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EVOLUTION OF BROWN TOWHEES: ALLOZYMES, MORPHOMETRICS AND SPECIES LIMITS[1]

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Abstract. Variation in the Brown Towhee (*Pipilo fuscus*) complex was studied by using morphometric and electrophoretic methods. Study taxa, distributed primarily in the aridlands of southwestern North America, included Abert's Towhee (*P. aberti*), White-throated Towhee (*P. albicollis*), and two major components of the Brown Towhee (eastern *fuscus* group and western *crissalis* group); a sample of Brown Towhees from Baja California (*crissalis* group) was also included. Goals were to assess phenotypic (29 skeletal characters) and genetic (allozymic) patterns of differentiation, test current species limits, estimate phylogenetic relationships, and examine concordance in morphometric and genetic variation. Evolution in skeletal size and proportions has occurred primarily in the skull; taxa are not each distinct in principal component space. Phenograms based on taxonomic distances and correlation coefficients failed to reflect currently recognized species limits. A survey of 39 genetic loci revealed typical levels of genetic variation within and among taxa. However, the genetic distance between *P. albicollis* and *P. fuscus* from Arizona was nearly zero. The *fuscus* and *crissalis* groups were genetically distinct. Branching diagrams (phenograms, distance Wagner trees, maximum likelihood trees) summarizing genetic distances derived from a matrix of allelic frequencies suggest the following ordering of taxa: Abert's Towhee, Brown Towhee (*fuscus*) plus White-throated Towhee, and Brown Towhees from California and Baja California (*crissalis*). Based on the genetic data, the Brown Towhee as currently recognized is paraphyletic. The two forms of the Brown Towhee should be considered distinct species (*Pipilo fuscus* and *Pipilo crissalis*).

Key words: Brown Towhee; electrophoresis; morphometrics; genetic variation; phylogeny; speciation and species limits.

INTRODUCTION

Ornithologists have recently incorporated biochemical techniques into analyses of geographic variation and speciation (Barrowclough 1980, Corbin 1983, Johnson and Zink 1983, Zink 1986). These techniques are useful because they permit study of the geography of genetic variation and comparison of genetic variation with variation in morphological and other types of features. I analyzed patterns of genetic (allozymic) and morphologic variation among taxa in the Brown Towhee (*Pipilo fuscus*) complex, a group of sparrows distributed primarily in the aridlands of North America (Hubbard 1973; Fig. 1). My purpose was not a thorough survey of geographic variation in the forms, an excellent beginning at which was made by Davis (1951). Instead, I analyze variation in a few point samples with respect to species limits, which are controversial (AOU 1983), and I attempt to infer evolutionary patterns of diversification. Additionally, I add to the growing body of data concerning genetic variation within and among avian populations and species, and I comment on the covariation of genetic and morphologic patterns.

REVIEW OF PREVIOUS STUDIES OF THE BROWN TOWHEE COMPLEX

Davis (1951) provided a detailed analysis of variation in external measurements and coloration and behavior in the Brown Towhee complex. Davis recognized three species: *P. fuscus* (Brown Towhee), *P. aberti* (Abert's Towhee), and *P. albicollis* (=*P. rutilus*; White-throated Towhee). *Pipilo aberti* occurs in central and southern Arizona (and parts of adjacent states) and northern Mexico and *P. albicollis* occurs in Puebla, Guerrero, and Oaxaca. *Pipilo fuscus* includes three groups of subspecies: the *crissalis* group (eight subspecies occurring in Oregon, California, and Baja California), the *perpallidus* group (eight subspecies occurring in Arizona, New Mexico, Texas, Oklahoma, and Mexico south to Sonora) and *fuscus* (three subspecies occurring in Hidalgo and Oaxaca). I follow the AOU Checklist (1983) and refer to *fuscus* as a combination of *perpallidus*

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and *fuscus* groups. Unless otherwise noted, mention of either *crissalis* or *fuscus* refers to the subspecies groups. The *fuscus* and *crissalis* groups have been considered species (Davis 1951). Members of the *fuscus* group possess a distinct breast spot. However, Davis advocated conspecific status because morphological variation in several mensural traits and general coloration grades between the two groups. The form of the *crissalis* group most phenotypically similar to the *fuscus* group is the southernmost one in the Baja peninsula, *P. fuscus albigula.* However, gradation in several phenotypic characteristics is continuous from California to the Cape region of Baja California. Therefore, *P. f. albigula* is included in the *crissalis* group of subspecies.

