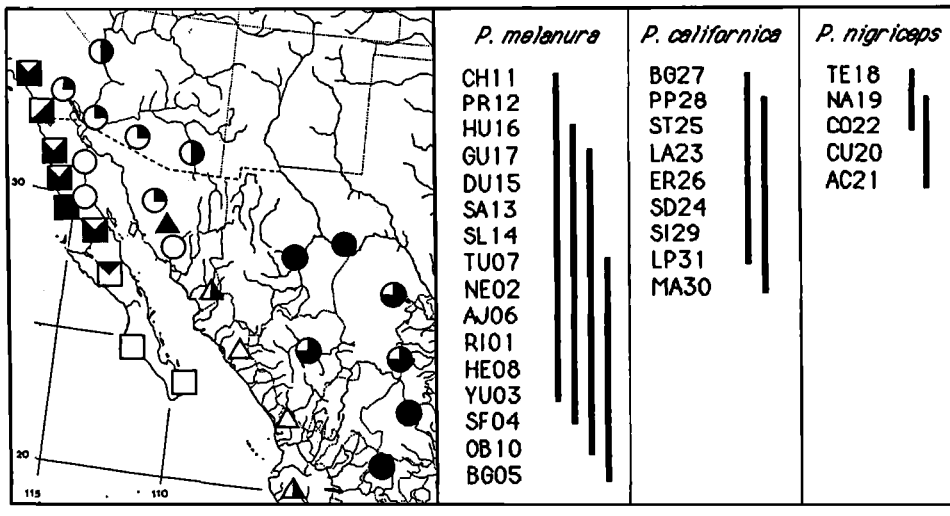


FIG. 34. Variation in PC1 scores in three species of *Polioptila* (males). See legend to Figure 22. Vertical lines to the right of the sample areas for each species indicate maximal nonsignificant subsets determined by the Sum of Squares Simultaneous Test Procedure (SS-STP).

huahuan and Sonoran desert populations. Sample areas SF04, BG05 and OB10 were all characterized by small (strongly negative) values on PC1. The plot of means for PC1 in *P. californica* similarly resembled those of TLEN and P6LEN for this species, with uniformly large values obtained from areas north of approximately 27°N latitude and distinctly smaller mean PC1 scores from populations in the Cape region of Baja California (SI29, MA30, LP31). In *P. nigriceps,* the plot of PC1 means indicated a clinal pattern of geographic variation, similar to that repeatedly observed in univariate analyses.

Less clear patterns of geographic variation were demonstrated by mean scores for PC2 (Fig. 35); single nonsignificant subsets of sample means were identified in all three species by SS-STP. Most Chihuahuan desert samples of *P. melanura* segregated together along PC2, although SL14 obtained a low (negative) value on this axis. No obvious pattern of geographic variation was evident for PC2 scores in *P. californica.* In *P. nigriceps,* where PC2 scores were highly correlated with TLEN as opposed to R5SSH in both *P. melanura* and *P. californica* (Table 15), a pattern of north-south clinal variation was evident.

SS-STP identified two maximally nonsignificant subsets of mean PC3 scores in both *P. melanura* and *P. nigriceps* (Fig. 36); only a single subset was calculated for *P. californica.* Chihuahuan desert populations of *P. melanura* varied clinally in the morphological characteristics summarized by PC3, with small values obtained in northern sample areas (CH11, PR12) and large values in the south (HU16, GU17). Sonoran desert samples of *P. melanura* showed no evident pattern of geographic variation in mean PC3 scores. The three sample areas located in the center of *P. nigriceps* distribution (NA19, CU20, AC21) were plotted as uniformly large in mean PC3 values, with smaller scores being obtained from localities to the north (TE18) and the south (CO22).

Potential hybrid specimens.—Of particular interest in this study are the morphological characteristics of "black-tailed" gnatcatchers obtained from the region

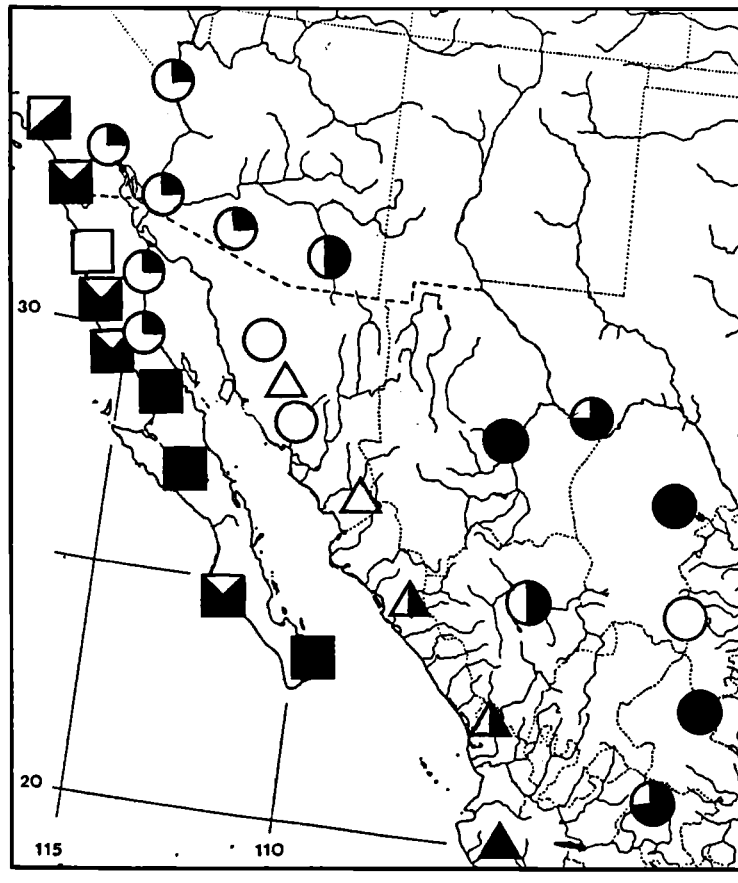


FIG. 35. Variation in PC2 scores in three species of *Polioptila* (males). See legend to Figure 22. The Sum of Squares Simultaneous Test Procedure (SS-STP) identified only single nonsignificant subsets for each species.

of overlap between *P. melanura* and *P. californica.* I obtained no evidence of mixed pairs of *P. melanura* and *P. californica* where the two putative species occurred sympatrically, nor did I record individuals with intermediate vocal characters (see above). Do specimens collected from this region show any intermediate morphological characteristics that might indicate hybridization?

