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PATTERNS AND EVOLUTIONARY SIGNIFICANCE OF GEOGRAPHIC VARIATION IN THE SCHISTACEA GROUP OF THE FOX SPARROW (*PASSERELLA ILIACA*)

BY

ROBERT M. ZINK
Museum of Vertebrate Zoology and
Department of Zoology
University of California
Berkeley, California 94720

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Author, Robert M. Zink, Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720. *Present address:* Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803

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". . . one of the basic problems in evolutionary biology is to explain the nature and origin of the differences between different populations of the same species."
(Merrell 1981)

INTRODUCTION

Geographic Variation: Significance of Patterns, Evolutionary Inferences, and Goals of Analysis

Merrell's remark nicely illustrates that the study of intraspecific, or geographic, variation can contribute to the understanding of evolutionary processes (Mayr 1980). In fact, Gould and Johnston (1972: 457) stated that "the foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the verification of predictions made about it." The evolutionary significance of geographic variation traditionally rests upon two assumptions. First, natural selection is thought to increase the degree to which populations are adapted to locally differing environments. Hence, a pattern of geographic variation can indicate a series of adaptive responses to geographically varying selection regimes. Secondly, many biologists believe that the processs of geographic differentiation is also a model of the origin of species. That is, speciation is usually envisioned to consist of the conversion of genetic variation from within to among populations coupled with the origin of reproductive isolation (Mayr 1942, 1963, 1970). At the least, analysis of geographic variation might clarify the nature of phenotypic and genotypic change, and possibly the evolution of reproductive isolation (Zink and Remsen, in press). These basic assumptions about the evolutionary significance of geographic variation are not without challenge. Differential patterns of gene flow, constrictions in effective population size, and random genetic drift can generate geographic patterns of variation in the absence of natural selection (Rohlf and Schnell 1971; Lande 1985). There is also some opposition to the classical notion that speciation is merely an extension of the process of infraspecific differentiation (Goldschmidt 1940; Eldredge and Cracraft 1980; Cracraft 1983). Nonetheless, whether or not one accepts either assumption or both of them, study of geographic variation is of value because it might expose aspects of the processes of adaptation and speciation.

A primary objective in the analysis of geographic variation is to identify patterns of variation and explain their evolution. In recent years both the methods and geographic scale of analysis have changed. New methods involve types of data gathered and techniques and theories of data analysis. Biochemical tools are being used with increasing frequency to study the genetics of the microevolutionary process (Barrowclough 1983). Quantitative, computer-assisted analyses have greatly improved the description of patterns of geographic variation. In particular multivariate statistical methods have been widely employed because, as eloquently stated by Sokal and Rinkel (1963), "Geographic variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is doubtless a multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and ranges probably overlap in a rather complex fashion." Implicit in the characterization of geographic variation by Sokal and Rinkel is a message that the types of traits often surveyed for geographic variation might have complex genetic bases, re-

quiring quantitative genetic analyses to distinguish genetic vs environmental contributions to phenotypic variation as well as the genetic responses to potentially antagonistic forces of natural selection. Although description and analysis of variation in traits traditionally considered will continue to be of value, quantitative genetic studies (Price et al. 1984b) of polygenic traits, comparison of geographic differences in ontogenetic "trajectories" (Alberch et al. 1979), and analysis of biochemical characters for which the genetic basis of variation is known (e.g., Barrowclough 1983), will be necessary directions for future studies of geographic variation. In addition, even time-honored definitions of species and speciation should be evaluated (Cracraft 1983).

An important objective of studies of geographic variation is to determine the extent of population subdivision or differentiation. In other words, on a continuum from panmixia to complete subdivision and cessation of gene flow, what is the genetical population structure of a particular species (no matter how species are defined)? The nature of population structure influences the processes of adaptation (Wright 1978) and speciation (Templeton 1980b; Slatkin 1985b). Hence, empirical estimates of population structure are of interest. Traditionally the extent of genetic differences among populations was inferred from the extent of differentiation in external morphology. Electrophoretic analysis of enzyme loci has provided a tool for documenting genetic variation in natural populations (Lewontin 1974; Ayala 1976, 1982; Smith et al. 1982), although relatively few surveys of avian species exist (Barrowclough 1983; Barrowclough et al. 1985). In contrast to traditional types of characters analyzed in studies of geographic variation, one can determine an individual's genotype at each of up to 100+ loci (the limits on the number of loci are as much financial and logistical as they are technical). These genetic data, analyzed in light of quantitative predictions of population genetic models, can elucidate the genetic structure of populations, levels and patterns of gene flow, effective population sizes, strength and nature of natural selection, and the pattern of evolutionary divergence of populations and species. A further advantage of molecular characters is the approximately uniform, time-dependent rate of evolution, a "molecular clock," which allows a temporal perspective on the divergence of groups of individuals. Thus, because evolution ultimately consists of genetic change, biochemical methods that expose the geography of genetic variation are of considerable interest if the goal is to estimate the pattern and timing of the fragmentation of populations and patterns and mechanisms of speciation.

Analyses of covariation of morphology and proteins indicate whether they evolve in concert or are "decoupled" (Schnell et al. 1978; Patton et al. 1979; Smith 1981; Yoshiyama and Sassaman 1983), although Lewontin (1984, 1986) suggests some cautions to be used in interpreting patterns of covariation. Significant genetic divergence has been found where an absence of morphological differentiation would have been interpreted previously as evidence of a lack of population structure. Conversely, morphological patterns of variation might not reflect the historical genealogy of populations because of nongenetic environmental influences (Chernoff 1982). In birds, morphological differences among populations are often accompanied by no or few detectable differences at enzyme loci, unlike some other vertebrates (Barrowclough 1983). Nevertheless, the goal is to explain how and why populations have their particular sets of phenotypic and genotypic attributes. Hence, all data sets have relevance, especially when the

strengths and weaknesses of each are recognized. Biochemical and morphological data sets should be viewed as complementary.

Some recent studies of geographic variation have included assessment of "microgeographic" patterns of variation (Patton and Feder 1978, 1981; Chesser 1983). This trend toward documentation of microgeographic patterns stems from a desire to discover the smallest aggregation of individuals in nature that might function as an evolutionary unit (Ehrlich and Raven 1969; Jackson and Pounds 1979; Cracraft 1983). For example, if all individuals from a species were studied, one could pool individuals, beginning with a randomly drawn one, until either genetic and/or morphological gaps were encountered or all specimens were in one group (a taxon without infraspecific variation). A gap could be quantitative, such as nonoverlapping ranges in some trait, or a meristic, discrete phenotypic state. If consistent groupings of individuals obtain, whatever their taxonomic designation, it is then necessary to discover their evolutionary relationships and how and why their pattern of relationships arose.

An extensive ornithological literature exists on patterns of geographic variation in a variety of traits (Zink and Remsen, in press). An examination of this literature has allowed evaluation of some important topics in evolutionary biology, such as local adaptation, hybridization, sexual dimorphism, ecological isolation, Pleistocene speciation, and others (Johnson 1980). Study of patterns of geographic variation in birds contributed to the development of the theory of allopatric speciation (e.g., Huxley 1942; Mayr 1942; Streseman 1975). However, recent treatises (Endler 1977; White 1978; Bush 1982) on speciation were constructed largely without input from modern analyses of avian geographic variation. Ornithologists will continue to contribute to these research areas, especially when newer methods of data gathering and analysis discussed above are used to complement traditional types of studies.

Objectives of the Present Study

The goal of this study is to determine what evolutionary forces influence the historical origin and current maintenance of geographic variation in the Fox Sparrow (Fig. 1). The analysis was restricted to some members of the Schistacea group (Fig. 2) because they provide an opportunity to study and compare levels and patterns of population structure from morphological and genetical perspectives. In fact, Kenneth Parkes stated (in Arbib 1981) that "It is quite apparent that *Passerella iliaca* must have the most extreme variations in bill size and shape of any emberizine, certainly in North America and probably in the world." This study was not intended as a taxonomic revision, although it produced results with taxonomic implications. Individuals were collected from isolated breeding populations and more-or-less continuously distributed habitat, different breeding habitats, and from regions in which individuals possess different morphological characteristics (Fig. 3). The sampling protocol was designed to allow study of geographical and ecological correlates of variation, such as isolation and habitat, respectively.

Because variation is the raw material in the evolutionary process, considerable attention has been focused on documenting variation in natural populations. I use quantitative analyses of genetic and morphological variation to describe variation within and among populations. Covariation of morphological and environ-

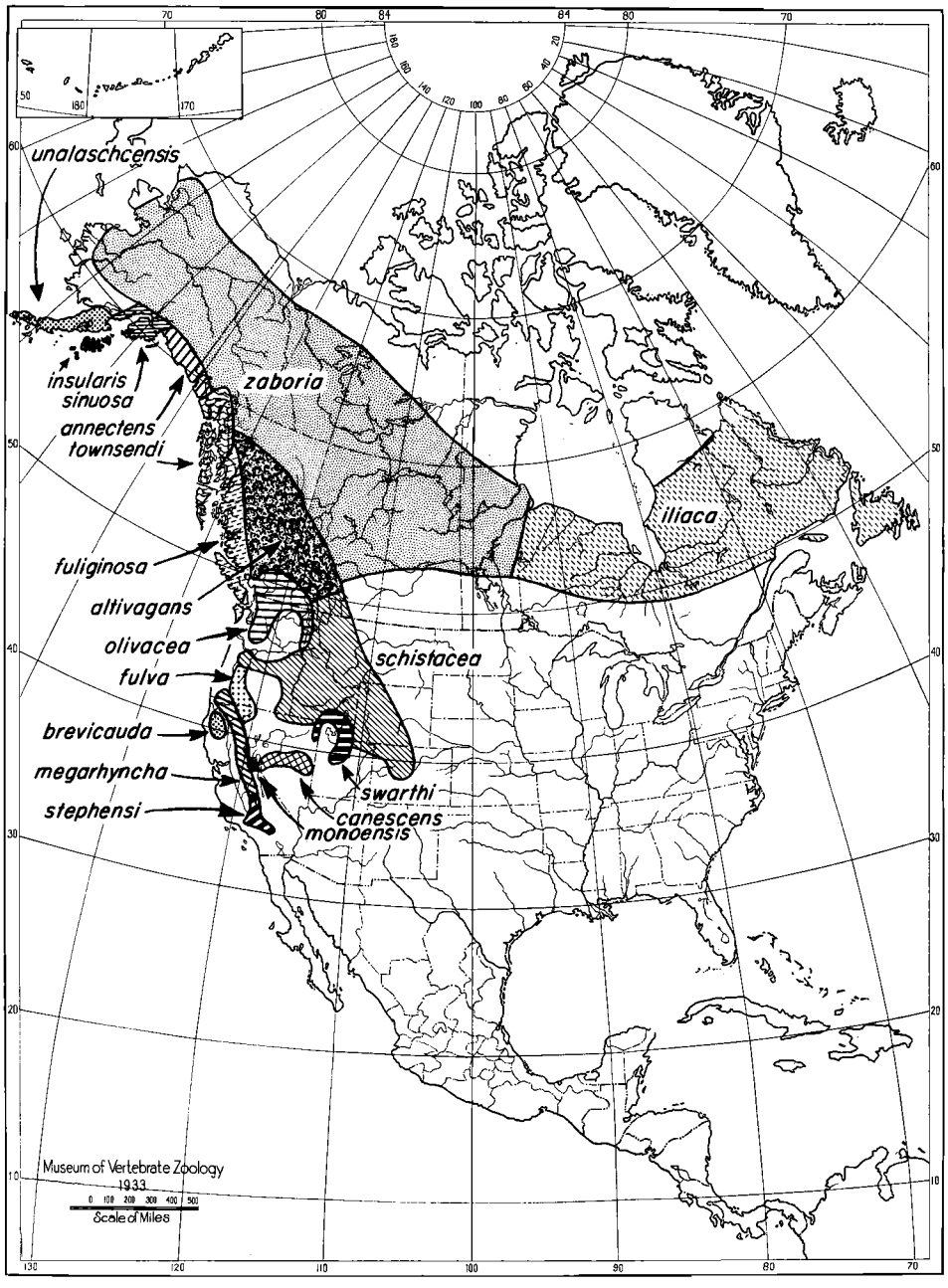

FIGURE 1. Breeding ranges of the 18 subspecies of the Fox Sparrow in North America. Subspecific taxonomy follows the A. O.U. Check-list (1957); see also Miller (1956). The ranges are generalized, because breeding Fox Sparrows are not continuously distributed over the range of each subspecies. Three subspecies groups are recognized (Swarth 1920): Iliaca (*iliaca, altivagans, zaboria*), Unalaschcensis (*unalaschcensis, insularis, sinuosa, annectens, townsendi, fuliginosa*), and Schistacea (*schistacea, megarhyncha, stephensi, brevicauda, fulva, canescens, olivacea, swarthi, monoensis*). Winter range is the southern United States, extreme northern Mexico, and coastal regions of the western United States.

mental features is used to assess the geography of adaptation. For example, is phenotypic variation consistent with expectations of ecogeographic rules? Do characters covary in similar ways, and do the sexes show similar patterns of variation? Assessment of variation at 38 enzyme loci allows a genetic perspective on morphological traits, as well as contributing information on genetical population structure and gene flow. How is genetic variation apportioned in indiviudals and populations and among populations? Are isolated populations relatively less variable or genetically differentiated? What is the nature of gene flow? Can a historical pattern of fragmentation, or evolutionary history, of populations be discerned? If geographic variants are a stage in the speciation process (Simpson 1953; Rensch 1959; Gould and Johnston 1972; Bock 1979; Charlesworth et al. 1982), then the origin of interspecific differences might be deduced from studies of populations of Fox Sparrows differentiated to various degrees (Vuilleumier 1980). Thus, I compared variation among local populations, subspecies, and recently evolved species (Zink 1982) to elucidate potential morphological and genetic correlates of the speciation process. Thus, in these ways I address the evolutionary significance of geographic variation in the Fox Sparrow.

Previous Studies of Geographic Variation in Fox Sparrows

The Fox Sparrow was the subject of two intensive, broad-scale surveys of geographic variation (Swarth 1920; Linsdale 1928). Swarth (1920) studied characteristics of external morphology such as wing and tail lengths, bill size, and coloration to clarify subspecies limits. Swarth recognized three distinct subspecies groups: Iliaca, Unalaschcensis, and Schistacea (see legend to Fig. 1). The Iliaca group, represented by three subspecies, ranges in summer throughout northern North America, exclusive of the northwest coast. Birds are typically reddish with relatively short tails and streaked backs. The Unalaschcensis group is distributed along the northwest coast, and birds are typically dark brown in coloration, with relatively short tails and medium-sized bills, the latter character showing a north to south clinal increase in size; seven subspecies are recognized. A notable feature of this group is the leap-frog pattern of migration wherein subspecies with the darkest coloration winter in humid conditions, south of the winter range of the subspecies breeding to the south of them. The darker subspecies breed in relatively more arid conditions, where one might expect a lighter coloration. Thus, coloration seems influenced by conditions of the winter and not the breeding environment. The third subspecies group, Schistacea, breeds in the mountains of the western United States, and contains eight subspecies. Members of the Schistacea group have gray backs with reddish wings and tails, a relatively long tail, and marked variation in bill size over short geographic distances.