Davis (1951) argued that the ancestor of brown towhees originated in northern Mexico and spread northward concomitant with the spread of the Madro-Tertiary flora in the Miocene. Separation into two groups occurred in the middle Pliocene along with the disappearance of towhees from the Great Basin. By the middle Pliocene, towhees had spread into Oregon and into southern California. Towhees in Baja California presumably immigrated from the north. Davis suggested that in general wherever habitats changed over time, towhee phenotypes changed in response. For example, Davis posited that the habitat in the Cape region of Baja California had remained similar to that inhabited by eastern *fuscus* populations; he considered *P. f. albigula* to be a "nondifferentiate," closer to the ancestral phenotype (*fuscus*) than other forms of *crissalis.*

Davis' analysis of the speciation history of towhees results in a paraphyletic taxon, *P. fuscus.* He suggested that an east-west split isolated *crissalis* and *fuscus* groups in the middle Pliocene, and that in the early Pleistocene, *P. aberti* evolved from the *crissalis* group (which also became darker), owing to uplifting of southern California mountains isolating *crissalis* and "proto-*aberti.*" Thus, according to Davis, *P. aberti* is the sister species of *crissalis* instead of *crissalis* plus *fuscus* groups. Based on geological and paleobotanical evidence, Davis suggested that whereas *aberti* evolved in a million years, *crissalis* and *fuscus* had not reached species-level distinction in six million years, an apparent disparity in rates of speciation. *Pipilo albicollis* was presumed to have arisen from *fuscus* stock isolated in southern Mexico.

Marshall (1960, 1964) reviewed evidence on the interrelations of sympatric *P. aberti* and *P. fuscus mesoleucus* [*fuscus* group]. Marshall (1960: 49) wrote "In the field, the Canyon Towhee [=*P. fuscus mesoleucus*] is not even recognizably the same species as the populations of California [*crissalis* group]; it is rather the Abert's Towhee which in form, posture, voice, and abundance seems the counterpart of the birds of coastal California." Nonetheless, Marshall (1960:63) concluded that "Although *P. f. mesoleucus* differs in many respects from *P. fuscus* [*crissalis* group] of California, its similarity in ecology and those other behavioral and vocal traits necessary to keep open the capability of interbreeding tend to substantiate the conclusion of Oberholser and Davis that they are subspecies." The two forms of the Brown Towhee were retained as subspecies in the most recent AOU Checklist (1983).

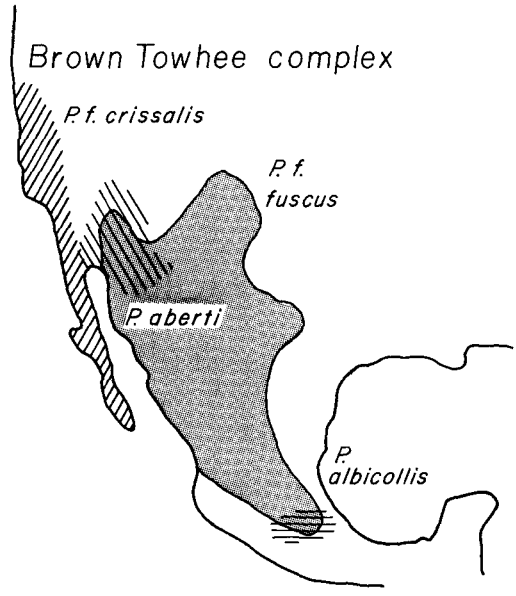

FIGURE 1. Outline map of the approximate distributions of taxa in the Brown Towhee complex.

MATERIALS AND METHODS

Samples for electrophoresis were taken from the following localities (N; taxon and locality code [*P. fuscus* only]): Napa County, California (8; *P. fuscus*-CA, *crissalis* group); Baja California, Mexico (7, *P. fuscus*-BA, *crissalis* group); Oaxaca, Mexico (4, *P. albicollis*); Cochise County, Arizona (10, *P. fuscus*-AZ, *fuscus* group); Pima County, Arizona (2, *P. fuscus*-AZ, *fuscus* group; 10, *P. aberti*). One specimen of the Green-tailed

TABLE 1. Eigenvectors for skeletal characters on the first three principal components. D = depth, L = length, W = width.