Canonical discriminant analysis (CDA) was used to compare phenetically the 20 specimens collected in the zone of sympatry between *P. melanura* and *P. californica* with specimens of both species taken in nearby regions of allopatry. The results of CDA are presented in Figure 37; 88.9 percent of the total variation was accounted for by the first two canonical variables. Scores of individual specimens from the zone of overlap (BG05, BG27) fell within the range of variation found in allopatric samples of either *P. melanura* (YU03, SF04) or *P. californica* (ER26, PP28). No morphological intermediacy was indicated.

Discriminant function analysis (DFA), based on 22 morphological characters (BLEN, BWID, BDEP, TARTOE, P3–10LEN, TLEN, R4–6PCT, R5–6SSH, R5–6SPCT, R5–6WEB), was also used to compare the 20 specimens from BG05 and

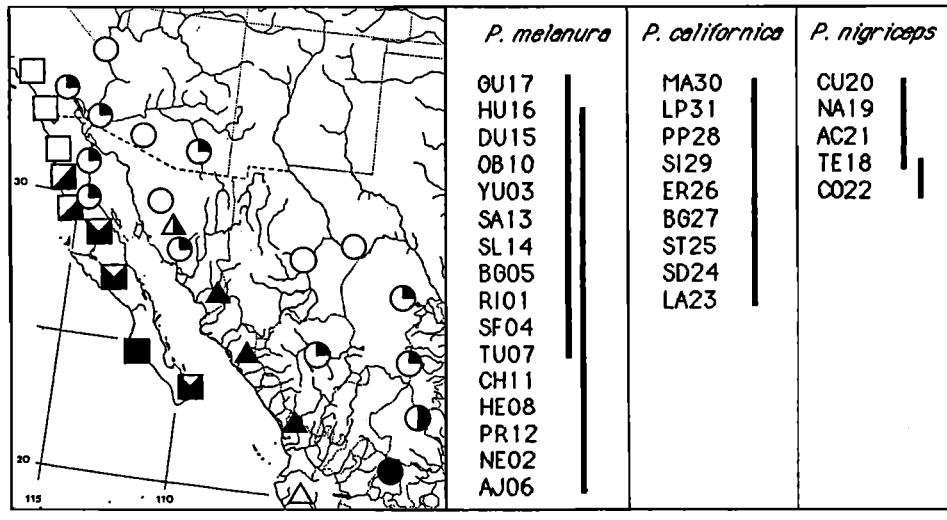


FIG. 36. Variation in PC3 scores in three species of *Polioptila* (males). See legend to Figure 22. Vertical lines to the right of the sample areas for each species indicate maximal nonsignificant subsets determined by the Sum of Squares Simultaneous Test Procedure (SS-STP).

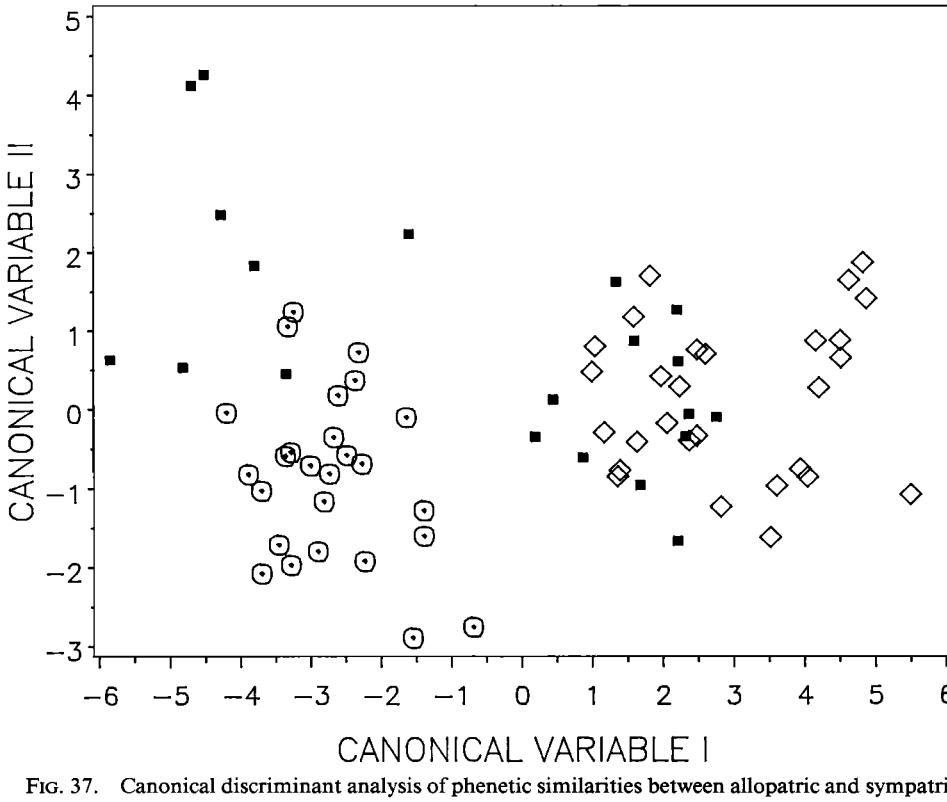


FIG. 37. Canonical discriminant analysis of phenetic similarities between allopatric and sympatric samples of *Polioptila melanura* and *P. californica*. Individual specimens are plotted on the first two canonical axes. Specimens collected in the zone of sympatry (BG05, BG27) are indicated by solid squares. Specimens of *P. melanura* from allopatric areas (YU03, SF04) are indicated by circles, and specimens of *P. californica* from allopatric areas (ER26, PP28) by diamonds.

BG27 with specimens taken in areas of allopatry (YU03, SF04, ER26, PP28). In all cases, specimens from the overlap zone that had been identified on the basis of vocalizations as either *P. melanura* (N = 8) or *P. californica* (N = 12) were correctly classified by DFA (using morphological characters) into the appropriate species.

DISCUSSION

Species Limits and Taxonomy

In describing processes of avian speciation, most modern ornithologists have generally based their analyses on Mayr's (1963) biological species concept, in which species are considered to be "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." Dissatisfaction with this definition and its application to evolutionary problems has substantially increased in recent years (see reviews by Ehrlich 1961; Sokal and Crovello 1970; Cracraft 1983), leading some authors to conclude that "the biological species concept is in need of a major overhaul" (Zink 1986). In particular, Cracraft (1983) has proposed adoption of a phylogenetic species concept, in which populations that are characterized by at least one distinguishing trait or "evolutionary novelty" are considered to be species, regardless of whether or not these populations are reproductively isolated from other such groups.