Swarth concluded that the Iliaca and Unalaschcensis groups were most similar (closely related?), and he developed a historical scenario to explain overall patterns both in the species and within each of the three groups.

Linsdale (1928) determined that patterns of geographic variation in 16 skeletal characters paralleled those obtained by Swarth. Linsdale was one of the first to document concordance between character sets, now termed a test of the "nonspecificity hypothesis" (Sneath and Sokal 1973).

Thus, it has been appreciated for over 50 years that extensive geographic vari-

ation exists in Fox Sparrows, both in coloration and in skin and skeletal features. In fact, the number of subspecies, 18, ranks third in North America, behind the Song Sparrow (*Melospiza melodia*) and Horned Lark (*Eremophila alpestris*) (A.O.U. 1957). Because of the marked morphological differentiation among subspecies, and the monographs by Swarth and Linsdale, it was decided to undertake a quantitative description of genetic variation that could be used to contrast with morphological patterns of variation, the latter of which was also assessed using modern analytical techniques.

STUDY SITES, SAMPLING DESIGN AND TECHNIQUES, AND BRIEF SUMMARY OF NATURAL HISTORY

The precise localities of the 31 sample sites are given in the Appendix and depicted more generally in Figure 2 and Table 1. Site codes, elevation, habitat type, an estimate of population density, sample sizes, and subspecific designation for the population at each site are also given in Table 1. The general breeding ranges of the subspecies are shown in Figure 3; scale drawings of heads of male Fox Sparrows depict geographic variation in bill size and shape.

Swarth (1920) and Linsdale (1928) described the natural history of Fox Sparrows, and I found their accounts to be highly accurate. Martin (1979) discusses geographic variation in song. Aspects of the breeding distribution and ecology of Fox Sparrows are summarized in Table 2. Fox Sparrows breed in two distinct habitats in the region I surveyed. In the Great Basin, Fox Sparrows breed in riparian thickets consisting of alder (*Alnus* sp.), water birch (*Betula occidentalis*), willows (*Salix* spp.), *Ribes,* and other species. These habitats are generally linearly distributed along stream courses, becoming somewhat more expansive at canyon heads. Densities of Fox Sparrows in riparian situations are generally lower than in chaparral (discussed beyond). Breeding sites in the Great Basin occur from about 1,980 m to 3,050 m. Riparian habitats are often disjunct, being separated by large expanses of uninhabitable (to breeding Fox Sparrows) sagebrush desert, an environment typical of much of the Great Basin. Because many of these water courses are fed by springs, I assume that this habitat is available annually to breeding Fox Sparrows, without periods of local habitat extinction.

West of the Great Basin in the Sierra Nevada, Cascades, North Coast Ranges, and Transverse Range (Fig. 3), Fox Sparrows breed in a *very* different environment, namely, montane chaparral (see Ornduff 1974). These brush fields, occurring from 1,220 m to 3,000 m, include a variety of plant species, most commonly *Arctostaphylos patula, Ceanothus* spp., and *Castanopsis sempervirens.* However, in the Greenhorn Mountains, south of the main Sierra Nevada, Fox Sparrows are found in elderberry (*Sambucus* sp.) thickets.

Montane chaparral occurs both on soils and slopes too steep or poor in nutrients for timber and as the natural successional vegetation on lands deforested by fires or logging (Beaver 1976). As a result, montane brush fields vary in age, size, and vegetation structure. As a post-fire successional stage, montane chaparral reaches a density sufficient to support Fox Sparrows within approximately 10 years (Bock and Lynch 1970). For example, at the Cherry Lake (CHER) site, the forest burned in 1966 and by 1978 the brush was sufficient to support a low density of Fox Sparrows, which doubtless immigrated from nearby breeding sites. Fox Sparrow densities change as the brush field matures and apparently peak at approximately

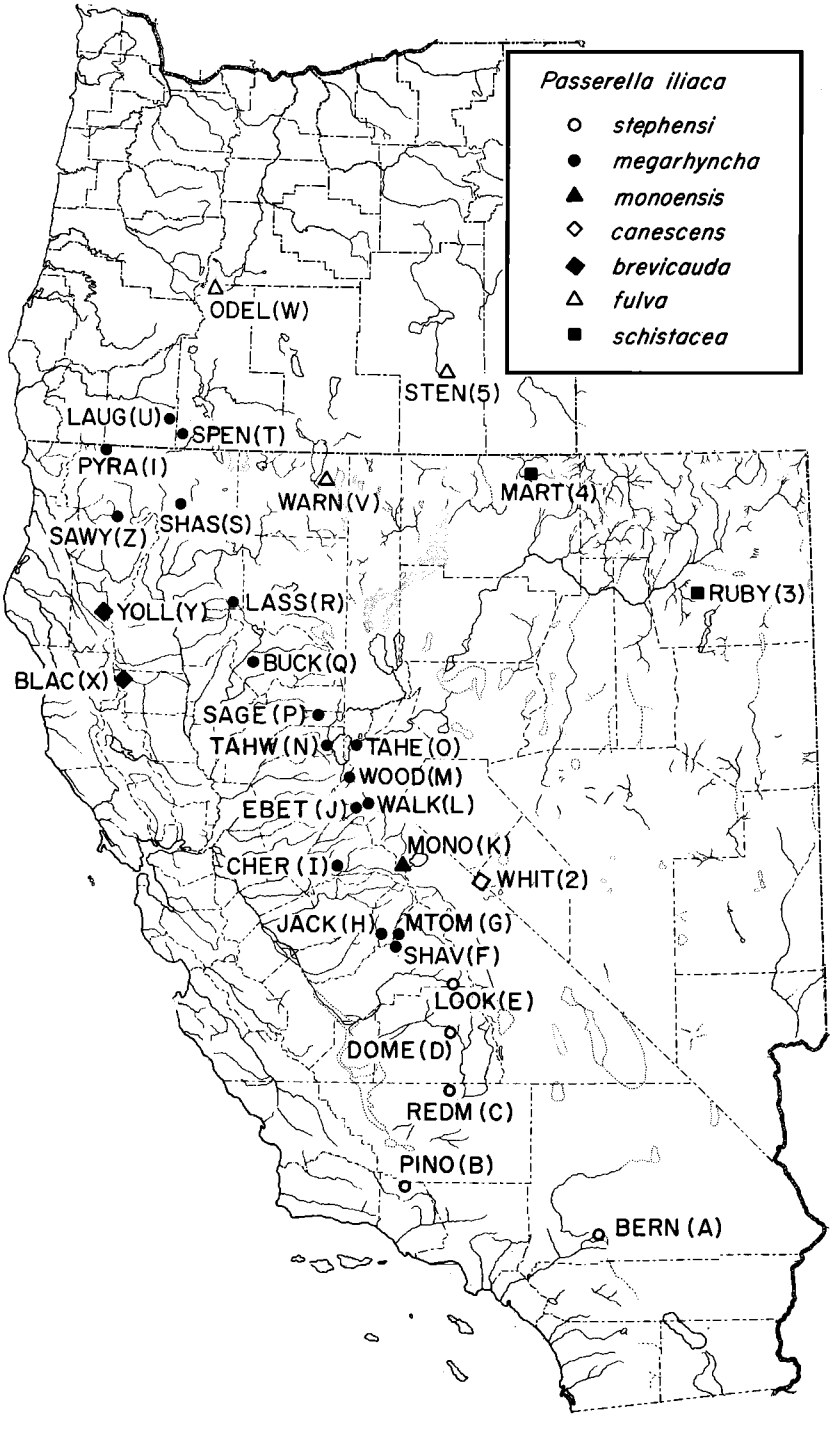

FIGURE 2. Location of the 31 collecting sites; for precise locations see Appendix I. The subspecific designation of each sample is indicated by symbols.

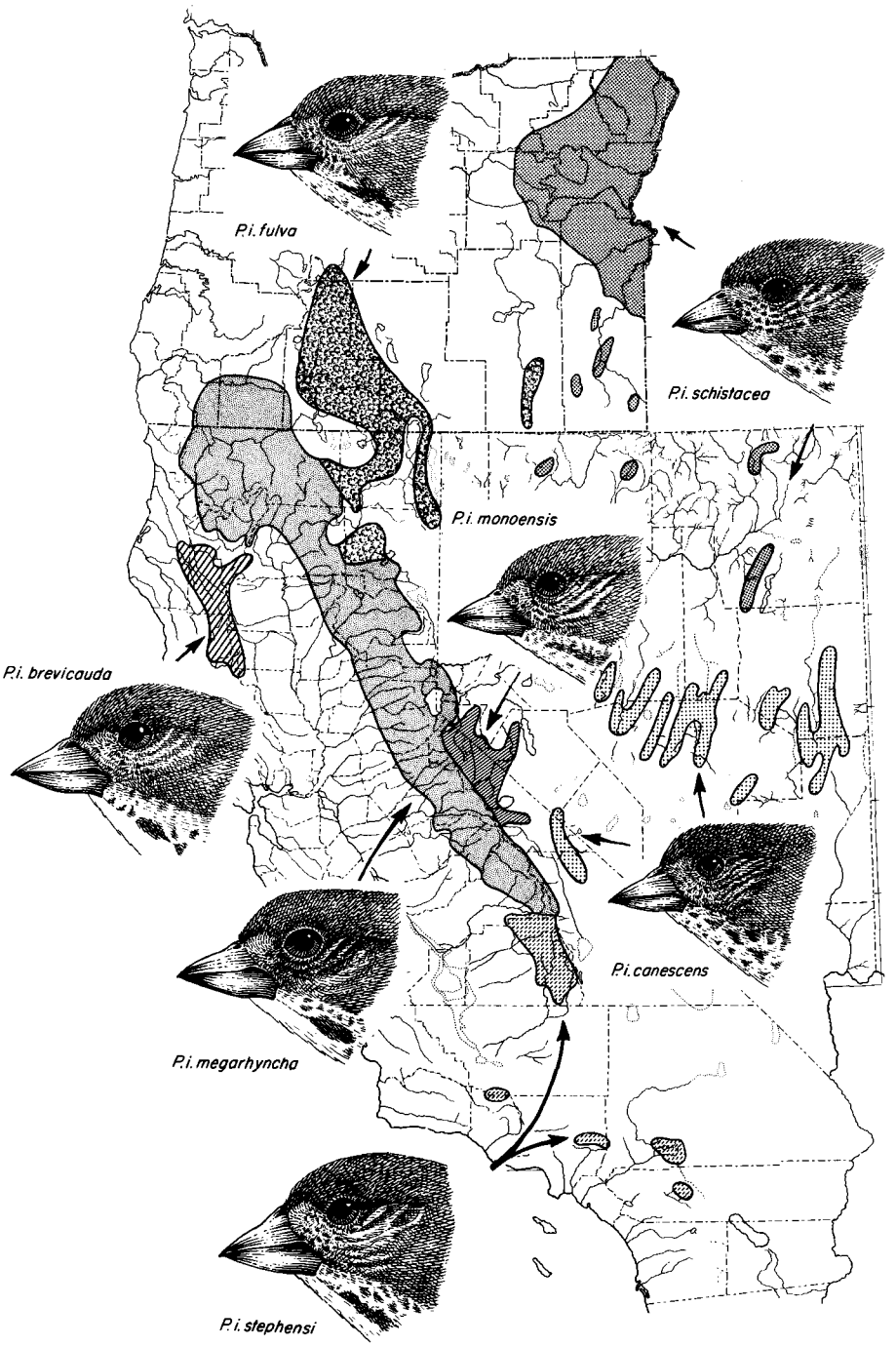

FIGURE 3. Breeding distribution of seven subspecies of the Fox Sparrow in Oregon, Nevada, and California. Ranges are generalized because breeding Fox Sparrows are not continuously distributed within the boundaries of each subspecies. Scale drawings of heads of males illustrate geographic variation in bill size and approximate shape only. Subtle plumage differences shown here are typical of individual variation in all populations and are not meant to indicate diagnostic geographic differences.

TABLE 1

DESCRIPTION OF STUDY SITES (FIG. 2) FOR SAMPLES OF FOX SPARROWS. PRECISE LOCALITY DESCRIPTIONS ARE GIVEN IN APPENDIX I. SAMPLE SIZES INCLUDE ALL INDIVIDUALS COLLECTED AT EACH SITE. IN SOME ANALYSES, NOT ALL SPECIMENS WERE USED BECAUSE OF DAMAGED CHARACTERS. SUBSPECIFIC TAXONOMY FOLLOWS GRINNELL AND MILLER (1944)

Site	Code	Elevation (m)	Number of			Habitat[1]	Density[2]	Subspecies
			Males	Females	Immatures			
A.	BERN	2,210	22	5	1	C	4	*stephensi*
B.	PINO	2,530	18	8	0	C	4	*stephensi*
C.	REDM	1,920	16	3	0	C	3	*stephensi*
D.	DOME	2,410	19	6	0	C	4	*stephensi*
E.	LOOK	2,350	17	8	1	C	4	*stephensi*
F.	SHAV	1,650	29	6	3	C	4	*megarhyncha*
G.	MTOM	2,230	11	6	0	C	3	*megarhyncha*
H.	JACK	2,010	17	6	3	C	4	*megarhyncha*
I.	CHER	1,550	4	5	3	C	1	*megarhyncha*
J.	EBET	1,890	13	4	1	C	3	*megarhyncha*
K.	MONO	2,290	6	3	4	C	2	*monoensis*
L.	WALK	2,410	8	8	1	C	2	*megarhyncha*[3]
M.	WOOD	1,950	15	4	5	C	3	*megarhyncha*[3]
N.	TAHW	2,010	17	5	0	C	4	*megarhyncha*
O.	TAHE	2,130	9	1	1	C	2	*megarhyncha*
P.	SAGE	1,920	14	4	3	C	5	*megarhyncha*
Q.	BUCK	1,650	11	2	2	C	2	*megarhyncha*
R.	LASS	1,830	34	18	13	C	5	*megarhyncha*
S.	SHAS	1,800	17	11	2	C	4	*megarhyncha*
T.	SPEN	1,220	10	3	2	R	2	*megarhyncha*[4]
U.	LAUG	1,430	11	5	1	C	3	*megarhyncha*[4]
V.	WARN	1,860	18	11	3	C	3	*fulva*
W.	ODEL	1,580	12	4	0	C	3	*fulva*
X.	BLAC	2,070	15	4	0	C	3	*brevicauda*
Y.	YOLL	1,370	22	8	8	C	4	*brevicauda*
Z.	SAWY	1,650	9	8	0	C	2	*megarhyncha*
1	PYRA	1,580	12	4	0	C	2	*megarhyncha*
2.	WHIT	2,680	22	8	3	R	3	*canescens*
3.	RUBY	2,680	10	3	0	R	2	*schistacea*
4.	MART	2,070	3	2	1	R	1	*schistacea*
5.	STEN	2,230	8	3	1	R	2	*fulva*
			449	176	62			

[1] C = montane chaparral; R = riparian.
[2] Density estimates are subjective estimates of the density of breeding Fox Sparrows and the extent of suitable habitat at each site. A 1 indicates the lowest density and a 5 represents a dense, extensively distributed, local breeding colony.
[3] Samples treated as intergrades between *monoensis* and *megarhyncha* by Grinnell and Miller (1944).
[4] Essentially on the border of *megarhyncha* and *fulva*.

one pair per hectare (Bock and Lynch 1970; Bock et al. 1978; Savage 1978). Although the populations in the Transverse Range (PINO, BERN) are isolated (Fig. 3), in general the distance between suitable chaparral habitats is less than that between riparian thickets in the Great Basin. Patches of montane chaparral are sufficiently dense and widespread to effect a quasi-continuous distribution in the Sierra Nevada and Cascades.