Character	PC I	PC II	PC III
Pre-maxilla L	0.12	0.07	0.18
Bill L	0.10	0.18	0.30
Bill D	−0.06	0.38	0.02
Nasal bone W	0.10	0.08	0.09
Interorbital W	−0.10	0.57	0.26
Post-orbital W	0.07	0.02	−0.04
Maximum skull W	0.10	0.06	−0.07
Maximum skull L	0.11	0.05	0.11
Mandible L	0.10	0.07	0.17
Mandible minimum L	0.15	0.06	0.19
Mandible D	0.00	0.52	0.06
Coracoid L	0.24	0.07	0.00
Scapula head W	0.22	0.26	−0.15
Sternum L	0.22	0.04	−0.23
Sternum W	0.19	−0.03	0.12
Sternum D	0.21	0.17	−0.33
Posterior synsacrum L	0.31	−0.12	−0.05
Fused vertebrae L	0.25	−0.15	0.25
Anterior synsacrum L	0.22	0.06	0.05
Synsacrum minimum W	0.19	−0.03	0.02
Synsacrum maximum W	0.21	0.05	−0.17
Femur distal end W	0.21	−0.09	0.21
Femur L	0.19	−0.04	0.12
Tibiotarsus L	0.24	−0.14	0.25
Tarsus L	0.23	−0.10	0.35
Humerus trochanter L	0.23	−0.03	−0.18
Humerus L	0.21	0.07	−0.14
Ulna L	0.20	0.07	−0.22
Carpal L	0.23	0.08	−0.27

Towhee, *P. chlorurus,* was used as an outgroup for rooting phylogenetic trees. Samples for morphometric analysis included the above specimens in addition to 10 from the American Museum of Natural History, New York, where voucher specimens are deposited; frozen tissue samples are preserved at the Museum of Zoology, Louisiana State University.

ELECTROPHORESIS

Samples of liver and pectoral muscle were taken from each specimen within a few hours after death and preserved in liquid nitrogen. Pieces of liver and muscle were pooled, minced with a razor blade, combined with 25 μl of deionized water, and spun at 36,000 × g for 25 min at 4°C. The aqueous supernatant was preserved at −70°C for subsequent electrophoresis and the tissue pellet discarded. Horizontal starch gel electrophoresis followed standard procedures (Selander et al. 1971, Harris and Hopkinson 1976, Johnson et al. 1984). Acronyms for protein loci follow Harris and Hopkinson (1976). Single locus genotypes were pooled and tested for departures from Hardy-Weinberg equilibrium expectations using χ^2 tests. Individual heterozygosity was determined by direct count and averaged across loci for each sample. Percentage of loci polymorphic and number of alleles per locus were computed. From genotypes, estimates of gene frequencies were used to derive genetic distances of Nei (1978) and Rogers (1972). To depict patterns of genetic similarity among samples and to estimate evolutionary history, phenograms (UPGMA; see Sneath and Sokal 1973) and distance Wagner trees (Farris 1972) were constructed. The above genetic analyses were performed by the computer program BIOSYS-1 (Swofford and Selander 1981). The computer program PHYLIP, version 2.7 (written by J. Felsenstein), was used to produce a maximum likelihood unrooted tree (program "CONTML") from square-root transformed gene frequencies (Felsenstein 1981), and a minimum-length tree (program "FITCH") from Rogers' distances via the least-squares procedure.

MORPHOLOGY

A total of 47 skeletons was measured for 29 characters (see Table 1); these measurements are described in Robins and Schnell (1971). Measurements were recorded to the nearest 0.05 mm using dial calipers.

Data analysis followed principles of numerical taxonomy (Sneath and Sokal 1973, Baker 1985). Raw data were $\log_{10}$-transformed and subjected to principal components analysis (PCA), the principal components being extracted from the covariance matrix using the computer program "PRINCOMP" (SAS Institute 1982). From character means, which were first variance-standardized, a matrix of taxonomic distances (Sneath and Sokal 1973) was constructed and used as a basis for construction of a UPGMA phenogram. Although the data were standardized, this phenogram is likely influenced by the size of individuals. Therefore, a second matrix was produced, the elements of which were Pearson product-moment correlation coefficients, and a second UPGMA phenogram was produced. The latter phenogram is intended as a gross estimate

TABLE 2. Allelic frequencies for polymorphic loci, observed and expected heterozygosity (and their standard errors), percentage polymorphic loci, and mean number of alleles per locus for six taxa of towhees. Alleles are coded by letter, with frequencies in parentheses.