The advantages and disadvantages of the phylogenetic species concept have been discussed by Zink and Remsen (1986). By focusing on the results of evolution, namely, differentiated taxonomic units, the study of speciation based on phylogenetic species is unencumbered by preconceived notions concerning the evolutionary processes that might have caused the observed pattern being investigated. Furthermore, the need for subjective decisions regarding whether certain morphological, behavioral or genetic differences between allopatric populations might result in reproductive isolation is avoided. Difficulties with the phylogenetic species concept are mainly practical in nature; for example, species might undergo considerable independent evolution without the appearance of a diagnostic characteristic, and, therefore, not be easily recognizable (Zink and Remsen 1986), or apparently diagnostic traits might reflect the influence of environmental factors rather than true divergence (James 1983).

In this study I have presented several lines of evidence supporting the hypothesis of at least two distinct species (under both Mayr's and Cracraft's species definitions) of gnatcatchers with mostly black outer rectrices. Although primarily allopatric in their distributions, *P. californica* and *P. melanura* are currently sympatric in at least two distinct areas, where assortative mating occurs without hybridization. Therefore, on the basis of the biological species concept, *P. melanura* and *P. californica* are "good" species. Furthermore, *P. californica* and *P. melanura* differ sharply from each other vocally, and subtle contrasts in morphology and ecology also exist. The presence of such distinguishing features indicate that these two "black-tailed" gnatcatchers also meet the definition of phylogenetic species.

As to the taxonomy of the "black-tailed" gnatcatcher group, *P. melanura* and *P. californica* should certainly be restored to full specific status, as originally described by Baird (1854) and Brewster (1881). Regardless of which species concept is used, considering these populations as conspecific is unjustified. The mor-

phological similarity between Sonoran desert populations of *P. melanura* and populations of *P. californica* from the Cape region of Baja California, which formed the basis of Grinnell's (1926) decision that the two should be considered conspecific, is better interpreted as evolutionary convergence. In an exactly parallel situation, Davis (1951) considered the California-Baja California populations of Brown Towhee (*Pipilo fuscus*; A.O.U. 1983) to be conspecific with forms occurring in the Chihuahuan-Sonoran deserts based on morphological similarities between Cape region and eastern populations; Zink (1988) has recommended that these populations be considered specifically distinct.

A more difficult question concerns the formal taxonomy of the Chihuahuan and Sonoran desert forms of *P. melanura.* These two allopatric populations are moderately distinct morphologically, especially using multivariate character analyses; these differences suggest some degree of independence in their evolutionary histories. No obvious differences in vocalizations exist between these two forms (although careful statistical analyses might reveal subtle variations not examined here). Comparative genetic information is not available.

According to Cracraft's (1983) criterion of "diagnosability," I consider the Sonoran and Chihuahuan desert populations of "black-tailed" gnatcatchers to be probable phylogenetic species, although the overall level of phenetic divergence is not great. Whether these allopatric populations are also biological species (Mayr 1963), I do not know. My opinion is that vocalizations are of greater importance as reproductive isolating mechanisms in *Polioptila* than morphological traits, and that Sonoran and Chihuahuan desert populations of *P. melanura* would probably interbreed. However, in the absence of sympatry this is pure speculation. I cannot rule out the possibility that morphological, genetic, or subtle behavioral differences might prevent reproductive compatibility between Sonoran and Chihuahuan desert populations of *P. melanura.*

At the present time, I recommend that the name *P. melanura* be retained for both the Sonoran and Chihuahuan desert populations of "black-tailed" gnatcatchers. Despite the fact that each population is an evolutionary diagnosable unit, and that they are, therefore, arguably "species" (*sensu* Cracraft 1983), I nonetheless would advise against a nomenclatural change now. The rationale for this recommendation is more practical than philosophical. I concur with Zink and Remsen (1986) that phylogenetic species "should be the units used in historical analyses of phylogeny, biogeography, and speciation." However, until the phylogenetic species concept has become more widely accepted, inclusion of such "species" in systems of formal nomenclature that presently are largely based on an entirely different species definition seems more likely to confuse than to clarify discussions of evolutionary relationships.

The use of subspecies in avian taxonomy has similarly been debated recently (Phillips 1982; Johnson 1982; Barrowclough 1982), and their application in the present context is dependent upon how species are defined. Taxonomic arrangement for *P. melanura,* based on the biological species concept, would (as is presently the case; A.O.U. 1957) ascribe subspecific status to the Chihuahuan desert (*P. m. melanura*) and Sonoran desert (*P. m. lucida*) groups of "black-tailed" gnatcatchers. Inherent in this approach is the assumption that these vocally and (to a lesser degree) morphologically similar allopatric populations would interbreed should they ever come in contact. Under the phylogenetic species concept,

the use of subspecies is generally avoided because the basic taxonomic (and evolutionary) entity is considered to be the species. As discussed above, *P. m. melanura* and *P. m. lucida* might legitimately be considered phylogenetic species based on the presence of morphological differences between the two populations.

Although available specimen material from the isolated population of *P. melanura* on Isla Tiburón is limited, at the present time I recommend tentative retention of *P. m. curtata* (van Rossem 1932). I know of no specimens of this species from Isla San Esteban, and only a single specimen exists from Isla Ángel de la Guarda. All of these island populations of *P. melanura* warrant further study.

Clinal variation in multiple morphological characters was found in populations of *P. californica* north of the Cape region of Baja California; at approximately 25°N latitude, many characters showed a relatively sharp transition or step. Under the biological species concept, two subspecies of *P. californica* would be reasonably recognized: *P. c. californica* in the northern portions of the species' range, and *P. c. margaritae* in the Cape region. I see no compelling reason to maintain *P. c. pontilis* for populations in central Baja California, which in most characters merely seem to exhibit smooth, clinal variation with populations farther north; in fact, this subspecies was originally defined in terms of these "transitional" characters (van Rossem 1931a).

Strict application of the phylogenetic species concept might consider *P. c. californica* and *P. c. margaritae* to be "species" on the basis of diagnostic morphological differences (*P. c. margaritae* having relatively short tails and more extensive white on the outer rectrices). However, Cracraft (1983) conceded that "under some circumstances . . . subspecific names could be applied to populations showing clinal variation, and subspecies boundaries could then be determined by sharp gradients in character variation." The phenetic differences between *P. c. californica* and *P. c. margaritae* are not as profound as those between *P. m. melanura* and *P. m. lucida.* Certainly *P. c. californica* and *P. c. margaritae* should not be considered biological species (no distributional disjunction or evidence of reproductive isolation exist), and because of the relatively slight differentiation between them I consider the two forms only marginal species by the phylogenetic definition. Assuming concordance between genetic and phenetic divergence as well as similar rates of evolution within these groups (both somewhat questionable assumptions; Zink 1988), *P. c. californica* and *P. c. margaritae* diverged more recently from one another than did *P. m. melanura* and *P. m. lucida.* A study of genetic differences between these four major populations of "black-tailed" gnatcatchers would be most instructive. Also, additional specimen material from populations of *P. californica* on islands in the Gulf of California would be desirable.