Specimens were obtained from isolated sites, areas of continuous distribution, sites of different elevation, riparian thickets (Great Basin), and chaparral of various ages (western mountains). General collecting areas were determined from range maps in Grinnell and Miller (1944) and Miller (1956), and precise collecting sites

TABLE 2

ASPECTS OF THE BREEDING DISTRIBUTION AND ECOLOGY OF FOX SPARROWS OF THE SCHISTACEA SUBSPECIES GROUP

Aspects of:	Sierra Nevada, Cascades, Coast and Transverse ranges	Great Basin
Distribution	Continuous to disjunct	Disjunct
Elevation	1,200 to 3,000 m	2,300 to 3,000 m
Habitat type	Montane chaparral	Riparian (e.g., willows)
Habitat stability	Seral states (ephemeral)	Relatively stable
Breeding density	Low to high	Usually low
Breeding site	2-dimensional	Linear
Bill size	Medium to Large	Small

were chosen while in the field; collecting localities were spaced at about 40 km intervals, except for a few instances when the samples were more closely spaced for analysis of microgeographic variation. Some sites were chosen to duplicate samples taken in the 1920s by Lindsdale (1920); the recent samples were analyzed for temporal variation (Zink 1983). Birds were collected in June, July, and August of 1978–1980, using a shotgun or mist-nets. The timing of the collecting effort insured that individuals collected would represent the local breeding community. Precise dates, itineraries, and site descriptions are on file at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, California.

Specimens were prepared as either study skins plus partial skeletons or as complete skeletons. Below, "skin" refers to a standard study skin preparation. For both types of skeleton preparations, specimens were dried (out of sunlight), and then cleaned by a dermestid beetle colony. On complete skeleton preparations, standard skin measurements (described below) were taken on completely dried "roughed-out" specimens prior to use of beetles. These "skin" measurements are comparable to those taken on prepared (and dried) study skins (see Johnson et al. 1984 for further comments on methods).

MATERIALS AND METHODS

ELECTROPHORESIS

Within three hours of collection of each specimen, samples of liver, heart, kidney, and pectoral muscle were frozen in liquid nitrogen. Samples were subsequently stored at −76°C until used for electrophoresis. Tissue extracts were prepared by mincing approximately 0.5 cm^3 of tissue (liver and muscle combined; heart and kidney not used) and combining it with an equal volume of de-ionized water, and then centrifuging this mixture at 16,000 rpm for 40 min at 4°C. The supernatant (aqueous tissue extract) was frozen at −76°C and the tissue pellet discarded.

Gels for horizontal electrophoresis were made of 12% starch and the appropriate buffer solution. Electrophoretic conditions for the 38 presumptive genetic loci examined are given in Table 3. After electrophoresis, the gel was sliced horizontally and each slice stained differentially using protein assays described by Selander et al. (1971) and Harris and Hopkinson (1976). Interpretation of bands on gels

TABLE 3

ELECTROPHORETIC CONDITIONS USED FOR STUDY OF FOX SPARROWS

Gel type[1]	Volts–hours		Loci[2,3]
LiOH (2)	300	3	liver: LGG; LA-1,2; NP; GDA; LAP; EST-1,4; AB1,2
TC 8 (5)	130	4	liver: ICD-1,2; MDH-1,2; Acp (=EAP); PGM-2; LDH-1,2; GPT muscle: ADA; MPI; GOT-1,2; GPD-1,2; AK
TM (9)	100	4	liver: 6-PGD; G-6-PDH; ADH; GDH; SOD-1,2
Poulik (3)	250	3	muscle: GPI; AB-3,4; ACON; CK-1,2
Phos-Cit[4]	200	3	muscle: GaPDH

[1] Numbers refer to buffer types in Selander et al. (1971).
[2] Abbreviations for loci follow Harris and Hopkinson (1976).
[3] Many loci are scorable on several gel types and with several tissues.
[4] Conditions available from author.

followed Harris and Hopkinson (1976), Barrowclough and Corbin (1978), and Avise et al. (1980a). Unless variation was unambiguous, a locus was not scored. Stained gels were photographed and saved.

For each population I constructed a table of allelic frequencies for each locus. Measures of within-population genetic variability were: (1) percentage of loci polymorphic, calculated as the number of loci with two or more alleles divided by 38 (POLY99 and POLY95, depending on whether the frequency of the most common allele was <99% or 95%, respectively), (2) average number of alleles per polymorphic locus (NALL), and (3) average individual heterozygosity (H). H was calculated by averaging individual heterozygosities in each population. That is, if an individual was heterozygous at three loci, its H estimate is $\frac{3}{38}$ or 0.079. Values for each individual in a population sample were then averaged (±s.e.). Also, the expected H, H_{exp}, assuming Hardy-Weinberg equilibrium, was calculated as

$$H = \frac{1}{N}\sum_{i=1}^{N}\left[1 - \sum_{j=1}^{k_i} x_{ij}^2\right]$$

where x_i is the frequency of the jth allele at the ith locus, k_i is the number of alleles at the ith locus, and N is the total number of loci examined (38). The variance of H_{exp} has a theoretical expectation which may differ from the empirical s.e. described above (Nei 1978; Corbin 1981).

To test the observed frequency of genotypes for departures from Hardy-Weinberg expectations, I followed Barrowclough (1980a) by comparing with a chi-square test the observed and expected numbers of heterozygotes summed over all variable loci in a population. The degrees of freedom (d.f.) for this test are the number of alleles minus one at each locus summed over all loci. Loci at which only one heterozygote was expected were combined (Lewontin and Felsenstein 1965).

To detect patterns in measures of within-population genetic variation, partial correlation and multiple regression analyses were used. The sample size, latitude, longitude, and elevation at each site were coded as independent variables, and the following characteristics served as dependent variables: H, POLY99, POLY95, NALL, and the frequency of the most common allele at the most polymorphic

loci (LGG, LA-2, EST-D, EAP, ADA, GPI, and NP). The analysis (BMDP6R; Dixon 1979) controls for correlations among the independent variables, gives partial correlation coefficients among the dependent variables, and assesses whether or not the independent variables can statistically predict values of the dependent variables when used in a multiple regression analysis.

Population structure was examined with *F*-statistics, following the methods of Wright (1978). Three different methods of computing F_{ST} were used: "Wright's," uncorrected, and corrected, the latter of which involves subtraction of an error term because of finite sampling of genes per population. The F_{ST} value calculated over all variable loci was divided with its empirical s.e. and probably can be treated as a *t* statistic, with the d.f. equal to the number of loci minus one (see Barrowclough 1980a for a brief description of the terminology).

The genetic distance measures of Nei (1978) and Rogers (1972) were computed to measure the degree of differentiation between populations. These measures, used extensively for other organisms, permit comparisons across taxa (see Avise and Aquadro 1982). A phenogram, portraying the geographic pattern of genetic distances, was constructed from the matrix of Rogers' *D*-values; the unweighted pair-group method using arithmetic averages was used (UPGMA; see Sneath and Sokal 1973). Phenograms group samples as a function of levels of similarity (i.e., low distances are similar). Theoretically, when using genetic distances, samples with a common evolutionary history, or those connected by gene flow, should cluster together if rates of character state change are uniform (Felsenstein 1982). Other methods exist for constructing branching diagrams from distance matrices (e.g., Farris 1981; Swofford 1981; see Felsenstein 1982 for a review). However, the genetic distances in this study are so low that confidence in any branching structure is tenuous.

Slatkin (1981) proposed a method to estimate levels of gene flow in natural populations using allelic frequency data. The simulations of Slatkin showed that the conditional average frequency of an allele [$p(i)$] is basically independent of the assumed selection intensity and mutation rate but depends heavily on the overall level of gene flow. The data required are the average frequency of an allele conditioned on the number of populations in which it occurs, $p(i)$, and the occupancy number, *i*, the number of samples in which the allele was detected. Slatkin then showed that by plotting $p(i)$ versus i/d (d = total number of localities or samples), levels of gene flow can be assessed as high, low, or medium. Use of a recent refinement (Slatkin 1985a) of the 1981 method did not alter conclusions about gene flow in the Fox Sparrow (Zink, unpubl. data).

Morphology

Study Skin Measurements

Nine characters were measured with dial calipers (recorded to nearest 0.05 mm) on study skins, or dried specimens prior to preparation as skeletons: (1) ORETL—length of the outer rectrix, measured from point of insertion of the central rectrices to tip of the outer rectrix. (2) WINGL—length of the outer primary, measured as the chord of the unflattened wing from the bend of the wing to the tip of the outermost primary. Excessive wear of the longest primary prevented use of this

character. (3) HINTL—length of hind toe plus claw, measured from the ventral base of the hind toe to the tip of the hind claw. Variance due to curvature of the toe and claw on dried specimens was not sufficient to necessitate deletion of the character. (4) TARSL—length of tarsus, measured from the mid-point of the posterior surface juncture of the tibiotarsus and the tarsometatarsus to the anterior lower edge of the last large scute on the tibiotarsus, a point consistently apparent on each specimen. (5) BILL-1—length of bill from anterior rim of nares to the tip of the upper mandible. (6) BILL-2—length of lower mandible, from the anterior-most inner edge of ramus to the tip of the lower mandible. (7) BILLW—width of lower mandible measured at its base (widest point). (8) BILLD-1—depth of bill measured through a plane passing perpendicular through the anterior-most tip of the nostril. (9) BILLD-2—depth of bill measured from the base of the lower mandible (the widest point, on lateral aspect) to a point on the culmen directly above the anterior edge of the nostril.

Skeletal measurements

Measurements of 15 skeletal characters judged relatively accurate (Zink 1983) were taken on each specimen: (1) SKULW—maximum width of skull across the bullae, (2) SKULL—partial length of skull measured from suture at posterior end of bulla to a notch on the anterior face of the post-orbital process, (3) CORAL—length of coracoid, (4) SCPEW—width of the proximal end of the scapula, (5) STERL—length of the sternum, (6) PSYNL—posterior synsacrum length, (7) SYNMW—maximum width of the synsacrum, (8) FEPEW—width of the proximal end of the femur, (9) FEDEW—width of the distal end of the femur, (10) FEMRL—length of the femur, (11) TIBOL—length of the tibiotarsus, (12) HTROL—length of the trochanter (humerus), (13) HUMRL—length of the humerus, (14) ULNAL—length of the ulna, and (15) ULPEW—width of the proximal end of the ulna. Most of these measurements are pictured and described more fully in Robins and Schnell (1971).

Numerical Analysis of Skin and Skeletal Characters

Study skin (SKIN) and skeletal (SKEL) data were analyzed separately as were males and females because of known sexual dimorphism (Linsdale 1928). For each population sample, means, variances, and coefficients of variation (CV) were computed for each character. Missing values, due to damaged or missing bones, were replaced by population and sex means to allow multivariate analysis. However, inserting means weights the population mean, decreases the variance, and increases the d.f., all of which are factors that exaggerate differences between groups. Hence, if a specimen lacked more than 2 skin or 3 skeletal characters, it was excluded from analysis beyond the calculation of basic univariate statistics.

Analysis of variance (ANOVA) was used to assess geographic heterogeneity for each character. Inspection of product-moment correlation coefficients, computed for each pair of characters (and based on all individuals) revealed which characters in each data set exhibited similar patterns of variation. Geographic variation for some characters was illustrated with pie diagrams. Although no two characters showed exactly the same geographic pattern, inspection of the character plots and

correlation coefficients between pairs of characters depicts the geography of character variation.

To estimate the size component of geographic variation, correlation coefficients were computed between sample means for each character and the mean cube-root of mass per site. In addition, a regression analysis was used to determine the amount of variance in a character that is "explained" by cube-root of mass.

Multivariate analysis of variance (MANOVA) was performed on each data set to test the hypothesis that the group centroids are significantly heterogeneous in multivariate space. Principal components analysis (PCA) was used to explore the general pattern of phenotypic similarity among population samples in multivariate morphometric space, and to identify linear combinations of variables that best summarize character variation within and among samples. Raw data were first $\log_{10}$ transformed. The principal components are orthogonal, unrotated, and extracted from the covariance matrix calculated over all individuals. To compare within-sample character variation at different sites, 10 of the largest samples were analyzed separately, and the relative values of character "loadings" inspected for similarity.

Individuals' scores on the first three principal components were analyzed with the SS-STP method (Gabriel 1964; Gabriel and Sokal 1969; Power (1970) and Johnson (1980) provide examples of this technique in avian studies). This analysis delimits a group of population samples for a given character, such that addition of another sample would result in a significant F-value (ANOVA). The resultant "maximally non-significant subsets," computed for each principal component, are illustrated on a map of localities and provide indications of the geographic structure of variation in PC scores. Samples are ranked by PC values from largest to smallest, rather than by geographic proximity. The scheme used to code pie diagrams for character variation was used also here to depict locality mean scores on the first three principal components, portraying a complex pattern of morphological variation in one dimension.

Cluster analysis was used to explore further the pattern of phenetic relationships among the samples. The taxonomic distance (d_{jk}) measure and correlation coefficient, computed from variance-standardized character means for each population, were used to construct an Operational Taxonomic Unit (OTU) by OTU matrix of distances or correlation coefficients. The UPGMA and WPGMA (Sneath and Sokal 1973) algorithms were used on the OTU by OTU matrices. The degree to which a phenogram represents the similarity or distance matrix was evaluated with the cophenetic correlation coefficient (r_{cc}).