Locus	*Pipilo chlorurus*	*P. albicollis*	*P. fuscus* Arizona	*P. fuscus* Northern California	*P. fuscus* Baja	*P. aberti*
Lgg	A (1.00)	B (1.00)	B (0.96) C (0.04)	A (1.00)	A (0.57) B (0.36) D (0.07)	A (0.70) B (0.30)
La-1	A (1.00)	C (1.00)	A (0.04) B (0.08) C (0.88)	C (1.00)	C (1.00)	C (1.00)
La-2	A (1.00)	A (0.88) B (0.12)	A (0.83) B (0.17)	A (0.94) C (0.06)	A (0.86) C (0.14)	A (1.00)
Est-D	A (1.00)	A (1.00)	A (0.92) B (0.04) C (0.04)	A (1.00)	A (0.86) B (0.14)	A (1.00)
α-Gpd	A (1.00)	A (1.00)	A (0.88) B (0.12)	A (1.00)	A (0.93) B (0.07)	A (1.00)
Np	A (1.00)	D (1.00)	B (0.21) C (0.04) D (0.75)	D (1.00)	D (1.00)	A (1.00)
Sod-1	A (1.00)	A (1.00)	A (0.96) B (0.04)	B (1.00)	B (1.00)	B (1.00)
Fum	A (0.50) C (0.50)	A (0.25) C (0.75)	A (0.46) B (0.13) C (0.41)	B (1.00)	B (1.00)	A (1.00)
Icd-1	A (0.50) B (0.50)	A (1.00)	A (0.88) B (0.08) C (0.04)	A (1.00)	A (1.00)	A (1.00)
Ada	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (0.86) B (0.14)
Pgm-2	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (0.85) B (0.15)
Sdh	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (1.00)	B (1.00)
Gpi	A (1.00)	A (1.00)	A (1.00)	A (0.94) B (0.06)	A (1.00)	A (1.00)
Mpi	A (1.00)	A (0.88) B (0.12)	A (1.00)	A (1.00)	A (1.00)	A (1.00)
Ldh-1	A (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)
Ldh-2	A (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)
Got-1	A (0.50) B (0.50)	B (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)
Gpt	A (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)
6-Pgd	A (0.50) B (0.50)	A (1.00)	A (1.00)	A (1.00)	A (1.00)	A (1.00)
Gda	A (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)	B (1.00)
$H_{obs.}$	0.103	0.026	0.064	0.006	0.026	0.020
(SE)	0.049	0.015	0.025	0.004	0.016	0.016
H_{exp}	0.103	0.024	0.060	0.006	0.032	0.025
(SE)	0.049	0.014	0.022	0.004	0.018	0.014
P	10.3	7.7	23.1	5.1	10.3	7.7
A	1.1	1.1	1.4	1.1	1.1	1.1

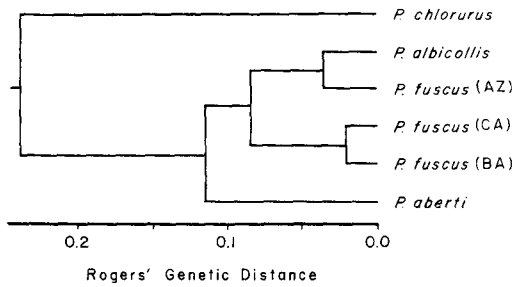

FIGURE 2. UPGMA phenogram based on Rogers' (1972) genetic distance.

of patterns of shape variation. The program package NTSYS (Rohlf et al. 1974) was used to construct phenograms.

RESULTS

ELECTROPHORESIS

Protein products of 39 presumptive genetic loci were resolved. Nineteen loci were monomorphic and fixed for the same allele in all taxa: CK-M, Ck-H, Mdh-1, Mdh-2, Eap, Got-2, Gsr, General protein (visualized with amido black) 1 and 2, Gdh, G-6-Pdh, Acon-1, Acon-2, Dia-1, Dia-2, Hk, AcP, Lap, and Icd-2. Twenty loci were variable, in that either polymorphism (heterozygosity) or interspecific differences were detected (Table 2). Within populations, no statistically significant ($P > 0.05$) departures were detected from expectations of Hardy-Weinberg equilibrium. Measures of genetic variability are shown in Table 2. Heterozygosity per sample ranged from 0.006 (*P. fuscus*-CA) to 0.064 (*P. fuscus*-AZ), and the average for all samples was 0.028. The percentage of loci polymorphic ranged from 5.1 (*P. fuscus*-CA) to 23.1 (*P. fuscus*-AZ); the average was 10.7%. The average number of alleles per locus was 1.1 for all samples except *P. fuscus*-AZ (1.4).

Patterns of variation at single loci (Table 2) exhibit several characteristics. Nine loci are polymorphic to a similar degree across samples, and, excluding the outgroup, contribute little to among-sample patterns of variation: La-1, La-2, Est-D, α-Gpd, Icd-1, Ada, Pgm-2, Gpi, and Mpi. Five loci contribute substantially to among-sample patterns: Lgg, Np, Sod-1, Fum, and Sdh. In the remaining loci variation is limited to the outgroup: Gda, 6-Pgd, Gpt, Got-1, Ldh-1, and Ldh-2.