A third member of the genus *Polioptila,* the mostly "white-tailed" *P. nigriceps,* was included in this study for comparative purposes. Although several of the important vocalizations of *P. nigriceps* resemble those of *P. californica,* the overall vocal repertoires of *P. nigriceps* and *P. californica* are more different from each other than are the vocalizations of *P. californica* and *P. melanura* from each other. An electrophoretic analysis of these three species indicated that *P. nigriceps* was sharply different from Sonoran desert samples of *P. melanura* and specimens of *P. californica* from northern Baja California and California; the "black-tailed" gnatcatchers were indistinguishable based on the limited number of loci that were studied (R. Matson, pers. comm.). Thus, morphological, behavioral, and genetic

analyses all support the contention that *Polioptila melanura* (Sonoran desert group) and *Polioptila californica* are more closely related to each other than either is to *Polioptila nigriceps.*

In summary, two or three species of *Polioptila* with mostly black outer rectrices exist, depending on whether "species" is defined as a reproductively isolated unit (*sensu* Mayr) or as a distinguishable evolutionary group (*sensu* Cracraft). Following Amadon's (1966) use of brackets in designating superspecies and allospecies, my arrangement of the "black-tailed" gnatcatcher complex is as follows:

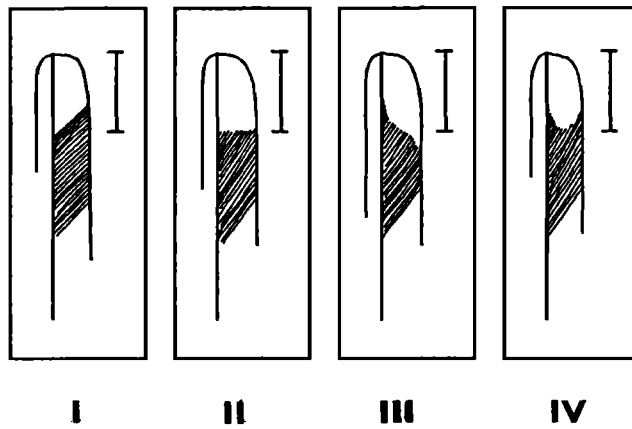
Superspecies:	*Polioptila* [*melanura*]
Allospecies:	*Polioptila* [*melanura*] *melanura*
	Polioptila melanura melanura
	Polioptila melanura lucida
	Polioptila melanura curtata (tentative)
Allospecies:	*Polioptila* [*melanura*] *californica*
	Polioptila californica californica
	Polioptila californica margaritae

The following key to these species, based on the data set used in this study (island populations excluded) and using only morphological characters (as opposed to distributional information), correctly identified 97 percent of the specimens that were examined with 90 percent accuracy. Most misidentifications involved females of *P. m. lucida* that were identified as *P. m. melanura,* and specimens of *P. californica* from the Cape region of Baja California (*P. c. margaritae*) that were confused with *P. m. lucida.* Incorporation of distributional data into such a key would result in virtually 100 percent accuracy; populations occurring in the only regions of overlap between *P. californica* and *P. m. lucida* are easily distinguished morphologically, and distributional characters could be used to separate populations that are phenetically convergent.

KEY TO THE "BLACK-TAILED" GNATCATCHER COMPLEX[a]

1A. Outer web of rectrix 6 not completely white ..... *P. californica*
1B. Outer web of rectrix 6 completely white *and* tail length < 47.5 mm *and* rectrix 6 tail spot shape Type III or IV ..... *P. californica*
1C. Not as above 2
2A. Formula A > 0.95 *or* length of tail spot on rectrix 6 ≦ 3 mm 3
2B. Not as above 4
3A. Length of tail spot on rectrix 6 < 6.5 mm ..... *P. californica*
3B. Length of tail spot on rectrix 6 > 6.5 mm ..... *P. m. lucida*
4A. Formula B < 102 *and* rectrix 6 tail spot shape Type I or II .. *P. m. lucida*
4B. Formula B < 102 *and* rectrix 6 tail spot shape Type III ..... *P. californica*
4C. Formula B > 112 ..... *P. m. melanura*
4D. Not as above 5
5A. Formula C > 2,420 *or* length of tail spot on rectrix 6 > 8 mm ..... *P. m. lucida*
5B. Length of tail spot on rectrix 6 ≦ 6 mm ..... *P. m. melanura*
5C. Not as above ..... unknown

[a] rectrix 6 tail spot shape and length defined as follows:



Key formulas, based on measurements in mm, defined as follows. Wing length is unflattened wing chord.

Formula A = (Wing length/tail length)
Formula B = ((Formula C) × (Tail length − length of rectrix 6 tail spot))/1,000
Formula C = (Wing length × tail length)

Common Names

The common name Black-tailed Gnatcatcher should be retained for *Polioptila melanura.* I reject a return to the principal English name (Plumbeous Gnatcatcher) that was earlier associated with this species for the following reasons: (a) avoidance of potential confusion with the Middle and South American *Polioptila plumbea* (Tropical Gnatcatcher); (b) agreement between English name and specific epithet; (c) recognition that in reality most populations of *P. californica* are more truly "plumbeous" (i.e., lead-colored) than is *P. melanura*; and (d) recognition that the common name Black-tailed Gnatcatcher is currently widely used by both professional and amateur field ornithologists for populations of *Polioptila melanura.*

I suggest that *Polioptila californica* be referred to as the California Gnatcatcher. Reasons for this recommendation include (a) clear agreement of the specific scientific epithet with this English name; (b) historical usage of the similar names California Black-capped Gnatcatcher by Baird (1854) and California Black-tailed Gnatcatcher by Grinnell (1926) for *P. californica*; and (c) the fact that *P. californica* is restricted to California and Baja California. To return to the now obsolete association of the English name Black-tailed Gnatcatcher with *P. californica* seems certain to create needless confusion.