UPGMA phenograms were also computed from matrices of taxonomic distances and correlation coefficients that had been constructed from character means for males that were first divided by the mean cube-root of male mass at each site and then transformed to $\log_{10}$. This procedure produced groupings of samples, perhaps less influenced by size, which might portray patterns of variation in shape.

A canonical correlation analysis (BMDP6M, Dixon 1979) was performed, using sample means for each character (sexes separate) and the following locality and climatic variables: elevation (ELEV), latitude (LATI), longitude (LONG), May mean temperature (MAYT), average maximum May temperature (MAYX), average minimum May temperature (MAYM), June mean temperature (JUNT),

average maximum June temperature (JUNX), average minimum June temperature (JUNM), average July temperature (JULT), average maximum July temperature (JULX), average minimum July temperature (JULM), April precipitation (APPR), and total annual precipitation (ANNP). The weather data were taken from recent U.S. Forest Service publications. Most of the weather stations were located within 20 km of the collecting sites, but often differed in elevation. As a consequence, temperature values were corrected for elevation by adjusting the value used by 1°F for every 400-foot difference in elevation between the collecting site and weather station (Hopkins 1938). The canonical correlation analysis tests for independence of patterns between two data sets. In this analysis, the objective is to "explain" morphological patterns of variation in terms of the environmental data. If independence is refuted, the analysis indicates which environmental variables are primary determinants of the non-independence of the two data sets.

Randomness in Geographic Patterns: Mantel Tests

Mantel's (1967) test compares two distance matrices for congruence of pattern. It tests the hypothesis that the pattern of distances in one matrix (dependent) is independent of the pattern of distances in the second matrix (hypothesis). Here, two hypothesis matrices are a matrix of minimum geographic distances (GEOG) between each pair of sites, and a matrix of the reciprocals of geographic distances (REGE). For dependent matrices, I use genetic and morphological distances (males only). Many alternative hypothesis matrix structures exist (Sokal 1979). For example, if population samples were taken on opposite sides of a barrier to gene flow, e.g., a mountain range, the minimum geographic distance between sites (across the range) would not be as appropriate as the path distance around the mountain range, a more biologically realistic gene flow corridor. Use of reciprocals of geographic distance "in effect consider all longer distances to be about equal while emphasizing differences between short distances. This procedure increases the statistical power of the analysis to reveal local geographic patterning whereas tests involving actual distances are more useful in evaluating regional geographic patterns" (Jones et al. 1980).

If, for example, matrix comparisons indicated that genetic and geographic distances were independent, then the pattern of genetic distances might not be a simple function of isolation by distance (as represented by the particular hypothesis matrix). In this study, GEOG and REGE "hypothesis" matrices were used because I lacked information on patterns of gene flow among these samples of Fox Sparrows. Because any two matrices can be compared, genetic and morphological matrices were contrasted as well. In addition to t-values resulting from Mantel's test, matrix correlation coefficients are also computed to illustrate further the degree of matrix association. Douglas and Endler (1982) and Schnell et al. (1985) provide further notes on methodology, and Jones et al. (1980) provide a useful empirical demonstration.

The Mantel procedure generates a matrix of t-values between distance matrices. When testing several matrices, Douglas and Endler (1982) recommended that a corrected t-value be used to reject the null hypothesis of independence of the matrices. For the present study, nine t-values were computed; thus, the corrected

probability value for a Type 1 error is 0.05/9, or 0.0056, for which the corresponding t-value is 2.88. Therefore, an observed t-value must exceed 2.88 to reject the null hypothesis (independence); if a t-value exceeds 2.88, then the matrices share a common structure to some degree.

RESULTS

Electrophoretic Analysis

Locus Level

An initial survey at 38 loci of 150 individuals representing most collecting sites indicated that 14 loci were sufficiently polymorphic to survey for remaining individuals (breeding adults only). Therefore, 14/38 (36.8%) loci were considered polymorphic, and all calculations that follow assume 24 loci to be monomorphic and fixed for the same allele in all 31 population samples.

Barrowclough and Corbin (1978) and Avise et al. (1980a) describe the electrophoretic phenotypes of heterozygous individuals for several loci in various species of wood-warblers and thrushes. My results agree with these studies, and with those documented for the same loci in other vertebrates. Therefore, I refer to electrophoretic phenotypes (= electromorphs) as alleles.

Notes follow on electrophoretic patterns for loci that are sometimes difficult to interpret. (1) *Esterase-D* (EST-D; 4-methylumbelliferyl acetate esterase). The three-banded pattern of heterozygotes at this locus is consistent with the interpretation that the active state of this enzyme is a dimeric condition (Harris and Hopkinson 1976). A fluorescent lamp was used in a darkroom to cause the bands (alleles) to fluoresce. After scoring gels for EST-D, the position of the alleles was marked by punching a hole in the gel with a stirring rod. Gels were then rinsed with deionized water and treated with a visual esterase assay (alpha NP + FBRR salt; Harris and Hopkinson 1976); this caused a complex series of bands to appear. Other than the most anodal locus (EST-1), the other bands were not interpreted because it seemed that gene products of several loci had similar mobilities, thus obscuring resolution of single loci. The visual stain did not detect EST-D, because none of the colored bands was coincident with the position of bands at EST-D, thereby implicating single-locus control of EST-D. (2) *Erythrocyte Acid Phosphatase* (EAP; 4-methylumbelliferyl phosphatase). Presumed heterozygotes at this locus showed a two-banded phenotype consistent with the interpretation (Harris and Hopkinson 1976) that the active form of this enzyme is monomeric. This locus was clearly different from the visual acid phosphatase (ACP), because heterozygotes at the latter locus exhibited the expected three-banded pattern (the ACP locus was not used here). (3) *Peptidases.* Four loci were scored on LiOH gels, LAP, LGG, LA-1, and LA-2. No variation was detected at LAP. Using leucyl-glycyl-glycine as substrate, a locus (LGG) with two-banded heterozygotes was observed. Using leucyl-alanine as a substrate, two zones of activity appeared, representing two presumptive genetic loci (LA-1 and LA-2). Heterozygotes at LA-1 showed a three-banded pattern, and at LA-2 a two-banded pattern, suggesting dimeric and monomeric status for these enzymes, respectively.

Considering the 14 polymorphic loci and all (619) individuals (Table 4), the number of alleles per polymorphic locus ranged from two (SOD-1, ICD-1, MPI) to six (LA-2), and averaged 3.5; the average across all loci was 1.9 (including

TABLE 4

NUMBER OF ALLELES PER LOCUS, OBSERVED AND EXPECTED FREQUENCIES, AND NUMBERS OF HETEROZYGOTES AT VARIABLE LOCI, BASED ON POOLING OF ALL 619 INDIVIDUALS. ESTIMATES OF INBREEDING COEFFICIENTS (F) CALCULATED AS $1 - (H_o/H_e)$.

Locus	Number alleles	Heterozygotes observed		Heterozygotes expected		F
		Freq.	N	Freq.	N	
LA-2	6	0.316	194	0.316	195.7	0.009
ADA	5	0.246	150	0.242	147.4	−0.018
LGG	3	0.192	119	0.194	120.0	0.008
EST-D	5	0.145	90	0.151	93.7	0.039
NP	3	0.141	87	0.139	86.3	−0.008
SOD-1	2	0.115	71	0.120	73.9	0.039
EAP	4	0.108	67	0.108	67.0	0.000
PGM	4	0.053	33	0.052	32.3	−0.022
GPI	3	0.044	27	0.044	26.9	−0.003
ICD-1	2	0.034	21	0.033	20.7	−0.014
LA-1	3	0.031	19	0.033	20.7	0.082
6-PGD	4	0.029	18	0.029	17.8	−0.011
α-GPD	3	0.011	7	0.011	6.9	−0.014
MPI	2	0.006	4	0.006	3.9	−0.026
Overall	49	0.039	907	0.039	913.2	0.007

monomorphic loci). Observed heterozygote frequencies varied from 31.61% (LA-2) to 0.65% (MPI), which illustrates that loci differ markedly in levels of polymorphism. Notable is the close correspondence between numbers of observed and expected heterozygotes, both per locus and over all loci. The largest discrepancy for any locus, that at LA-1, is trivial. The *F*-values quantify these comparisons, and provide a measure of inbreeding (Hartl 1981) (these values are evaluated as if all individuals were sampled from a single breeding population). Negative values indicate an excess of heterozygotes. None of the *F*-values differs from expectation (Table 4). Furthermore, the eight negative and six positive *F*-values indicate no consistent trends, such as heterozygote excess. Given divergence among populations, pooling individuals from different populations results in significant *F*-values because of a "Wahlund Effect" (e.g., Barrowclough and Corbin 1978). The absence of significant *F*-values both within each sample and the total array of individuals (Table 4) is evidence for panmixis.

INDIVIDUAL LEVEL

The observed heterozygosity for Fox Sparrows over all individuals is 3.85%, and ranges from 0 to 13.2%. The latter value means that the most heterozygous individual was polymorphic at 5 of 38 loci. Observed heterozygosities were equivalent for males and females.

Interpretation of electrophoretic measures of genetic variation requires that electromorphs are inherited in a Mendelian fashion. For some mammals, electromorphs of some esterase loci, transferrin, and leucine amino-peptidase (LAP) do not exhibit Mendelian inheritance (Bowen and Yang 1978; McGovern and Tracy 1981; Davin et al. 1984). Of these loci, only LAP and two esterases (EST-

TABLE 5

ALLELIC FREQUENCIES FOR 14 VARIABLE LOCI IN POPULATION SAMPLES OF FOX SPARROWS. SAMPLE ACRONYMS AS IN TABLE 1. SAMPLE SIZES ARE IN PARENTHESES

Locus (allele)	PINO (26)	BERN (23)	REDM (19)	DOME (23)	LOOK (24)	SHAV (36)	WHIT (29)	MONO (11)	STEN (11)	JACK (23)	MTOM (17)	CHER (12)
GPI												
a		.044	.026		.042	.028	.017			.043	.029	
b	1.00	.956	.974	1.00	.958	.958	.983	1.00	.954	.957	.971	1.00
c						.014			.046			
EAP												
a	.019	.087	.053	.087	.021	.042	.035	.136		.065	.029	.125
b												
c	.981	.913	.947	.913	.979	.958	.965	.864	1.00	.935	.971	.875
d												
SOD												
a	.789	.978	.974	.891	.958	.986	.845	.955	.818	.891	1.00	.958
b	.211	.022	.026	.109	.042	.014	.155	.045	.182	.109		.042
6-PGD												
a	.038	.044	.026		.021					.022	.029	
b	.962	.956	.947	.957	.979	.986	1.00	1.00	1.00	.978	.971	1.00
c				.022								
d			.027	.021		.014						
ICD												
a		.043		.022	.021	.028				.022	.088	
b	1.00	.957	1.00	.978	.979	.972	1.00	1.00	1.00	.978	.912	1.00
MPI												
a									.091		.029	
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.919	1.00	.971	1.00
α-GPD												
a												
b	1.00	1.00	1.00	.978	1.00	.986	.983	1.00	1.00	1.00	1.00	.972
c				.022		.014	.017					.028
ADA												
a						.014						
b	.019	.087					.017					
c	.039		.105	.087	.167	.097	.138	.136	.273	.152	.177	.333
d	.942	.891	.895	.913	.833	.889	.845	.864	.727	.848	.794	.667
e		.022									.029	

TABLE 5
CONTINUED

Locus (allele)	PINO (26)	BERN (23)	REDM (19)	DOME (23)	LOOK (24)	SHAV (36)	WHIT (29)	MONO (11)	STEN (11)	JACK (23)	MTOM (17)	CHER (12)
LGG												
a	.058	.044	.132	.174	.146	.167	.069	.046		.087	.088	.167
b							.017			.130	.059	
c	.942	.956	.868	.826	.854	.833	.914	.954	1.00	.783	.853	.833
LA-1												
a								.045	.136	.022	.029	
b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.955	.864	.978	.971	1.00
c												
PGM												
a			.026						.045	.044		.041
b	1.00	.978	.974	1.00	.938	.972	1.00	.955	.955	.935	1.00	.917
c		.022										
d					.062	.028		.045		.021		.042
NP												
a	.058	.022	.026	.130	.063	.208				.065	.029	.125
b	.942	.978	.974	.870	.937	.792	1.00	1.00	1.00	.935	.971	.875
c												
LA-2												
a	.134	.152	.053	.239	.104	.083	.138		.227	.196	.118	.208
b	.019					.028	.017	.046	.046			.042
c	.808	.696	.842	.761	.875	.889	.845	.954	.727	.804	.882	.750
d	.039		.105		.021							
e		.152										
f												
EST-D												
a			.026	.044	.021	.014	.017	.181		.065	.029	.042
b	.904	.978	.921	.870	.854	.944	.948	.727	1.00	.913	.942	.833
c	.019			.021	.042	.028						
d	.058		.053	.022	.021	.014				.022		
e	.019	.022		.043	.062		.035	.092			.029	.125
H_{obs}	3.24	3.20	3.32	4.81	3.73	4.24	3.36	4.07	4.78	5.15	4.18	4.17
s.d. of H_{obs}	2.47	3.17	2.45	3.69	2.56	3.10	2.32	2.46	3.07	3.59	2.80	2.62
H_{exp}	3.43	3.57	3.37	4.84	4.11	3.92	3.19	3.68	4.60	5.12	3.86	6.03
s.e. of H_{exp}	1.36	1.43	1.15	1.58	1.34	1.33	1.26	1.50	1.85	1.61	1.32	2.11
POLY99	8	11	10	10	11	12	8	8	7	12	11	9
NALL	2.63	2.18	2.30	2.40	2.36	2.42	2.50	2.13	2.14	2.25	2.27	2.33
χ^2 (d.f.)	0.10 (9)	0.63 (7)	0.59 (8)	0.76 (10)	1.36 (11)	1.40 (11)	0.49 (6)	0.35 (5)	0.84 (7)	0.73 (11)	0.44 (8)	0.33 (4)