Table 3 gives genetic distances among samples. The average genetic distance (Nei 1978) between the outgroup and samples of *P. fuscus* and *P. aberti* was 0.210. The average distance between *P. aberti* and *P. fuscus* samples was 0.094. Considering the remaining samples, the average distance was 0.043, and ranged from 0.002 (*P. albicollis* vs. *P. fuscus*-AZ) to 0.075 (*P. albicollis* vs. *P. fuscus*-CA). The value resulting from comparison of *fuscus*-AZ and *fuscus*-CA (*crissalis*) was 0.069.

The matrix of Rogers' (1972) genetic distances can be used as a basis for the inference of phylogenetic trees. Given the assumption of uniform rates of allozyme evolution, a UPGMA phenogram (Fig. 2) provides an estimate of evolutionary history. *Pipilo albicollis* and *P. fuscus*-AZ and *P. fuscus*-CA and -BA are each distinct pairs of taxa, each more similar to one another than either is to *P. aberti*. A distance Wagner tree (not shown) had the same topology and branch lengths roughly equivalent to those in the phenogram. An unrooted tree (not shown) produced by the maximum likelihood method exhibited a branching sequence identical to the UPGMA phenogram. The minimum length tree (not shown) places *P. aberti* as a sister taxon to *P. fuscus*-CA and -BA; whether this tree is statistically better than the previous three is unclear. The congruence of the first three branching diagrams suggests that the pattern in Figure 2 is independent of three different methodologies for tree construction. The

TABLE 3. Nei's (1978) and Rogers' (1972) genetic distances below and above diagonal (respectively).

	1	2	3	4	5	6
1. *P. chlorurus*	—	0.231	0.223	0.243	0.260	0.246
2. *P. albicollis*	0.205	—	0.031	0.082	0.077	0.128
3. *P. fuscus*–AZ	0.193	0.002	—	0.091	0.078	0.126
4. *P. fuscus*–CA	0.226	0.075	0.069	—	0.019	0.095
5. *P. fuscus*–BA	0.236	0.058	0.051	0.004	—	0.096
6. *P. aberti*	0.216	0.112	0.097	0.084	0.083	—

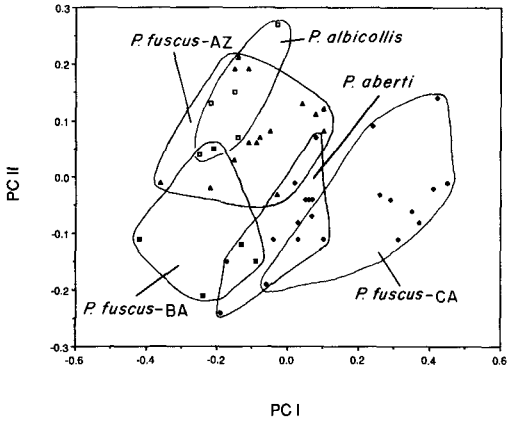

FIGURE 3. Plot of individuals on principal components I and II.

conclusions reached below will not depend on the differences between the two genetic tree structures.

Alleles were analyzed cladistically, by considering those found in the outgroup, *P. chlorurus,* to be ancestral and other alleles as synapomorphies or autapomorphies. Few alleles qualify for the latter two categories, a result consistent with many other avian electrophoretic surveys. In the towhees, the relationships of the *fuscus, crissalis,* and *albicollis* samples are of most interest. The distance analysis groups *fuscus* and *albicollis* because they share similar frequencies of alleles at Fum ("A" and "C"), Sod-1 ("A"), and Lgg ("B"). These conditions, however, are not absolute. Also, the similarity of *fuscus*-AZ and *albicollis* is due to sharing apparently ancestral alleles at Fum and Sod-1 (assuming that alleles in *P. chlorurus* represent the ancestral condition).

MORPHOMETRIC PATTERNS

In a plot (Fig. 3) of PC I × PC II, there is considerable overlap among several samples. Most individuals of *P. fuscus*-CA have relatively high scores on PC I (44.9% of the variance), whereas towhees from Baja California have relatively low scores. On PC II (14.9% of variance) samples are dispersed between *P. albicollis* and *P. aberti.* Postcranial characters contribute most to variation on PC I, whereas variation in skull characters (especially bill depth, interorbital width, and mandible depth), contributes most to separation on PC II (Table 1). On PC III (10.0% of variance), no particular body region contributes disproportionately to the separation of samples.