Historical Biogeography

The value of a comparative biogeographical approach in the study of speciation has been summarized by Cracraft (1982, 1983). By examining the geographical ranges of various groups of phylogenetic species, congruent distributional patterns can be identified. Shared patterns of distribution among unrelated taxa suggest that the historical factors or events associated with the speciation process might

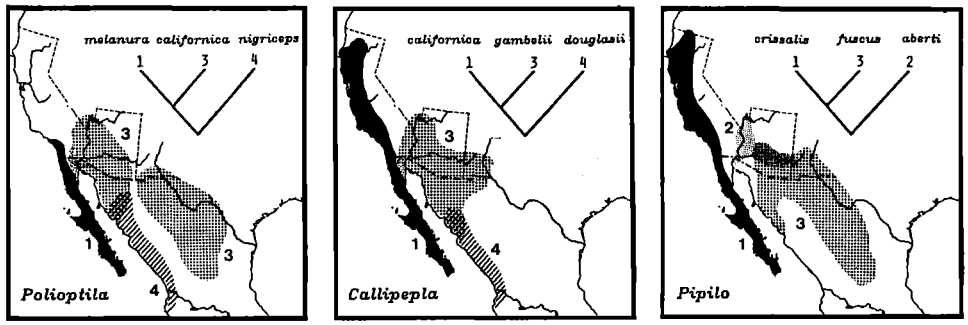


FIG. 38. Phylogenetic relationships and distribution in three taxa of North American xeric-adapted birds. Hypothesized cladistic relationships based on this study (*Polioptila*), Gutierrez et al. (1987) (*Callipepla*), and Zink (1988) (*Pipilo*). 1 = taxa restricted to the California-Baja California region; 2 = taxa restricted to the Sonoran desert; 3 = taxa restricted to the Sonoran and Chihuahuan deserts; 4 = taxa restricted to the arid lowlands of the western Mexican mainland.

have been similar for each lineage; species groups with different distributional patterns would presumably have different evolutionary histories.

I have attempted to apply these principles to three genera of birds with members distributed in the arid regions of western North America: *Polioptila* (gnatcatchers), *Pipilo* (towhees), and *Callipepla* (quail). Specific phylogenetic relationships have been recently hypothesized for each of these groups (Fig. 38).

Repeated patterns or species "tracks" (Wiley 1981) are evident from the distributional maps of these taxa. Three species (*Polioptila californica, Pipilo crissalis* [*sensu* Zink 1988], and *Callipepla californica*) are restricted to California and/or Baja California. Three species (*Polioptila melanura, Pipilo fuscus* [*sensu* Zink 1988], and *Callipepla gambelii*) occur in both the Chihuahuan and Sonoran deserts. *Polioptila nigriceps* and *Callipepla douglasii* share similar ranges along the arid western coast of mainland Mexico, and *Pipilo aberti* is restricted to specialized habitats in the Sonoran desert (Davis 1951).

Cladistically, all three of the species that are restricted to the California-Baja California region (*Polioptila californica, Pipilo crissalis,* and *Callipepla californica*) have as their closest relatives species that are distributed in both the Sonoran and Chihuahuan deserts (*Polioptila melanura, Pipilo fuscus,* and *Callipepla gambelii*) (Fig. 38). *Polioptila californica* is not most closely related (cladistically) to *Polioptila nigriceps* of the western coast of mainland Mexico, nor are the similarly distributed *Callipepla californica* and *C. douglasii* sister species.

Various hypotheses have been suggested to explain the distributional patterns exhibited by the biota of Baja California. Most early authors, assuming a geological permanence to the peninsula, accounted for present-day distributions and species relationships through invasions of Baja California by northern faunas coupled with the ecological effects of climatic changes (Grinnell 1928; Savage 1960; Stager 1960; Hubbard 1974). However, Murphy (1983a, b) has convincingly argued that most of the distributional and phylogenetic patterns characteristic of the amphibians and reptiles of Baja California are better explained by the effects of geologic events associated with the peninsula's formation. Murphy (1983a) noted two especially important vicariance events in the evolution of the herpetofauna of Baja California. First, during the mid-Miocene (approximately 14 MYBP), land masses that eventually formed the Cape region of Baja California began rifting

northward from their origin on the Mexican mainland near the present-day state of Colima; these Cape islands probably became connected with developing northern parts of the peninsula in the Pliocene. Secondly, expansion of the proto-Gulf of California began in the Pliocene (approximately 5 MYBP), resulting in (a) isolation of the peninsula from mainland regions located north of the present-day state of Sinaloa, and (b), for xeric-adapted forms, isolation of the peninsula from areas north of the mesic San Gorgonio Filter Barrier, located near present-day Palm Springs, California. In Murphy's scenario, establishment of the Gulf of California was responsible for the formation of several east-west sister taxa of reptiles distributed in Baja California and the Chihuahuan-Sonoran deserts. Most of the species that Murphy (1983a) hypothesized to have dispersed onto the peninsula from northern mainland regions during the Pleistocene are widespread Chihuahuan-Sonoran desert forms that presently are restricted to the extreme northeastern coastal region of Baja California; north-south dispersals to or from the peninsula during the Pliocene were limited to mesophilic species able to cross the San Gorgonio Filter Barrier.

To what extent is the present-day distribution of birds in Baja California a reflection of Pliocene geologic events? Are patterns of distribution and phylogeny better explained by dispersal between mainland and peninsular desert regions or by vicariance associated with various geologic events?

The patterns shown by *Polioptila* (Fig. 38) are consistent with both trans-Gulf vicariance and north-south dispersal models. Assuming an ancestral population of "white-tailed" *Polioptila* (proto-*nigriceps*) on the west coast of Mexico, "black-tailed" gnatcatchers might have evolved on the Baja California peninsula following its separation from the mainland. As the San Gorgonio Filter Barrier was eliminated in the late Pliocene and Pleistocene (Murphy 1983a), "black-tailed" gnatcatcher stock dispersed northward (and eastward) from the Baja California peninsula into the Chihuahuan-Sonoran desert regions. Further elevation of the Peninsular ranges (Gastil et al. 1975) and continuing aridity trends (Axelrod 1966, 1975, 1979) sharpened the developing ecological contrasts between the California-Baja California region and the Chihuahuan-Sonoran deserts. Populations of "black-tailed" gnatcatchers in each of these two areas are hypothesized to have undergone allopatric speciation, with secondary sympatry being established as the already differentiated *Polioptila melanura* dispersed from the Sonoran desert into the arid coastal zone of northeastern Baja California.

The alternative hypothesis, invoking dispersal of "black-tailed" gnatcatchers into Baja California from the north, is also tenable in its explanation of phylogenetic relationships. In both cases, *Polioptila melanura* and *P. californica* are sister species, and populations of *Polioptila californica* in California and Baja California are predictably similar. However, none of the reptiles thought to have dispersed southward into Baja California during the Pleistocene are distributed throughout the entire peninsula as is *P. californica,* and none have sister species located in the Chihuahuan-Sonoran desert regions (Murphy 1983a). Earlier (Pliocene) dispersal of xerophilic taxa was prevented by the presence of mesic habitats which extended from the head of the Gulf of California westward to the Los Angeles basin of southern California (Murphy 1983a).