TABLE 5

CONTINUED

Locus (allele)	EBET (17)	TAHW (20)	SAGE (21)	BUCK (13)	LASS (51)	WALK (16)	WOOD (17)	TAHE (10)	RUBY (13)	MART (6)	WARN (30)	SHAS (28)	SPEN (15)
GPI													
a				.077	.010			.050	.038	.167	.017		
b	1.00	1.00	1.00	.923	.990	1.00	1.00	.950	.962	.833	.983	1.00	1.00
c													
EAP													
a	.029	.050	.095	.154	.029	.031	.079	.050		.083	.050	.036	.033
b													
c	.971	.950	.905	.846	.971	.969	.921	.950	1.00	.917	.950	.964	.933
d													.034
SOD													
a	.971	.925	.976	.962	.912	1.00	.947	1.00	1.00	.750	.933	1.00	.967
b	.029	.075	.024	.038	.088		.053			.250	.067		.033
6-PGD													
a			.048		.010							.018	
b	.971	1.00	.952	1.00	.980	1.00	1.00	.950	1.00	1.00	1.00	.982	1.00
c													
d	.029				.010			.050					
ICD													
a		.025			.029	.031		.050			.033	.018	
b	1.00	.975	1.00	1.00	.971	.969	1.00	.950	1.00	1.00	.967	.982	1.00
MPI													
a			.024										
b	1.00	1.00	.976	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
α-GPD													
a													
b	1.00	.975	.976	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
c		.025	.024										
ADA													
a												.018	
b	.029	.025											.067
c	.088	.175	.167	.192	.098		.106	.100	.154	.083	.167	.143	.100
d	.883	.800	.833	.808	.902	1.00	.894	.900	.846	.917	.833	.839	.833
e													

TABLE 5
CONTINUED

Locus (allele)	EBET (17)	TAHW (20)	SAGE (21)	BUCK (13)	LASS (51)	WALK (16)	WOOD (17)	TAHE (10)	RUBY (13)	MART (6)	WARN (30)	SHAS (28)	SPEN (15)
LGG													
a	.118	.075	.071		.098	.031	.079	.100	.038		.150	.089	.133
b		.125											
c	.882	.800	.929	1.00	.902	.969	.921	.900	.962	1.00	.850	.911	.867
LA-1													
a	.029		.024		.020				.077	.167	.017	.018	.067
b	.971	1.00	.976	1.00	.970	1.00	1.00	1.00	.923	.833	.983	.982	.900
c					.010								.033
PGM													
a	.029	.050			.029							.018	.067
b	.942	.900	1.00	1.00	.942	.969	1.00	1.00	1.00	1.00	1.00	.964	.933
c													
d	.029	.050			.029	.031						.018	
NP													
a	.088	.200	.119	.077	.088	.063	.053	.100	.039		.083	.018	.133
b	.912	.800	.891	.923	.902	.937	.921	.850	.962	1.00	.917	.982	.867
c					.010		.026	.050					
LA-2													
a	.176	.150	.286	.077	.206	.313	.211	.050	.039	.167	.267	.161	.033
b			.071	.039		.031		.050			.033	.018	
c	.765	.850	.643	.884	.794	.625	.763	.900	.846	.750	.700	.821	.933
d	.059					.031	.026		.115				
e													
f										.083			.034
EST-D													
a	.029	.025			.029	.062					.017	.017	
b	.942	.900	.976	1.00	.952	.938	.947	.950	1.00	1.00	.917	.893	.867
c		.025											
d	.029	.025									.017	.036	
e		.025	.024		.019		.053	.050			.050	.054	.133
H_{obs}	4.02	5.13	4.89	3.04	3.56	2.30	2.91	3.68	2.63	4.39	4.47	3.20	4.56
s.d. of H_{obs}	3.73	2.49	2.25	2.60	3.02	2.69	2.46	2.83	3.56	3.19	2.41	2.62	3.51
H_{exp}	3.84	5.25	4.31	3.12	3.87	2.68	3.24	3.56	2.45	4.70	4.36	3.25	4.39
s.e. of H_{exp}	1.36	1.71	1.65	1.30	1.22	1.45	1.29	1.16	1.10	1.91	1.59	1.23	1.41
POLY99	10	10	11	6	12	7	7	9	6	6	10	10	9
NALL	2.40	2.60	2.09	2.17	2.42	2.29	2.29	2.22	2.17	2.17	2.30	2.50	2.44
χ^2 (d.f.)	0.18 (8)	0.60 (12)	2.29 (8)	0.43 (5)	3.70 (17)	0.60 (3)	1.83 (7)	0.10 (4)	0.20 (3)	2.14 (4)	3.08 (12)	0.16 (8)	0.31 (10)

TABLE 5

CONTINUED

Locus (allele)	LAUG (17)	ODEL (16)	BLAC (18)	YOLL (23)	SAWY (17)	PYRA (15)	F_{IS}	F_{ST}[1]	F_{ST}[2]	F_{IT}	χ^2 (corr.)	χ^2 (uncorr.)	d.f.
GPI							−0.009	0.047	0.008	0.043	17.8	111.9**	90
a	.059	.031		.043	.029								
b	.941	.969	1.00	.957	.971	1.00							
c													
EAP							0.011	0.034	0.033	0.035	18.1	123.3*	120
a	.029	.094	.111	.022	.177	.033							
b		.031											
c	.971	.875	.889	.978	.824	.967							
d													
SOD							0.015	0.072	0.042	0.079	51.0**	81.1**	60
a	.941	1.00	.917	.826	.971	.967							
b	.059		.083	.174	.029	.033							
6-PGD							−0.004	0.024	0.000	0.020	0.0	57.4	120
a						.033							
b	1.00	1.00	1.00	1.00	1.00	.967							
c													
d													
ICD							−0.006	0.028	0.003	0.028	2.7	33.7	60
a	.029			.022									
b	.971	1.00	1.00	.988	1.00	1.00							
MPI							−0.001	0.059	0.024	0.061	28.7	72.1*	60
a													
b	1.00	1.00	1.00	1.00	1.00	1.00							
α-GPD							0.000	0.019	0.000	0.022	0.0	45.0	90
a		.031											
b	1.00	.969	1.00	.988	1.00	1.00							
c				.022									
ADA							−0.007	0.040	0.005	0.022	20.8	194.1**	120
a													
b													
c	.235	.031	.250	.109	.176	.133							
d	.765	.937	.750	.891	.824	.867							
e		.032											

TABLE 5
CONTINUED

Locus (allele)	LAUG (17)	ODEL (16)	BLAC (18)	YOLL (23)	SAWY (17)	PYRA (15)	F_{IS}	F_{ST}[1]	F_{ST}[2]	F_{IT}	χ^2 (corr.)	χ^2 (uncorr.)	d.f.
LGG							−0.021	0.041	0.016	0.035	37.6	99.5*	60
a	.147	.031	.083	.152	.059	.067							
b													
c	.853	.969	.917	.848	.941	.933							
LA-1							−0.010	0.065	0.026	0.066	62.4	158.9**	60
a	.029		.056		.088								
b	.971	1.00	.944	1.00	.912	1.00							
c													
PGM							0.027	0.031	0.004	0.036	11.9	112.1	90
a	.059		.028		.059								
b	.941	1.00	.972	1.00	.941	1.00							
c													
d													
NP							−0.007	0.049	0.023	0.045	55.0	119.3*	60
a	.029	.031	.111	.022		.067							
b	.971	.969	.889	.978	1.00	.933							
c													
LA-2							0.043	0.047	0.019	0.097	112.6	285.9**	150
a	.059	.156	.139	.217	.118	.267							
b	.029	.031				.033							
c	.912	.812	.861	.783	.853	.700							
d					.029								
e													
f													
EST-D							0.070	0.045	0.018	0.057	85.1	218.8**	120
a				.044									
b	.883	.812	.889	.891	.912	.967							
c													
d	.029	.031	.028	.022									
e	.088	.156	.083	.044	.088	.033							
H_{obs}	4.33	3.29	4.53	4.23	3.56	3.29							
s.d. of H_{obs}	2.62	2.45	3.23	3.15	2.45	2.53							
H_{exp}	4.20	3.30	4.53	4.02	4.06	3.20							
s.e. of H_{exp}	1.38	1.34	1.51	1.48	1.40	1.40							
POLY99	11	8	9	10	9	8							
NALL	2.18	2.50	2.11	2.20	2.11	2.13							
χ^2 (d.f.)	1.47 (7)	0.45 (4)	0.60 (8)	0.35 (8)	1.98 (7)	0.13 (4)							

[1] F_{ST} and χ^2 not corrected for sampling error.
[2] F_{ST} and χ^2 corrected for sampling error following method of Wright (1978).
* $P < 0.05$; ** $P < 0.001$

1, EST-D) were scored for Fox Sparrows, with LAP and EST-1 showing no variation whereas variation at EST-D behaved in a Mendelian fashion. On three occasions, I collected two or three nestlings and their presumed parents. The occurrence of electromorphs at polymorphic loci within these family groups was consistent with a hypothesis of Mendelian inheritance. Johnson and Zink (1983) found the same result for sapsuckers (*Sphyrapicus*). However, these are not rigorous tests, and I encourage others to report similar data.

Population Level

The allelic frequencies at the 14 polymorphic loci for all samples are given in Table 5. At each locus, the same allele was the most frequent one in all population samples, indicating few if any qualitative differences between samples. For example, the frequency of the most common allele (c) at LA-2, the most variable locus and allele, ranges from 0.625 (WALK sample) to 0.954 (MONO sample). The highest frequency of a "private polymorphism" (Slatkin 1985a) involves the LA-2^e allele, which occurs only in the BERN sample at a frequency of 0.152. Four alleles occur at moderate frequency (5–15%) in some samples but not in others: SOD-1^b, LGG^b, LA-2^e, and NP^a. The detection of low frequency alleles is a function of sample size; hence, the significance of their pattern of occurrence is uncertain. Sample sizes used here are sufficient to show that few alleles occur in only one geographic region or habitat, although EST-D^c occurs mostly in the southern Sierra Nevada and Transverse Range.

A preliminary goal of this study was to test for the existence of genetic microstructuring. At several sites (Appendix I) samples were taken from between two and five km apart. Because inspection of genotypic results (not shown) indicated an absence of local genetic differentiation, individuals were pooled into 31 samples.

Summarizing allelic frequency data for all loci provides measures of within-locality (= population) genetic variation (Table 5). Average observed heterozygosity per individual per locality ranges from 2.3% (WALK) to 5.2% (JACK). The large standard errors for expected heterozygosities are due mostly to among-locus differences in levels of polymorphism (Table 4; Archie 1985). Inspection of heterozygosity values per site indicates no apparent trends. For example, the average heterozygosity for samples taken in riparian habitats in the Great Basin is 3.80%, very similar to the overall average (3.85%). Observed heterozygosities at sites with low densities of birds (Table 1) were 4.17% (CHER), 4.39% (MART), 2.63% (RUBY), indicating that no apparent effect of current population size is evident in average heterozygosity, with the possible exception of the RUBY sample. Sites with high densities had typical values of heterozygosity, such as SHAS (3.20%), SAGE (4.89%), LASS (3.56%), and SHAV (4.24%). Isolated colonies of both low and high density showed typical levels of heterozygosity, PINO (3.24%), MART (4.39%), BERN (3.20%), WHIT (3.36%) and STEN (4.78%).

The number of polymorphic loci per sample ranged from 6 to 12 (mean = 9.2) and the number of alleles per polymorphic locus ranged from 2.09 (SAGE) to 2.63 (PINO) (mean = 2.3). Variation among samples in these characteristics exhibited no geographic or ecological correlates.

The χ^2 tests showed no significant departures from Hardy-Weinberg equilibrium

expectations in any of the 31 Fox Sparrow population samples (Table 5). However, this should be viewed as a weak test because expected numbers in many genotype classes are less than five. Each locus in each population was also examined for departures from Hardy-Weinberg expectations (Hartl 1981) by the calculation of F_{IS} (Wright 1965). Average F_{IS} values (Table 5) for loci per sample, which range from -0.021 to 0.070, differ somewhat from F-values calculated over all individuals (Table 4) because they are weighted averages. These F-values, taken by locus or population, illustrate that genic variation within populations is not biased by departures from random mating, selection, drift, migration (gene flow), or mutation.

Genetic Distance between Population Samples

Inspection of Nei's (1978) genetic distances (D) between sites (Table 6) and their standard errors (not shown; available from author) show that few if any Ds are significantly different from zero or each other. The largest genetic distance ($D \pm$ s.e.) observed between any pair of localities is 0.0037 ± 0.0016 (SHAV–STEN). The negative values of Nei's D result from subtraction of a sampling error component from a value already close to zero. Negative genetic distances are biologically nonsensical and should be interpreted as zero (Nei 1978). Between any pair of samples, the degree of isolation and differences in habitat, elevation, and density do not covary with genetic distance. For example, an isolated, low-density sample taken in riparian habitat in the Great Basin (RUBY) showed a similar genetic distance when compared with an adjacent, ecologically similar sample (MART) as when it was compared with a geographically and ecologically disparate sample (YOLL). Overall, the D between pairs of localities in the same subspecies was 0.00032 ± 0.00041 (s.d.; N = 104), and between pairs of localities, each in different subspecies, 0.00083 ± 0.00076 (N = 327). Because values used to calculate these means are not independent, they are not compared statistically. These D-values illustrate that as the geographic distance between pairs of sites increases, D also tends to increase. However, because in many instances sites in different subspecies are geographically nearer than many comparisons within subspecies (such as *megarhyncha* and *fulva*), this aspect is examined in greater detail below.

Geographic Pattern of Protein Variation

A phenogram (Fig. 4) based on Rogers' D-values (Table 6) makes no "geographic" sense, because genetically similar samples are often widely disparate in geography and breeding habitat. The cluster BERN-WALK-ODEL represents a geographically heterogeneous group, and RUBY-BUCK groups a sample with small bills from a riparian environment (RUBY) with one from chaparral with large bills (BUCK). Although two samples from the Great Basin, MART and STEN, are genetically similar, other samples from this region are not (e.g., WHIT, RUBY, WARN). Populations from the same subspecies do not tend to cluster together, and samples from equivalent elevations or habitats are not similar genetically. For example, YOLL and WHIT cluster together, yet they represent the extremes in longitudinal, elevational, and habitat differences.