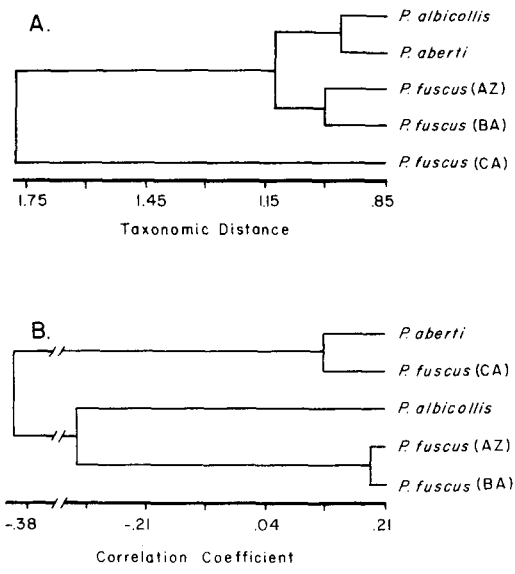

FIGURE 4. Phenograms summarizing patterns of morphometric similarity. A. Based on taxonomic distance, a "size" portrayal. B. Based on product-moment correlation coefficient, a "shape" portrayal.

In the phenogram (Fig. 4A) based on taxonomic distances (not shown, available from author), *P. aberti* and *P. albicollis,* and *P. fuscus*-AZ and -BA are paired, with the sample of *P. fuscus*-CA being an outlier to the other four samples. In the phenogram (Fig. 4B) based on correlation coefficients *P. aberti* and *P. fuscus*-CA are clustered together, as are *P. fuscus*-AZ and -BA; the sample of *P. albicollis* is phenetically most similar to the latter pair of samples. In none of the branching diagrams do the brown towhees from California and Arizona cluster together most closely.

To assess congruence between the taxonomic and genetic (Rogers) distance matrices, a Pearson product-moment correlation coefficient was computed. Its value, -0.43 ($df = 9$, $P > 0.05$), indicated no significant association between genic and morphometric patterns. However, the most genetically similar pair of samples was phenetically most distant, namely the samples of *P. fuscus* from California and Baja California.

DISCUSSION

GENETIC VARIATION

Levels of within-sample genetic variation at protein loci were consistent with those observed for other birds, although average heterozygosity,

0.028, was somewhat below the avian average (4–6%; Corbin 1983). Electrophoretic surveys of protein loci in birds have documented lower levels of genetic differentiation relative to those found in other vertebrates at comparable taxonomic ranks (Avise and Aquadro 1982). Genetic distances among most towhee taxa conform to this generalization. Typical interspecific congeneric distances (Nei 1978) for birds are 0.04 to 0.07 (Marten and Johnson 1986). However, the average distance from the congeneric outgroup (*P. chlorurus*) to the brown towhees is 0.21, three times that typically observed within genera. Davis (1951) suggested that the genus *Melozone* is actually closer to members of the *P. fuscus* complex than are other *Pipilo,* such as *chlorurus.* Although samples of *Melozone* were unavailable in this study, the large distance separating *P. chlorurus* from its congeners suggests that study of the monophyly of *Pipilo* (sensu AOU 1983) is warranted. Genetic distance values alone cannot be taken as proof of a nonmonophyletic situation; however, based on findings in other avian genera (Zink 1982), other noncongeneric taxa might be more closely related to the brown towhees than *P. chlorurus.*

The genetic distance between *P. aberti* and brown towhees, 0.094, is typical of well differentiated congeners. Most other distances are typical of interspecific comparisons; however, two of these taxa (brown towhees from Arizona and California) are currently considered conspecific by the AOU (1983). Also, two values are consistent with comparisons of avian conspecific populations, *P. albicollis* and *P. fuscus*-AZ (D = 0.002), forms ascribed species status by most if not all authors, and conspecific samples of *P. fuscus* from Baja California and California (D = 0.004).

Johnson and Zink (1983) and many other authors note that the magnitude of genetic distances among taxa is not an absolute measure of taxonomic rank—it must be used in conjunction with other information. There is some consistency between taxonomic rank and genetic distance, but the relationship is imprecise (Barrowclough 1983). For example, the low genetic distance between *P. albicollis* and *fuscus*-AZ is not by itself a strong argument for conspecificity; these forms seem specifically distinct based on morphological criteria (as do *fuscus* and *crissalis*).

GENETIC BIOGEOGRAPHY

It is possible to calibrate genetic distances and provide a temporal perspective on the phylogenetic framework. Considerable debate exists over the details of molecular clocks in general (e.g., Britten 1986, Vawter and Brown 1986) and in birds (e.g., Marten and Johnson 1986). Within the brown towhee complex, the Abert's Towhee originated approximately two million years before present (MYBP), the divergence of eastern (*fuscus*-AZ) and western *fuscus*-CA (*crissalis*) brown towhees about 1.5 MYBP, and the remaining taxa during the last one million years. These estimates of divergence dates, based on the calibration suggested by Marten and Johnson (1986), should be considered hypotheses for future testing.