Two recent studies have addressed the origin and differentiation of particular components of the avifauna of Baja California (Zink et al. 1987; Zink 1988). Assuming (probably correctly) that *Callipepla californica* is more closely related

to *C. gambelii* than to the unstudied *C. douglasii* (Gutierrez et al. 1983), Zink et al. (1987) hypothesized that "California Quail dispersed southward into Baja California subsequent to its connection to the southern California mainland;" if this species "was present on Baja while it moved northward, and subsequently dispersed northward into California . . . California Quail would be nearest relatives (cladistically) with quail . . . such as Elegant Quail (*C. douglasii*)." I believe the trans-Gulf vicariance model is equally consistent with this pattern. The hypothesized phylogeny of this group would be adequately explained by peninsular isolation and differentiation of pre-*californica-gambelii* stock from mainland Mexican populations (pre-*douglasii*), followed by range expansion of *californica-gambelii* across the San Gorgonio Filter Barrier and subsequent separation into Chihuahuan-Sonoran desert (*Callipepla gambelii*) and California-Baja California (*C. californica*) populations.

Comparable distributional patterns are also exhibited by members of the genus *Pipilo* (Fig. 38). Zink (1988) suggested that the "close relationship between brown towhees in Baja California and California . . . suggests that they dispersed into Baja from the north subsequent to the joining of the Baja peninsula to the California mainland." However, a Pliocene east-west vicariance event (separating proto-*fuscus* to the east and proto-*crissalis* on the Baja peninsula), followed by expansion of *crissalis* from Baja California north into California after elimination of the San Gorgonio Filter Barrier, could also be suggested as a viable hypothesis. Although the genetic data presented by Zink (1988) indicate a more recent date of divergence between these two species than that postulated by the trans-Gulf vicariance model, the calibration of molecular clocks remains open to much debate (Vawter et al. 1980; Britten 1986; Vawter and Brown 1986). Neither model can be excluded at the present time.

This discussion suggests caution in the construction of speciation scenarios for North American xeric-adapted birds, especially those that occur in Baja California. The paleogeography of the late Pliocene-early Pleistocene undoubtedly influenced patterns of differentiation and present-day distribution, but the extent of these effects is poorly known. Further information concerning relationships, paleoecology, rates of avian evolution, and the degrees of genetic divergence exhibited by these and other taxa of desert birds might eventually provide more definitive support for the north-south dispersal or trans-Gulf vicariance models, or suggest alternative hypotheses. Without such additional data the evolutionary histories of these xeric-adapted bird species must remain unclear.

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SUMMARY

All populations of *Polioptila* with mostly black outer rectrices are currently considered to be a single species, *Polioptila melanura.* However, two forms are reproductively isolated where they occur sympatrically; this fact, coupled with pronounced vocal differences and relatively subtle contrasts in morphology and ecology, indicate that *Polioptila melanura* and *P. californica* are biologically distinct species. Recognition of these species limits restores the original taxonomy proposed for the group. Under the phylogenetic species concept, it could be argued that three species of "black-tailed" gnatcatchers exist, with the Chihuahuan and Sonoran desert populations of *P. melanura* being evolutionary taxa on the basis of morphological differences.

Polioptila californica is primarily restricted geographically to Baja California, whereas *P. melanura* is distributed widely throughout the arid regions of the southwestern United States and Mexico. The two species occur sympatrically in three areas, principally on the north central Gulf coast of Baja California between 29°–30°N latitude. In this overlap zone assortative mating occurs, and no indication of hybridization has been found. Vocal, morphological, and ecological differences that distinguish the species where they occur allopatrically persist even in this area of sympatry.

Previously proposed evolutionary histories involving avian taxa occurring in Baja California have generally indicated invasions of the peninsula by species that differentiated in northern desert regions. However, comparison of geographic and phylogenetic patterns in the genera *Polioptila, Callipepla,* and *Pipilo* with those proposed for the herpetofauna of Baja California by Murphy (1983a) suggests that an alternative hypothesis, based on vicariance events associated with formation of the Gulf of California, might be equally tenable. At the present time, neither scenario can be easily rejected.

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APPENDIX I

LOCALITIES OF SPECIMENS USED IN MORPHOLOGICAL AND VOCAL ANALYSES

For each species, the localities of specimens used in the analysis of morphological variation are provided for each sample area. The locality code for each area is given following the sample area name. Modern localities that have been substituted for obsolete geographic names are indicated in brackets []. Localities of vocal recordings obtained during this study are also provided.

SPECIMEN LOCALITIES

Polioptila melanura

STUDY SKINS

RIVERSIDE COUNTY, CALIFORNIA RI01

California—Riverside Co.: Chiriaco Summit, 5 mi W; Chiriaco Summit, 9.6 mi E; Chuckwalla Springs; Coachella; Cottonwood Spr., Joshua Tree National Monument; Indian Wells, 2 mi S; Indio; Mecca; North Shore, 7 mi E; Palm Springs; Palm Springs, Deep Canyon; Pinto Wash, Joshua Tree National Monument; Thermal; Wiley Well; Imperial Co.: Fish Springs; Fish Springs, 5 mi W.

NEEDLES, CALIFORNIA NE02

Arizona—Mohave Co.: Alamo; Fort Mohave, Colorado River; Kingman, 18.5 mi W; Parker; California—San Bernardino Co.: Fort Piute, 4 mi W; Needles, 29 mi S; Vidal Jct., 9 mi N; "Nevada, Clark County, Needles Hwy., 4.6 mi S Hwy. 163" [= Needles, 19.4 mi N]; "Nevada, Clark County,

Needles Hwy., 5.7 mi S Hwy. 163" [= Needles, 18.3 mi N]; Nevada—Clark Co.: Snyder Ranch, 0.5 mi SW.

YUMA, ARIZONA YU03

Arizona—Yuma Co.: Yuma; Baja California—Cocopah Mtns; Laguna Salada; Cañon Los Palmas, 15 mi S of N end of Laguna Salada; Río Hardy; El Doctór; California—Imperial Co.: Bard; Brawley.

SAN FELIPE, BAJA CALIFORNIA SF04

Baja California—Arroyo El Cajón; Bahía San Felipe; San Felipe; San Felipe, 10 mi NW; San Felipe, 11 mi NW; San Felipe, 22 mi SSW; Valle de Trinidad.

BAHÍA SAN LUÍS GONZAGA, BAJA CALIFORNIA BG05

Baja California—Arroyo Calamajué; Campo Punta Finál, 5 mi W; El Crucero, 5 mi NW; Las Arrastras, 5.8 mi NW; Las Encantadas, 2 mi NW.

AJO, ARIZONA AJ06

Arizona—Pima Co.: Ajo, 9 mi SE; Gila Bend; Organ Pipe Cactus National Monument; Sonora—Sierra Pinacáte; Sonoyta; Sonoyta, 18.7 mi S.