TABLE 6

ROGERS' GENETIC DISTANCES (ABOVE DIAGONAL) AND NEI'S GENETIC DISTANCES (NEI 1978; BELOW DIAGONAL) BETWEEN SAMPLES OF FOX SPARROWS. LOCALITY CODES DEFINED IN TABLE 1. NEI'S *D*-VALUES ARE MULTIPLIED BY 100, AND ROGERS' *D*-VALUES BY 10

	PINO	BERN	REDM	DOME	LOOK	SHAV	WHIT	MONO	STEN	JACK	MTOM	CHER	EBET	TAHW	SAGE
PINO	—	.183	.150	.162	.168	.210	.110	.239	.241	.182	.204	.278	.143	.219	.202
BERN	.129	—	.152	.206	.195	.206	.182	.235	.286	.202	.182	.276	.171	.259	.161
REDM	.069	.073	—	.163	.113	.130	.136	.188	.289	.146	.140	.228	.097	.195	.183
DOME	.039	.106	.042	—	.163	.147	.165	.252	.313	.142	.220	.159	.140	.159	.156
LOOK	.095	.132	−.031	.021	—	.125	.143	.186	.289	.125	.126	.179	.124	.147	.198
SHAV	.181	.200	.053	.041	.026	—	.176	.244	.342	.183	.166	.216	.136	.132	.204
WHIT	.002	.107	.028	.050	.023	.159	—	.183	.195	.148	.143	.236	.148	.169	.177
MONO	.195	.241	.068	.182	.048	.219	.114	—	.313	.231	.227	.238	.207	.255	.242
STEN	.144	.233	.217	.221	.181	.371	.045	.317	—	.258	.266	.296	.256	.310	.258
JACK	.073	.124	.020	−.018	−.005	.083	.009	.144	.118	—	.161	.210	.136	.128	.194
MTOM	.153	.096	−.014	.075	−.039	.063	.028	.088	.126	−.009	—	.256	.156	.189	.183
CHER	.178	.155	.025	−.062	−.094	.030	.023	.046	.039	−.071	−.049	—	.187	.174	.188
EBET	.043	.023	−.049	−.039	−.029	.014	.020	.138	.120	−.024	−.009	−.050	—	.166	.140
TAHW	.141	.207	.076	.010	.000	−.005	.093	.186	.214	−.044	.028	−.121	−.005	—	.208
SAGE	.164	.068	.116	.016	.117	.149	.113	.304	.093	.067	.090	−.083	−.012	.091	—
BUCK	.155	.100	.043	.137	.059	.106	.049	.082	.135	.089	.023	−.014	.058	.092	.082
LASS	.035	.071	.027	−.019	.014	.061	.020	.175	.110	−.005	.030	−.002	−.053	.024	.032
WALK	.163	.054	.157	.079	.201	.242	.190	.348	.273	.155	.196	.199	.018	.235	.029
WOOD	.037	.017	−.003	−.034	.010	.073	.001	.135	.110	.002	.014	−.050	−.065	.045	.029
TAHE	.082	.056	−.057	.011	−.053	−.067	.036	.061	.240	.026	−.061	−.006	−.051	−.006	.075
RUBY	.137	.105	−.018	.167	.029	.108	.056	.133	.103	.102	−.010	.084	−.006	.126	.126
MART	.010	.101	.143	.132	.176	.304	−.009	.232	−.076	.073	.170	.233	.099	.259	.147
WARN	.107	.093	.063	−.040	.026	.102	.048	.235	.098	−.007	.031	−.119	−.035	.043	.034
SHAS	.108	.065	−.017	.042	−.031	.094	.025	.067	.125	.021	−.038	−.064	−.041	.062	.045
SPEN	.138	.175	.017	.066	−.025	.008	.086	.035	.246	.065	.015	−.040	.003	−.003	.181
LAUG	.147	.191	−.006	.097	−.066	.081	.016	.045	.116	.013	−.062	−.119	.029	.033	.168
ODEL	.115	.056	.046	.063	.053	.161	.091	.036	.292	.119	.079	.057	.034	.164	.101
BLAC	.117	.168	.043	.030	−.016	.075	.021	.053	.051	.011	−.004	−.196	.008	−.021	.043
YOLL	.008	.120	.044	−.031	.020	.148	−.029	.176	.099	−.021	.064	.011	.003	.092	.098
SAWY	.169	.101	.023	.109	.036	.177	.052	.005	.108	.058	.016	−.069	.033	.122	.090
PYRA	.071	.019	.039	−.012	.039	.111	.128	.228	.066	.018	.025	−.054	−.062	.067	−.078

TABLE 6

CONTINUED

	BUCK	LASS	WALK	WOOD	TAHE	RUBY	MART	WARN	SHAS	SPEN	LAUG	ODEL	BLAC	YOLL	SAWY	PYRA
PINO	.211	.137	.172	.127	.189	.185	.208	.180	.148	.230	.220	.168	.191	.122	.222	.129
BERN	.181	.172	.152	.140	.166	.174	.246	.183	.157	.250	.222	.156	.231	.195	**.197**	.136
REDM	.174	.133	.188	.117	.118	.125	.269	.146	.197	.164	.142	.161	.181	.137	**.161**	.129
DOME	.231	.116	.194	.111	.168	.254	.276	.113	.166	.195	.214	.190	.156	.111	.244	.146
LOOK	.162	.128	.199	.145	.141	.156	.314	.116	.101	.150	.094	.182	.156	.131	.160	.141
SHAV	.186	.140	.203	.162	.102	.189	.325	.157	.152	.165	.165	.209	.201	.170	.227	.174
WHIT	.162	.122	.199	.107	.164	.146	.200	.137	.106	.203	.160	.163	.151	.089	.152	.119
MONO	.180	.217	.253	.184	.225	.190	.297	.235	.167	.185	.192	.178	.177	.243	.141	.213
STEN	.248	.238	.284	.247	.336	.208	.193	.236	.245	.309	.247	.310	.230	.225	.233	.229
JACK	.198	.106	.208	.146	.194	.199	.268	.125	.134	.210	.159	.217	.170	.132	.192	.157
MTOM	.179	.155	.209	.168	.137	.141	.306	.150	.107	.204	.129	.193	.180	.176	.173	.154
CHER	.223	.201	.265	.177	.254	.287	.381	.165	.199	.187	.189	.217	.139	.219	.212	.201
EBET	.188	.068	.142	.095	.142	.153	.269	.116	.099	.143	.163	.184	.154	.150	.176	.096
TAHW	.215	.149	.240	.173	.195	.242	.350	.153	.160	.180	.175	.243	.151	.195	.218	.195
SAGE	.172	.155	.165	.113	.186	.183	.282	.118	.152	.218	.240	.200	.158	.214	.193	.080
BUCK	—	.193	.224	.143	.158	.136	.225	.180	.178	.213	.171	.169	.152	.222	.136	.156
LASS	.083	—	.143	.088	.132	.173	.246	.101	.103	.171	.157	.190	.139	.118	.188	.105
WALK	.243	.062	—	.137	.195	.188	.287	.152	.149	.257	.249	.162	.243	.196	.246	.112
WOOD	.020	−.033	.020	—	.126	.151	.218	.096	.105	.174	.180	.129	.127	.121	.154	.065
TAHE	−.035	−.011	.145	−.029	—	.157	.294	.157	.136	.170	.161	.176	.190	.180	.206	.147
RUBY	.013	.064	.191	.033	−.029	—	.224	.179	.131	.188	.170	.171	.185	.193	.142	.141
MART	.061	.059	.189	.060	.149	.082	—	.273	.270	.322	.306	.258	.279	.217	.245	.250
WARN	.116	−.004	.067	−.036	.043	.115	.122	—	.118	.182	.137	.195	.146	.114	.187	.085
SHAS	.045	.010	.103	−.026	−.026	.012	.157	.008	—	.164	.126	.134	.133	.133	.133	.102
SPEN	.075	.051	.293	.053	−.064	.039	.201	.108	.023	—	.140	.210	.141	.224	.161	.196
LAUG	.033	.063	.331	.057	−.030	.021	.154	.060	−.014	−.037	—	.209	.129	.155	.149	.196
ODEL	.070	.074	.086	−.008	.004	.106	.143	.090	.009	.059	.104	—	.187	.179	.161	.164
BLAC	−.027	.032	.260	−.004	−.007	.045	.105	.014	−.001	−.003	−.005	.076	—	.201	.125	.168
YOLL	.150	−.001	.133	−.004	.068	.135	−.002	−.001	.042	.118	.049	.099	.062	—	.215	.146
SAWY	−.032	.076	.224	.008	.023	.030	.052	.085	.000	.018	−.003	.014	−.047	.110	—	.180
PYRA	.062	−.026	−.016	−.072	.015	.052	.091	−.056	−.022	.119	.093	.038	.029	.002	.060	—

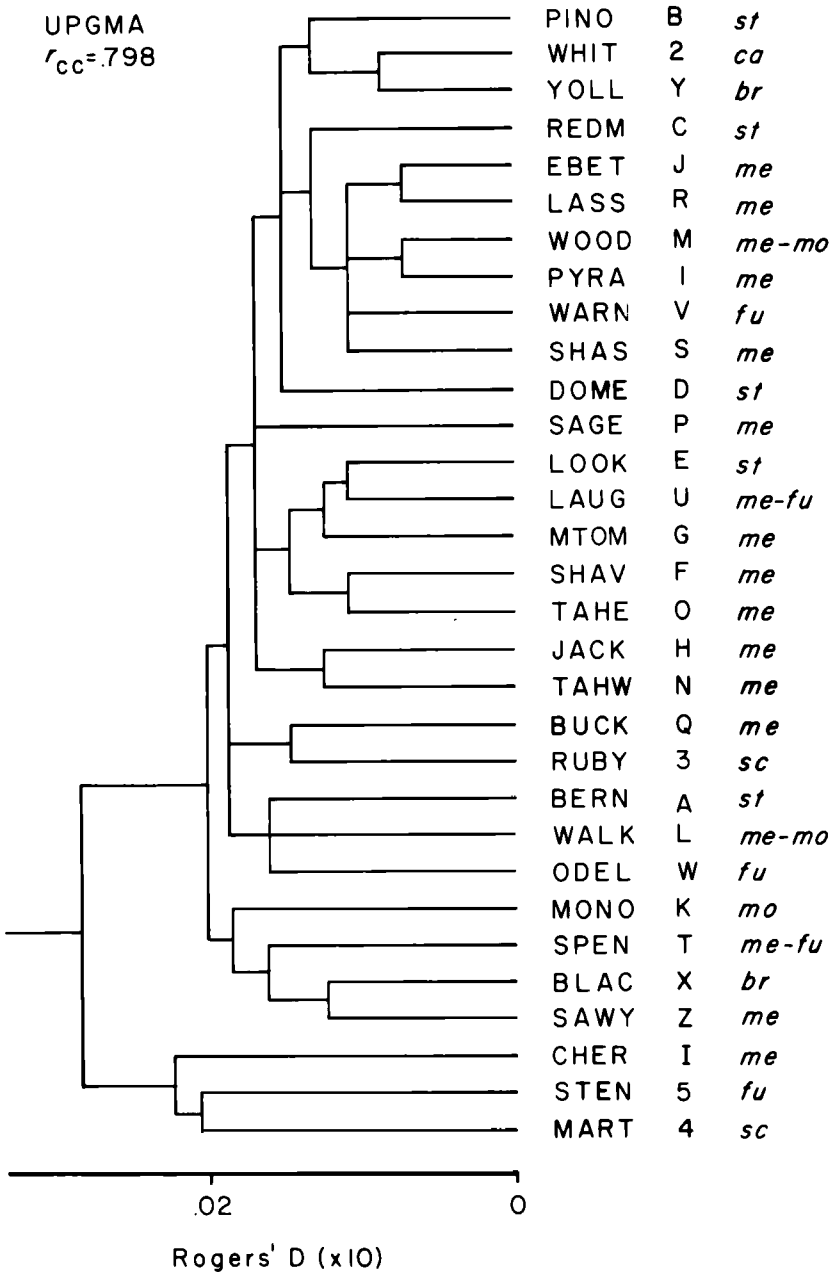

FIGURE 4. UPGMA phenogram derived from the matrix of Rogers' genetic distances (Table 6). Site codes and identifying letters, and two-letter codes are the first two letters of the subspecies name (Table 1).

TABLE 7

F_{ST} ANALYSIS OF ELECTROPHORETIC VARIATION AMONG FOX SPARROW SAMPLES FROM 31 LOCALITIES (N = 619).

	All variable loci (N = 14)	Loci with common allele ≤ 95% (N = 7)
Wright F_{ST}	0.0155	0.0165
Corrected F_{ST}[1]	0.0135 ± 0.0033[2]	0.0178 ± 0.0049
Uncorrected F_{ST}[3]	0.0428 ± 0.0041	0.0467 ± 0.0046

[1] Corrected according to Wright (1978).
[2] Standard error.
[3] Equivalent to Nei's G_{ST} (Wright 1978).

F-STATISTICS AND THE ANALYSIS OF GENETIC STRUCTURE AMONG POPULATIONS

The measure of population subdivision due to isolation and drift, F_{ST}, is shown for each locus in Table 5. The corrected F_{ST} values per locus range from 0 to 0.042 (SOD-1) and are considerably smaller than the uncorrected values (Table 5). The latter are reported because they are equivalent to Nei's (1975) G_{ST} values, and are comparable to other published studies.

The F_{ST} values for each locus can be converted to χ^2 tests of heterogeneity of allelic frequencies by the formula $\chi^2 = (k - 1)(2N_T F_{ST} - 1)$, where k is the number of alleles and N_T the number of individuals in the analysis (Workman and Niswander 1970). The degrees of freedom for this test are $(k - 1)(s - 1)$, where s is the number of populations sampled. The corrected and uncorrected F_{ST} values were used in calculating the chi-square values, the latter to produce a conservative test. Using the uncorrected F_{ST} values, the χ^2 tests show that all loci except PGM, α-GPD, 6-PGD, and ICD-1 exhibit significant geographic heterogeneity. Use of the corrected F_{ST} values obtained a significant chi-square value for only SOD-1. Although SOD-1, LA-1, NP, LA-2, EST-D, and LGG are geographically heterogeneous, I conclude that heterogeneity is biologically meaningful only for SOD-1. Values of F_{ST} for MPI are not considered biologically meaningful because the only variant allele (a) occurs in just three samples (STEN, SAGE, TAHW) and has an average frequency of 0.006 (considering all samples).

Three composite F_{ST} values, computed over all polymorphic loci (N = 14) and loci with the most frequent allele <95%, are shown in Table 7. The "Wright" F_{ST} values are 0.0155 and 0.0165. Correction for sampling error (different from the "Wrightian F_{ST}") is important. The uncorrected values are equivalent to Nei's G_{ST}. Throughout the remainder of this paper, I use the corrected F_{ST}, 0.0135 ± 0.0033 (empirical s.e.), which indicates that only 1.35% of the variance in allelic frequencies is distributed among populations.