These dates conflict with Davis' (1951) scenario in which Abert's Towhee arose one MYBP. If the phylogenetic sequence in Figure 2 is correct, Abert's Towhee evolved prior to the divergence of the other taxa. The Pleistocene separation of eastern and western components of the brown towhee is more recent than that suggested by Davis. Other avian taxa should be compared genetically between these arid regions to provide further perspective on the length of time taxa in them have been isolated. The genetic data also indicate a close relationship between brown towhees in Baja California and California, which suggests that they dispersed into Baja from the north subsequent to the joining of the Baja peninsula to the California mainland. Zink et al. (1987) suggest a similar explanation for the genetic similarity of samples of California Quail (*Callipepla californica*) from Baja California and California.

MORPHOMETRICS AND ITS COVARIATION WITH GENETIC PATTERNS

Many current workers challenge the concept that morphometric patterns reflect genealogical relationships of populations (Atchley 1983, James 1983, Zink 1986). Morphological variation might have a significant nongenetic (e.g., environmental) component or be influenced by natural selection, obscuring the history of evolutionary diversification. Because allozyme variants in birds are most likely selectively neutral (Barrowclough et al. 1985), they provide perhaps a better basis for the inference of phylogenetic relationships.

Few empirical studies of the covariation of genetic and morphometric patterns exist (Zink 1982, 1986; Barrowclough 1983; Capparella and Lanyon 1985). In this study, the insignificant correlation coefficient between genetic and morphological distances suggests that the morphometric patterns do not reflect phylogenetic patterns. However, the positioning of taxa in PC space (Fig. 3) does resemble the allozyme-based phylogeny, in that *fuscus*-AZ and *albicollis* are similar, *P. aberti* and *fuscus*-CA are distinct, but, unlike the allozyme results, *fuscus*-CA and *fuscus*-BA are distinct.

Irrespective of whether the morphometric patterns reflect phylogeny, they provide information about the evolution of towhees. The overlap of *species* taxa indicates that either speciation was not concomitant with movement of new species into a unique portion of "morphological space" or that if it was, species have secondarily converged. That is, morphometric analysis of skeletal characters does not recover species boundaries. In contrast to other analyses of avian skeletal data (Zink 1982, 1986; Baker 1985; Troy 1985), not all characters in the present analysis had high positive loadings on PC I (Table 1). Hence, it is unclear whether PC I is a "size" axis. Examination of character loadings suggests that evolution in size of postcranial characters accounts for the distribution of samples on PC I. On PC II, evolutionary change in skull shape is indicated. Thus, this analysis suggests that changes in both postcranial size and shape of the skull have been important in the evolution of brown towhees.

The two morphometric phenograms, albeit different, have elements in common, and support some previous taxonomic opinions. The phenogram based on correlations, presumably a measure of similarity in shape (but see Mosimann and James 1979, Bookstein et al. 1985) is strikingly similar to Davis' (1951) scenario of diversification of towhees. Davis suggested that *P. aberti* and *P. fuscus*-CA (=*crissalis*) were closely related, and that brown towhees from Baja California and Arizona were closely related; these patterns were observed in the shape phenogram (Fig. 4B) and the minimum-length tree (not shown) from the allozyme data. *Pipilo aberti* is genetically closer to samples of *crissalis* (0.084, 0.083; Nei's distance; Table 3) than to *fuscus* (0.097), and *fuscus*-AZ is closer to *fuscus*-BA (0.051) than to *fuscus*-CA (0.069). Davis believed that *P. albicollis* was derived from *P. fuscus*-AZ, a result consistent with the pattern of shapes and genetic distances. Thus, it seems evident that the traits and procedures used by Davis to judge systematic relationships closely conform to clustering taxa based on correlation coefficients. However, other nonconcordant patterns of skeletal shape and genetic variation suggest that the former may be a more reliable index to response to environmental features, much as implied by Davis (1951).