TUCSON, ARIZONA TU07

Arizona—Cochise Co.: Apache; Cave Creek; Chiricahua Mountains; Portal; Portal, 2 mi SE; Pima Co.: Continental; Huachuca Mtns., 15 mi E; Papago Indian Reservation, Robles Ranch, 14.8 mi W; Rincon Mtns., Vail; Santa Catalina Mtns., Sabino Canyon; Fort Lowell [= Tucson]; Sonora—Saric.

HERMOSILLO, SONORA HE08

Sonora—Carbo, 7 km W; Granádos; Granádos, 1.9 mi N in Río Bavispe Valley; Hermosillo; Hermosillo, 15 mi S; Opedope; Oputo [= Villa Hidalgo]; Querobabi, 3 mi S; Querobabi, 7 km W; Querobabi, 8 km W.

ISLA TIBURÓN, SONORA TI09

Sonora—Isla Tiburón.

CIUDAD OBREGON, SONORA OB10

Sonora—Batamotal; Camoa; Ciudad Obregon; Ciudad Obregon, 30 km N; Guaymas; Guaymas, 10 mi N; Guaymas, 37 mi NW; San Javier; Tecoripa.

CHIHUAHUA, CHIHUAHUA CH11

Chihuahua—Chihuahua; Chihuahua, 5 mi N; Ciudad Camargo; Ciudad Camargo, 5 mi SE; Ojo de Laguna.

PRESIDIO COUNTY, TEXAS PR12

Texas—Brewster Co.: Black Gap Headquarters, 2 mi E; Chisos Mtns., Pine Canyon; Chisos Mtns., 3 mi SE Lower Juniper Springs; Glenn Draw; Glenn Spring; Glenn Spring, 5 mi N; Hot Springs; Marathon; Rena Blanca Mountains; Río Grande, Johnson Ranch; San Vicente; Terlingua; Presidio Co.: locality unspecified; Presidio, 8 mi SE.

SABINAS, COAHUILA SA13

Coahuila—Ciudad Musquiz; Monclova, 12 mi N; Puerta del Carmen, 25 mi NW Monclova; Sabinas; Nuevo Leon—Rodriguez; Texas—Duval Co.: Freer, 10 mi SW; Webb Co.: Laredo; Laredo, 32 mi E.

SALTILLO, COAHUILA SL14

Coahuila—Presa El Tulillo, 3 mi S Hipolito; Cuesta Blanca, 12 mi W Saltillo; Saltillo, 20 mi W; Saltillo, 65 km W; Nuevo Leon—Monterey; Zacatecas—Concepción del Oro.

DURANGO, DURANGO DU15

Durango—Chocolate, 1 mi S; Chocolate, 2 mi S; Durango, 12 mi NE; Nombre de Díos, 2 mi NW; Pedriceña, 6 mi NE; Presa Francisco Zarco, 40 mi S Torreon; Rancho Baillón; Resvalón, 5 mi W San Juan del Río; Río Nazas, 110 mi N Durango; Rodeo, 2 mi N; San Juan del Río, 4 mi W.

EL HUIZACHE, SAN LUIS POTOSI HU16

San Luis Potosí—Huizache, 1 mi W; Huizache, 12 mi N; Huizache, 35 km ESE; Huizache, 40 km

ESE; Huizache, 45 km ESE; Matehuala, 6 mi S; Presa de Guadalupe, 33 mi SW Tula; Santo Domingo; Villa Hidalgo, 3.3 mi NE; Pendenera [= Zacatecas—Pendencia]; Tamaulipas—Jaimes.

GUANAJUATO, GUANAJUATO GU17

Guanajuato—Irapuato, 5 mi NW; San Pedro, 5 mi W Dolores Hidalgo; Hidalgo—"Jct. Rts 45 and 85" [= Ixmilquipan, 25 km WSW]; Jalisco—Lagos de Moreno, 5 mi S; Zacatecas—Estacion Lulu, 3 mi N.

VOCAL RECORDINGS

Arizona—Mohave Co.: Alamo Lake State Park; Topock, 2 mi NW; Yucca, 20 mi SE; Pima Co.: Quijotoa, 3 km SE; Tucson, 3 km SW San Xavier Mission; Why, 10 mi S; Why, 17 mi S; Why, 8 mi SE; Santa Cruz Co.: Chino Canyon.
Baja California—Arroyo Calamajué; Arroyo El Cajón; Arroyo El Cajón, 1 km E; Arroyo El Cajón, 1 mi N; Bahía de los Angeles, 5 mi N; Bahía Santa Maria, 2 km N; Bahía Santa Maria, 3 km N; Bahía Santa Maria, 5 mi SW; Cañon de Guadalupe; Cantu Palms; Cantu Palms, 10 km N; Coloradito, 3 km N; Crucero La Trinidad, 16 km N; Crucero La Trinidad, 18 km N; Crucero La Trinidad, 24 km W; Ejido San Matías, 2 km W; El Crucero, 5 mi NW; Las Arrastras, 5.8 mi NW; Las Encantadas, 2 mi NW; Mexicali, 29 km S; San Felipe, 10 mi NW; San Felipe, 22 mi SSW.
California—San Diego Co.: Bow Willow Canyon, Anza Borrego State Park; San Felipe; Riverside Co.: Chiriaco Summit, 10 mi E; Cottonwood Springs, Joshua Tree National Monument; Deep Canyon, Palm Springs; Imperial Co.: Finney Lake; San Bernardino Co.: Fort Piute, 2 mi W; Fort Piute, 4 mi W; Rice, 10 mi W.
Chihuahua—Ciudád Camargo, 5 mi NE; Ciudád Camargo, 5 mi SE; El Carmen, 2 km W.
Coahuila—Presa El Tulillo, 3 mi S Hipolito; Monclova, 22 mi S.
Durango—Chocolate, 2 mi S; Rodeo, 2 mi N; San Juan del Río, 4 mi W; San Juan del Río, 5 mi W.
Guanajuato—Dolores Hidalgo, 4 mi WSW.
San Luis Potosí—El Huizache, 12 mi N; El Huizache, 30 km E; Matehuala, 6 mi S.
Sonora—Bahía Kino, 6 km E; Ciudad Obregon, 25 km N; Ciudad Obregon, 30 km N; Guaymas, 10 mi N; Guaymas, 25 mi S; Querobabi, 7 km W; Querobabi, 8 km W; Ures, 7 mi W.

Polioptila nigriceps

STUDY SKINS

TECORIPA, SONORA TE18

Sonora—Ohuissa [= Huassa]; San Javier; Soyopa; Tecoripa; Ures, 13 mi W; Ures, 15 mi W.