RELATIONSHIPS AMONG ESTIMATES OF GENETIC VARIATION AND THEIR ENVIRONMENTAL AND GEOGRAPHIC CORRELATES

Measures of genetic variation such as heterozygosity and mean number of alleles per locus vary among sites (Table 5). Because the 31 sample localities span a wide range of latitudes, longitudes, and elevations, here I determine quantitatively whether within-locality genetic variation is related to these three site character-

TABLE 8

CORRELATION COEFFICIENTS BETWEEN CERTAIN VARIABLES USED IN THE ELECTROPHORETIC ANALYSIS. PARTIAL CORRELATION COEFFICIENTS BETWEEN THE DEPENDENT VARIABLES (SHOWN BELOW THE DIAGONAL) ARE CALCULATED BY REMOVING THE LINEAR EFFECTS OF THE INDEPENDENT VARIABLES. UNDERLINED VALUES INDICATE THAT THE DEPENDENT VARIABLE WAS SIGNIFICANTLY ASSOCIATED WITH THE INDEPENDENT VARIABLES IN A MULTIPLE REGRESSION ANALYSIS ($P < 0.05$, TWO-TAILED t-TESTS). ABBREVIATIONS FOR DEPENDENT VARIABLES ARE GIVEN IN TABLE 3 AND THE TEXT

Variable	2	3	4	5	6	7
Independent						
1. Sample size	−.01	−.12	−.20	−.05	.61**	.01
2. Elevation	—	.73**	−.51**	−.26	−.24	−.25
3. Latitude		—	−.54**	−.10	−.17	−.27
4. Longitude			—	.00	−.29	.04
Dependent						
5. Heterozygosity				—	.37*	.61**
6. POLY99				.44*	—	.26
7. POLY95				.60**	.25	—
8. NALL				.43*	.74**	.36
9. EAP-c				−12	.21	.01
10. SOD-a				−.37	.24	−.23
11. ADA-d				−.56**	−.30	−.27
12. LGG-c				−.56**	−.60**	−.58**
13. NP-b				−.32	−.08	−.48**
14. LA-2-c				.00	.12	.24
15. EST-D-b				−.24	−.18	.02

[1] For independent variables, the multiple R^2 is for each variable with the other variables, and the F-value tests the significance of multiple regression (d.f. = 3,27); for dependent variables, the multiple R^2 is the correlation of each variable with the independent variables, and the F-values test the significance of multiple regression (d.f. = 4,26).

* $P < 0.05$; ** $P < 0.01$.

istics. For example, RUBY from eastern Nevada at 2,680 m has considerably different environmental characteristics (besides habitat differences already noted) than those encountered by breeding Fox Sparrows at YOLL in the North Coast Range at 1,370 m, and one might predict that these differences, undoubtedly correlated with elevation, latitude, and longitude, would influence genetic variation.

The multiple R^2 values, correlation coefficients between all variables used in the multiple regression analysis, and the partial correlation coefficients between dependent variables are shown in Table 8. Among the independent variables, significant multiple R^2 values indicate that latitude, longitude, and elevation are significantly intercorrelated, but these are independent of sample size ($R^2 = 0.11$, $P > 0.05$). Among the dependent variables, only POLY99, NALL, and LGG[c] have significant R^2 values with the independent variables, which suggests that most measures of within-population genetic variation are not significantly related to sample size, elevation, latitude, or longitude.

As Gorman and Renzi (1979) found, sample size is not significantly correlated with H ($r = -0.05$; it would, however, be significantly correlated with the variance

TABLE 8
EXTENDED

8	9	10	11	12	13	14	15	Mul.[1] R^2	F
.71**	.29	−.03	.21	−.35*	−.23	−.12	.04	0.11	1.15
−.16	.28	−.15	.23	.23	.20	−.07	.17	0.56	11.49**
−.11	.23	−.09	.17	.13	.13	−.07	.26	0.60	13.47**
−.32	−.05	−.04	−.22	.26	.14	.08	.04	0.38	5.45*
.31	−.21	−.28	−.56**	−.55**	−.36*	.02	−.26	0.11	0.78
.88**	.17	.23	−.09	−.73**	−.32	.01	−.19	0.55	8.05**
.28	−.11	−.15	−.29	−.55**	−.50**	.24	−.09	0.11	0.78
—	.28	.16	.04	−.75**	−.43*	.07	−.25	0.63	10.94**
.31	—	−.21	.15	−.21	.00	−.05	.32	0.23	1.91
.19	−.14	—	.01	−.14	−.29	.02	−.17	0.05	0.32
−.17	.04	.04	—	.22	.06	−.33	.08	0.10	0.74
−.70**	−.33	−.08	.34	—	.51**	−.12	.32	0.31	2.95*
−.29	−.05	−.25	.09	.39*	—	−.01	.01	0.15	1.14
.26	.01	.01	−.30	−.19	−.02	—	−.33	0.02	0.14
−.38	.23	−.12	.04	.30	−.06	−.33	—	0.14	1.02

of H), although it is significantly correlated with POLY99 ($r = 0.61$) and NALL ($r = 0.71$). H is significantly correlated with POLY99, POLY95, and NALL, and is influenced by variation at ADA and LGG. A high partial correlation coefficient was obtained when comparing POLY99 and NALL ($r = 0.74$). That is, both "rare" and "common" alleles contribute to NALL, which is expected to be highly correlated with POLY99. The negative partial correlation coefficients between H and ADA and LGG (both -0.56) show that as H increases, the frequency of the most common allele decreases; that is, there are more non-M alleles (mostly present as heterozygotes). The frequency of LA-2^c, the most common allele at the most highly polymorphic locus, is uncorrelated with H. This result means that heterozygosity differences among sites are a result of variation at LGG, ADA, SOD-1, and NP, rather than LA-2, at which a fairly constant level of polymorphism occurs at most sites. The frequency of LGG^c shows significant negative correlations with H, POLY99, POLY95, and NALL, implying that variation at LGG (i.e., occurrence of non-M alleles) influences these parameters. Furthermore, the significant multiple R^2 (0.31) shows that the frequency of LGG^c is dependent on the "independent" variables, especially sample size (original $r = -0.35$). That is, as N increases, the frequency of LGG^c decreases, implying higher H for the locus.

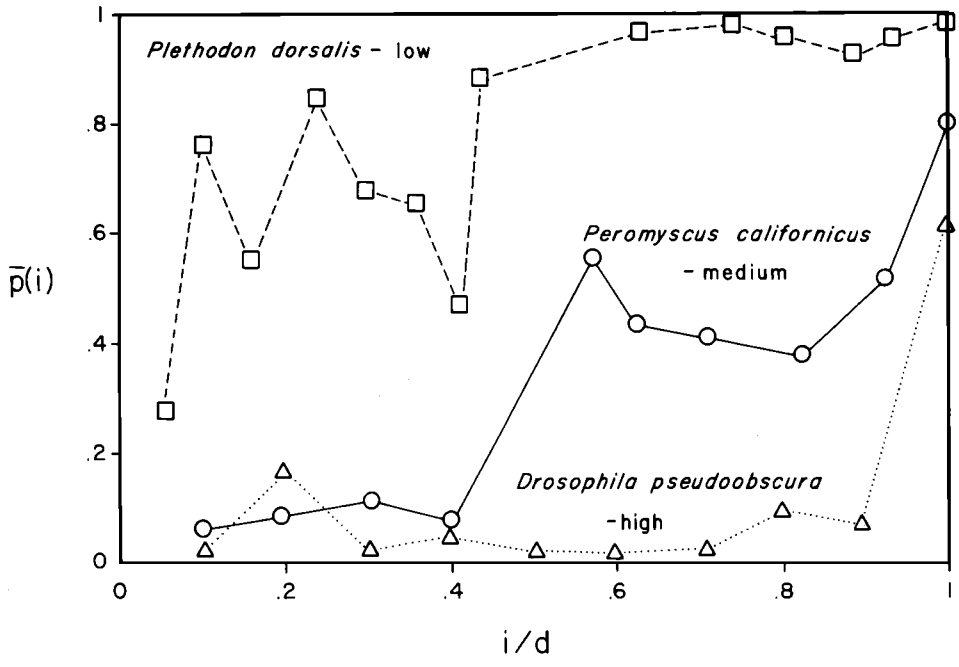

FIGURE 5. Examples of high, medium, and low levels of gene flow taken from Slatkin (1981). See text (p. 12) for explanation of axes and analysis.

The analysis permits evaluation of geographic trends in genetic characteristics of populations. The correlations of the dependent variables with elevation, latitude, and longitude range from −0.32 (longitude and NALL) to 0.28 (elevation and EAP^c). Although some of these correlations are significant, no obvious geographic trends exist for genetic variation within populations. For example, strong clinal patterns of variation at loci should result in consistently significant correlations between latitude and/or longitude and the frequency of alleles. The only significant trend is that values of *H*, POLY99, and NALL decrease with an increase in elevation.

Results of a multiple regression analysis are also shown in Table 8. Sample size is a significant predictor of POLY99, NALL, and EAP^c, elevation is a significant predictor of POLY99, latitude predicts NALL, and longitude predicts POLY99, NALL, and LGG^c. Because only 1 of 21 regression coefficients is significant for allele frequencies versus elevation, latitude, or longitude, I conclude that allelic frequencies exhibit no elevational or geographic trends, corroborating the correlation and phenogram analyses discussed above.

Analysis of Levels of Gene Flow

Representative plots of $p(i)$ vs i/d illustrate high, medium, and low levels of gene flow (Fig. 5). The data for Fox Sparrows suggest high levels of gene flow, evident by comparing the plot for the Fox Sparrow (Fig. 6) with that for *Drosophila pseudoobscura,* a species with presumably high levels of gene flow. These results parallel the low value of F_{ST}. *Plethodon dorsalis* (Fig. 5), with a highly subdivided population structure and a high F_{ST} (Larson and Highton 1978), has many alleles at high frequency which occur only in one or a few populations. Alternatively, a

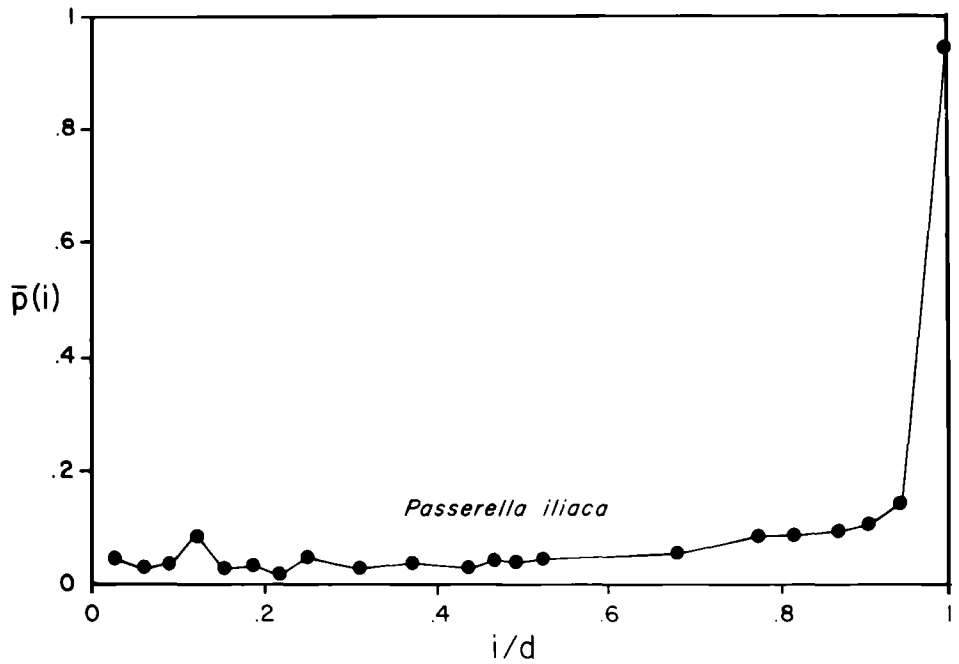

FIGURE 6. Analysis of gene flow in the Fox Sparrow using Slatkin's method of estimating level of gene flow from allelic frequency data (Table 5). Compare plot for the Fox Sparrow to that for *Drosophila pseudoobscura* (Fig. 5).

species with high gene flow would have little population subdivision, a low F_{ST}, and show a plot of $p(i)$ vs i/d like that of *D. pseudoobscura* and *P. iliaca.*

TEST OF THE NEUTRALITY HYPOTHESIS FOR ALLELIC POLYMORPHISMS WITHIN POPULATIONS

Results of the test of the Infinite alleles-Constant mutation rate (IC) model are shown in Fig. 7. The general expectation, and the results for the Fox Sparrow, are that most loci will be monomorphic, some slightly to moderately polymorphic, and a few highly polymorphic. In both the PINO and SAGE samples, the observed number of rare alleles, relative to alleles at intermediate frequencies, exceeds neutral expectations. However, neither PINO nor SAGE differed significantly from neutral distributions, either in the distribution of alleles by frequency class or in inter-locus heterozygosity; $D_{max} = 0.149$ for PINO, 0.049 for SAGE ($P > 0.05$ for both). Therefore, alleles segregating at polymorphic loci are selectively neutral on average. These results contrast with those obtained for the LASS sample, in which an excess of rare alleles (those with a frequency ≤ 0.05) resulted in a significant departure from the expected distribution of alleles by frequency class (Barrowclough et al. 1985).

MORPHOLOGICAL VARIATION

UNIVARIATE CHARACTER ANALYSES

Cube-root of mass of males.—A pronounced clinal pattern (Fig. 8) exists along a basically north–south axis, with the heaviest birds in the North Coast Range

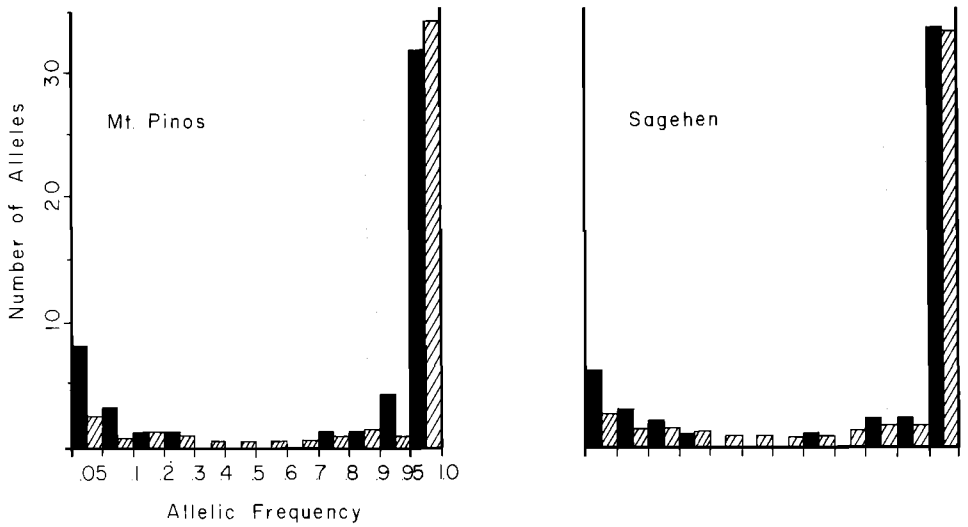

FIGURE 7. Expected (hatched) and observed (solid) distributions of alleles by frequency class in two samples of the Fox Sparrow. The expected distributions are obtained from the Infinite allele–Constant mutation rate model as described by Chakraborty et al. (1980).

and southern California, and the lightest ones in the Great Basin (STEN, MART, RUBY) and Cascades (e.g., ODEL, SPEN, SHAS). Birds from the White Mountains (WHIT), although generally smaller in morphometric characters (see below), are not as light (in mass) on average as birds from more easterly parts of the Great Basin. Although mass fluctuates daily, I presume that the sample means, transformed to cube-root of mass to effect linearity, reflect size (see also James 1970; Mosimann and James 1979). Because many females were in laying condition and consequently heavier, they were not used in the analysis of mass.