The phenogram based on taxonomic distance (Fig. 4A), presumably influenced by size, differs from the shape phenogram in the relative position of *P. fuscus*-CA. Although the cophenetic correlation coefficient, 0.873, is high, the information in the distance matrix is not necessarily portrayed faithfully (it would be if the correlation were 1.0). A minimum spanning tree (Sneath and Sokal 1973; Fig. 5), based also on the taxonomic distance measure (Sneath and Sokal 1973), reveals a different perspective on relationships. Here the relationship between *P. albicollis* and *P. fuscus*-AZ is closer than that implied by the phenogram, because *fuscus*-AZ is equidistant from *albicollis* and *fuscus*-BA. The distinctiveness of *P. fuscus*-CA from other *fuscus* is apparent, however. Thus, the pattern implied by the size phenogram (Fig. 4A) is of questionable significance; such phenograms are widely used, and should be interpreted with caution.

SPECIES LIMITS

Knowledge of the details of avian speciation has been obtained by comparing ecological, morphological, and behavioral traits of populations at different perceived levels of diversification. The remainder of this paragraph sets the general stage for considering the taxonomic status of brown towhee taxa. Comparison of conspecific populations usually reveals geographic variation in coloration and/or body proportions. Phenotypic and genotypic differences among populations are thought to be due usually to local adaptation, and particular differences may or may not be the "raw materials" from which new species-specific traits arise (Zink 1986). At the subspecies level, differences are often more marked, but not of species-level quality. Com-

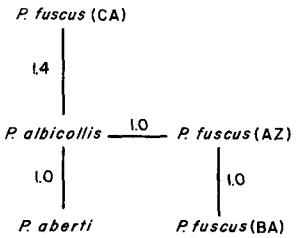

FIGURE 5. Minimum spanning tree based on taxonomic distance (shown along lines connecting samples).

parisons of sympatric, presumably closely related species are used to set the minimal limits for judging differences exhibited by newly-arisen but allopatric species. Speciation is usually considered to be a point in the divergence of conspecific groups of individuals at which they are reproductively isolated, an event acknowledged by most to be of fortuitous origin in allopatric units (Amadon 1950, Mayr and Short 1970). An analysis of geographic variation becomes a study of speciation when the investigator attempts to judge whether or not differences in traits of allopatric populations are equivalent to those observed between sympatric, noninterbreeding sister taxa (or at least congeners; see Banks 1964). Although phenotypic and genotypic divergence are correlated with reproductive isolation, the relationship is imprecise (Zink and Remsen 1986). Sometimes, comparisons of phenotypic variation among allopatric populations, judged in relationship to putative effects on reproductive isolation, will yield evolutionarily misleading taxonomic groupings. Either separate species will be grouped as one, or nonmonophyletic groupings will result (McKitrick and Zink 1988).

Reasoning involved in ascribing conspecific status to the *crissalis* and *fuscus* groups constitutes an exemplary application of the multidimensional Biological Species Concept (Mayr 1963, 1982). Differences in plumage and voice among these allopatric units were assumed by Davis (1951) and Marshall (1960) insufficient to serve as reproductive isolating mechanisms. Thus, evidence for the taxonomic distinctiveness of *crissalis* and *fuscus* was judged, inappropriately I maintain, of subspecies level. The logic used by Davis and Marshall, and followed by the AOU (1983), was internally consistent. However, the two towhee subspecies groups are genetically differentiated, as distinct as are most congeneric avian species pairs. The presence of a black spot on the chest of *fuscus* could serve as a species-specific, diagnostic trait (irrespective of one's definition of species). Therefore, I advocate species status for *crissalis* (California Towhee) and *fuscus* (Brown Towhee). The specific distinctiveness of *albicollis* rests in its plumage (Davis 1951).

Whether or not members of each group could interbreed is, in my opinion, an important issue that is nonetheless distinct from the delineation of species limits (Cracraft 1983, Zink and Remsen 1986, McKitrick and Zink 1988). Description of species limits should be based on the phenotypic and genotypic results of evolution (Cracraft 1983), and limits should be independent of the actual or presumed ability to interbreed. Reproductive compatibility (or its presumed existence) is equivalent to the retention of a primitive characteristic, which should not be used to unite groups as conspecific (Cracraft 1983). (Reproductive isolation affects the future fate of differences.) It seems logical that species, and not subspecies, limits should reflect phylogenetic patterns, and in the Brown Towhee (sensu AOU Checklist, 1983) they do not. The failure to appreciate (and to recognize) the actual distinctness and affinities of the towhees, based on subjective evaluation of similarities and differences, is potentially widespread in other species. The traits of *fuscus* and *crissalis* bespeak a period of evolutionary independence, deserving of recognition as phylogenetic species (Cracraft 1983). Furthermore, in the towhees, grouping allopatric units into biological species based on the presumed ability to interbreed has misrepresented evolutionary history, in that *crissalis* and *fuscus* are distinct species, and are almost certainly not each others nearest relative.

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