NAVOJOA, SONORA NA19

Sinaloa—Ahome; El Fuerte; San Blas, 14 km W, 26 km N; Sonora—Agiabampo, 6 mi SE; Alamos; Alamos, 19.5 mi NE; Alamos, 5 mi NE; Alamos, 6 mi W; Alamos, 7.5 mi SE; Alamos, 8 mi E; Alamos, 8.3 mi NW; Jori 5 mi W Bacum; Chinobampo; Ciudad Obregon; Ciudad Obregon, 9 mi N; Guirocoba; Tesia; Bahía Tobari.

CULIACAN, SINALOA CU20

Sinaloa—Chicorato, 3 mi S; Colmoa [= Durango—Coloma]; Copalito, 3 mi S Tecuciapa [= Capirato]; Cosala, 13 mi S; Culiacan; Elota; Portrerillo, 20 mi SE Cosala; San Lorenzo.

ACAPONETA, NAYARIT AC21

Nayarit—San Blas; Sauta, 7 mi S Santiago Ixquintla; Tepic; Tepic, 1 mi SE; Tepic, 16 km W; Tepic, 3 mi SE; Tepic, 3 mi SW; Tepic, 3 mi W; Tepic, 4.3 mi SSE; Tepic, 6 mi SW; Tepic, 7 mi NW; Sinaloa—Cacalotan, 15 mi E; La Guasimas; Labrados; Matatan; Mazatlan; Rosario; Villa Union, 5 mi E.

COLIMA, COLIMA CO22

Colima—Colima, 18 km S; Río Naranjo, 22 mi E Colima; Cualata; Periquillo, 12 km NW; Pueblo Juarez [= Coquimatlan]; Jalisco—Chacala; La Huerta; La Huerta, 3 mi S; Tuxpan.

VOCAL RECORDINGS

Colima—Colima, 18 km S.
Sinaloa—Villa Union, 5 mi E.
Sonora—Alamos, 12.7 km W; Guaymas, 20 mi S; Jori, 5 mi W Bacum.

Polioptila californica

STUDY SKINS

LOS ANGELES, CALIFORNIA LA23

California—Los Angeles Co.: locality unspecified; Arcadia; San Gabriel Wash, Azusa; Claremont; Monrovia; Palos Verdes Peninsula; Pasadena, Arroyo Seco; Port Ballona; Redondo; San Fernando; Taluca; Riverside Co.: Corona; Corona, 5 mi N; Lake Matthews; Menifee; Norco; Palm Springs; Riverside; San Jacinto Valley, Vallevista; San Bernardino Co.: Colton; San Bernardino.

SAN DIEGO, CALIFORNIA SD24

Baja California—Playa Santa Maria; Tijuana; California—San Diego Co.: Chula Vista; El Cajon; Jamul; National City; Point Loma; San Diego; San Diego, Sweetwater Reservoir.

SAN TELMO, BAJA CALIFORNIA ST25

Baja California—Colonet; San Quintín; Río Santo Domingo, San Ramon; San Telmo; Valle de Trinidad.

EL ROSARIO, BAJA CALIFORNIA ER26

Baja California—Cataviña; Cataviña, 3 mi N; Cataviña, 4.5 mi N; El Rosario; El Rosario, 10 mi E; El Rosario, 30 mi E; Guayaquil, 8 mi NW; San Agustin.

BAHÍA SAN LUIS GONZAGA, BAJA CALIFORNIA BG27

Baja California—Arroyo Calamajué; Campo Punta Finál, 5 mi W; Chapala, 2 mi NW; El Crucero, 5 mi NW; Las Arrastras, 5.8 mi NW; Las Encantadas, 2 mi NW.

PUNTA PRIETA, BAJA CALIFORNIA PP28

Baja California—Agua Amarga; Bahía de los Angeles, 10 mi W; Bahía de los Angeles, 22 mi W; Bahía de los Angeles, 8 mi W; Punta Prieta, 3 mi NW; Rosarito, 8 mi N; Rosarito, 8 mi SW; Rosarito, 9 mi SW; San Andres; San Borja.

SAN IGNACIO, BAJA CALIFORNIA (SUR) SI29

Baja California (Sur)—Bahía Concepción; Bahía San Francisquito; Bahía Santa Ana; Bahía Santa Teresa; San Bruno; Bahía San Francisquito; San Ignacio; San Lucas, 10 mi S Santa Rosalía.

BAHÍA MAGDALENA, BAJA CALIFORNIA (SUR) MA30

Baja California (Sur)—Isla Santa Margarita; Bahía Magdalena; San Jorge; Santa Rita, 17 mi SE; Santo Domingo, 15 mi S.

LA PAZ, BAJA CALIFORNIA (SUR) LP31

Baja California (Sur)—Bahía de los Muertos; Cabo San Lucas; El Cardonal, 15 km S; Bahía Frailes; La Paz; La Paz, 0.5 mi SW; La Paz, 0.8 mi SW; La Paz, 1 mi S; La Paz, 1 mi SW; La Paz, 3 mi S; La Paz, 3 mi SW; La Paz, 4 mi S; La Paz, 7 mi SW; Pichilingue, 1 mi SE; San Jose del Cabo; Santa Anita; Todos Santos.

ISLA ESPÍRITU SANTO, BAJA CALIFORNIA (SUR) ES32

Baja California (Sur)—Isla Espíritu Santo.

ISLA SAN JOSE, BAJA CALIFORNIA (SUR) SJ33

Baja California (Sur)—Isla San Jose.

VOCAL RECORDINGS

Baja California—Agua Amarga; Arroyo Calamajué; Arroyo El Cajón; Bahía de los Angeles, 3 mi N; Bahía de los Angeles, 30 mi NW; Cataviña, 3 mi N; Cataviña, 4.5 mi N; Colonet, 10 km E; El Crucero, 5 mi NW; El Crucero, 8.3 mi NE; El Rosario, 16 mi E; El Rosario, 32 mi E; Guayaquil, 8 mi NW; Las Arrastras, 5.8 mi NW; Las Encantadas, 2 mi NW; Meling Ranch, 11 km W; Meling Ranch, 6 km W; Campo Punta Finál, 5 mi W; Punta Prieta, 3 mi NW; Rosarito, 8 mi N; Rosarito, 8 mi SW; Ejido San Matías, 2 km W; San Telmo; San Vicente; San Quintín; Valle de Trinidad. Baja California (Sur)—El Cardonal, 15 km S; El Cardonal, 5 km S; El Cardonal, 8 km S; El Pescadero, 1 mi S; El Pescadero, 12 mi S; El Pescadero, 15 mi S; Mulege, 18 km S; Mulege, 30 km S; Pichilingue; San Ignacio, 1 km NW; Santa Rita, 15 mi SE; Santa Rita, 17 mi SE. California—San Diego Co.: Lake Hodges; Camp Pendleton Marine Corps Base; Jamul, 2 mi W; Riverside Co.: Lake Matthews; Los Angeles Co.: Palos Verdes Peninsula.

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