Skin characters.—ANOVA shows that each character is significantly heterogeneous across the 31 localities for both sexes (Table 9). For most characters, a large among-locality component of variance is evident, although not all characters exhibit the same degree of among-locality variation (compare among-sample sums of squares). Also, given a significant F-value in an ANOVA, one cannot assume that each sample differs statistically from all others. Inclusion of the small (Great Basin) and large (North Coast Range and southern California) specimens results in consistently significant ANOVAs for characters. If these small and large extremes were excluded, geographic heterogeneity would be less pronounced, and some regions of phenotypic uniformity would be evident, for at least certain characters; clinal variation would still be evident in most traits.

Correlation coefficients among the characters are given in Table 10. In general, the five bill measurements are highly intercorrelated, with coefficients ranging from 0.71 to 0.92 for males and 0.68 to 0.91 for females. The correlation coefficients among WINGL, TARSL, and HINTL, and their correlations with the bill measurements, are relatively lowest. Nonetheless, all correlation coefficients are positive and significant, suggesting some redundancy of information.

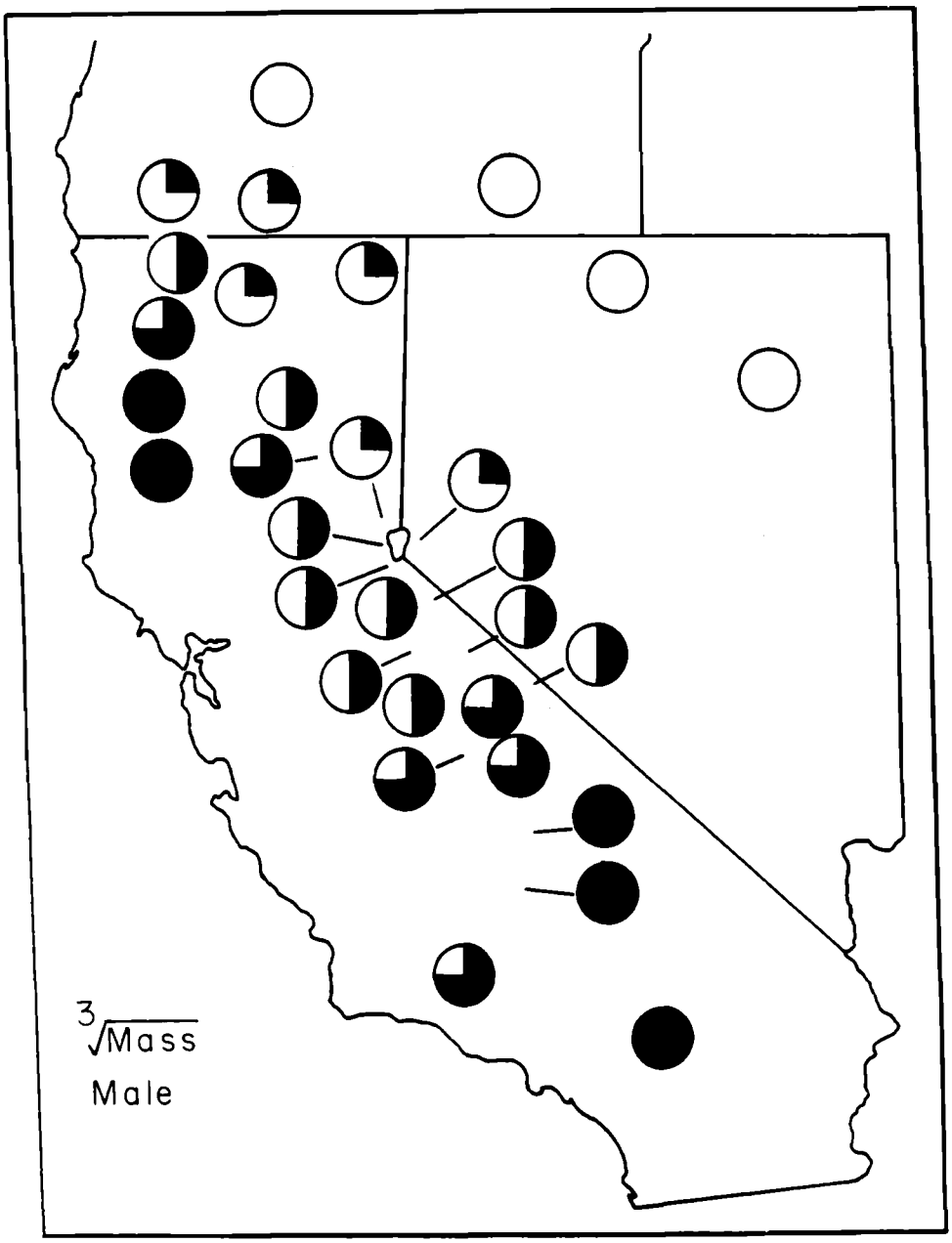

FIGURE 8. Variation in cube-root of mass for males. Circles are placed in approximate locations of sample sites (Fig. 2 and Appendix I). Range of variation in sample means was divided into five equal parts. Open circles represent the lowest one-fifth of the range of means, completely blackened circles the largest one-fifth. Intermediate values are denoted by progressively blackening-in fourths of the circle.

TABLE 9

ANOVA FOR SKIN CHARACTERS FOR MALES AND FEMALES

Character	Males						Females					
	d.f.	SS	MS	*F*	CV[1]	CV[2]	d.f.	SS	MS	*F*	CV[1]	CV[2]
WINGL												
Between groups	30	571.7	19.1	3.29**	.035	.032	27	247.9	9.2	2.03*	.032	.030
Within groups	394	2,286.0	5.8				118	532.5	4.5			
TARSL												
Between groups	30	79.7	2.6	5.99**	.034	.030	28	30.6	1.1	2.08*	.035	.032
Within groups	404	1,792.6	0.4				124	65.2	0.5			
HINTL												
Between groups	30	129.4	4.3	6.61**	.054	.046	28	74.6	2.7	1.93*	.056	.048
Within groups	406	265.1	0.7				126	173.9	1.4			
BILL-1												
Between groups	30	102.1	3.4	13.77**	.067	.049	28	29.7	1.1	4.20**	.065	.051
Within groups	403	99.5	0.25				122	30.9	0.25			
BILLW												
Between groups	30	408.4	13.6	89.25**	.097	.037	28	114.9	4.1	28.44**	.090	.037
Within groups	404	61.6	0.15				126	18.2	0.14			
BILLD-1												
Between groups	30	333.4	11.1	66.00**	.103	.044	28	106.7	3.8	25.40**	.101	.043
Within groups	405	68.2	.017				125	18.8	0.15			
BILL-2												
Between groups	30	134.1	4.5	23.28**	.069	.043	28	41.3	1.5	6.74**	.068	.047
Within groups	401	77.0	0.2				124	26.9	0.22			
BILLD-2												
Between groups	30	432.3	14.4	21.21**	.091	.039	28	112.1	4.0	18.20**	.084	.042
Within groups	407	276.5	0.68				126	27.7	0.22			

[1] Coefficient of variation (CV) for all individuals.
[2] Average CV per population.
** $P < 0.001$, * $P < 0.01$.

TABLE 10

CORRELATION COEFFICIENTS BETWEEN SKIN CHARACTERS. MALES BELOW DIAGONAL, FEMALES ABOVE. ALL VALUES ARE STATISTICALLY SIGNIFICANT ($P < 0.05$). ABBREVIATIONS FOR CHARACTERS DEFINED ON P. 12

	1	2	3	4	5	6	7	8	r-size[1,2]
1. WINGL	—	0.24	0.23	0.19	0.25	0.12	0.20	0.19	0.791
2. TARSL	0.28	—	0.22	0.38	0.45	0.44	0.41	0.45	0.849
3. HINTL	0.22	0.25	—	0.11	0.16	0.11	0.14	017	0.488
4. BILL-1	0.32	0.45	0.24	—	0.69	0.68	0.87	0.69	0.898
5. BILLW	0.39	0.51	0.26	0.72	—	0.89	0.75	0.91	0.925
6. BILLD-1	0.31	0.47	0.27	0.71	0.88	—	0.78	0.89	0.928
7. BILL-2	0.35	0.48	0.26	0.87	0.79	0.77	—	0.75	0.879
8. BILLD-2	0.30	0.46	0.24	0.71	0.92	0.89	0.78	—	0.915

[1] Size = cube-root of mass vs character means at each locality for males only.
[2] All values significant ($P < 0.001$) except HINTL ($P < 0.01$).

In Figures 9–11, I show plots of WINGL, TARSL, HINTL, BILLW, and ORETL for males, and WINGL for females, to illustrate the range of geographic patterns for characters. Females and males show similar patterns, an exception being WINGL and HINTL (not shown). Geographic variation of all bill characters for both sexes is similar to BILLW for males (Fig. 10). The degree of bill size variation (Fig. 3) exceeds differences between many avian species and genera. The Great Basin samples (STEN, RUBY, MART, WHIT) have relatively short and narrow bills of lesser depth, whereas bills are longer, wider, and deeper in the southern Sierra Nevada and North Coast Range samples (BERN, PINO, REDM, DOME, LOOK, SHAV, BLAC, YOLL); in the remainder of the samples there is a clinal increase in these dimensions from north to south, although allometry is apparent (see below).

Plots of TARSL, WINGL (for males), and HINTL differ from BILLW. TARSL varies clinally north to south, exceptions being BLAC, YOLL, MONO, and WHIT. WINGL for both males and females exhibits a more complex pattern, because there is not a pronounced cline. For example, samples of males from the central Sierra Nevada (e.g., TAHE, WALK) are small relative to adjacent samples, and are more similar to samples from ODEL, SPEN, PYRA, MART, and RUBY. For females, WINGL is largest at WHIT, BERN, and REDM, all samples from the southern part of the study area. However, short wings occur at dispersed sites, such as ODEL, SAWY, RUBY, and MTOM, sites with no obvious common habitat or elevational aspects (Table 1). Thus, patterns of variation of WINGL for females are not organized about any obvious geographic gradient. HINTL differs from previous characters because YOLL and BLAC are relatively small, although in the remaining samples there is a north-south cline similar to that found in BILLW (but values at SHAV, MTOM, and JACK interrupt the cline).

Because of worn central rectrices, the outer tail feather, which is shorter and usually less worn, was measured. Wear in all tail feathers of females prevented their use. No obvious geographic pattern was observed for ORETL (Fig. 11) except for the small values in the east-central Sierra Nevada and eastern Nevada. Sites with the longest outer rectrices, SPEN, BUCK, and BERN, are widely separated and share no apparent common habitat or elevational features.

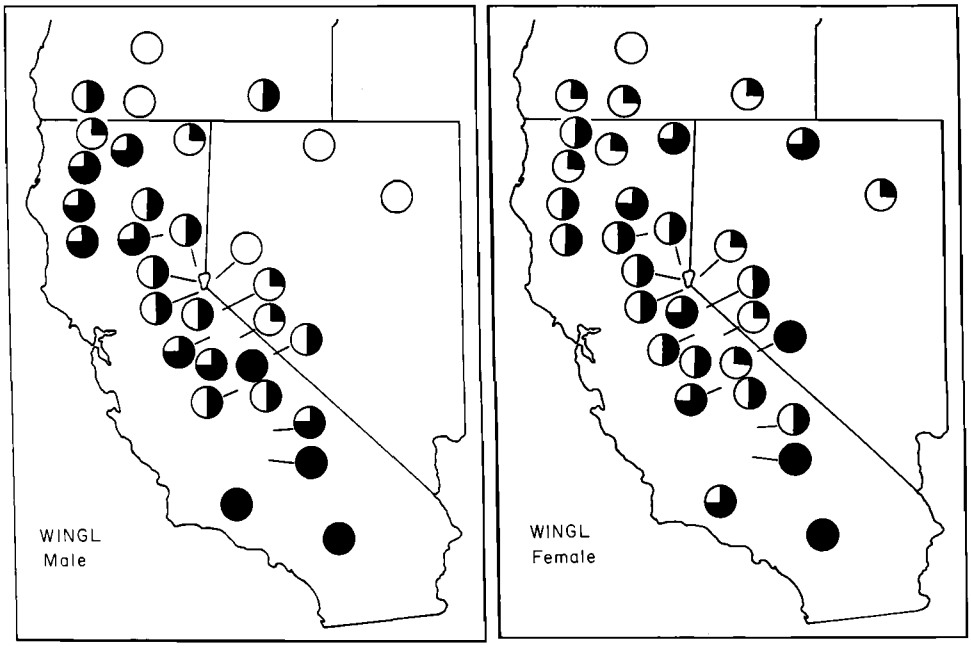

FIGURE 9. Pie diagrams depicting general pattern of variation in wing length for males and females. The circles are shaded according to the scheme outlined for cube-root of mass in Figure 8.

The length of the central rectrix is an important subspecific character for *brevicauda* (Swarth 1920). However, ORETL does not exhibit this feature—BLAC and YOLL have intermediate values. Thus, because *brevicauda* has relatively short central rectrices (Swarth 1920), and average length outer rectrices (Fig. 11), tail shape in *brevicauda* is not only shorter but also more squared-off than in other subspecies.

The coefficients of variation (CV) for skin characters (Table 9) illustrate variability at two levels. Considering all male specimens, BILLD-1 and BILLW have CVs of approximately 10%, whereas CVs for WINGL and TARSL are <4%. Relative levels of variability are apparent from inspection of the Sums of Squares (SS) from ANOVA (Table 9). BILLW and BILLD-1 have higher between-groups than within-groups SS than do WINGL and TARSL. Obviously, CVs summed over all individuals are biased because of different sample sizes per locality (and geographic variation). This bias is consistent for all characters and provides a relative measure of inter-character levels of geographic variability; these values should not be compared with other studies, however. The average CVs per population sample (Table 9), equivalent to CVs normally reported, illustrate that within populations characters show similar levels of variation, BILL-1 being the most variable (CV = 4.9%) and TARSL the least (CV = 3.0%).

For females, the results are similar to males because some characters exhibit high CVs when calculated over all individuals (e.g., BILLW and BILLD-1), whereas average CVs within populations are lower. Comparison of between- and within-groups SS shows results parallel to those obtained for males—characters with the

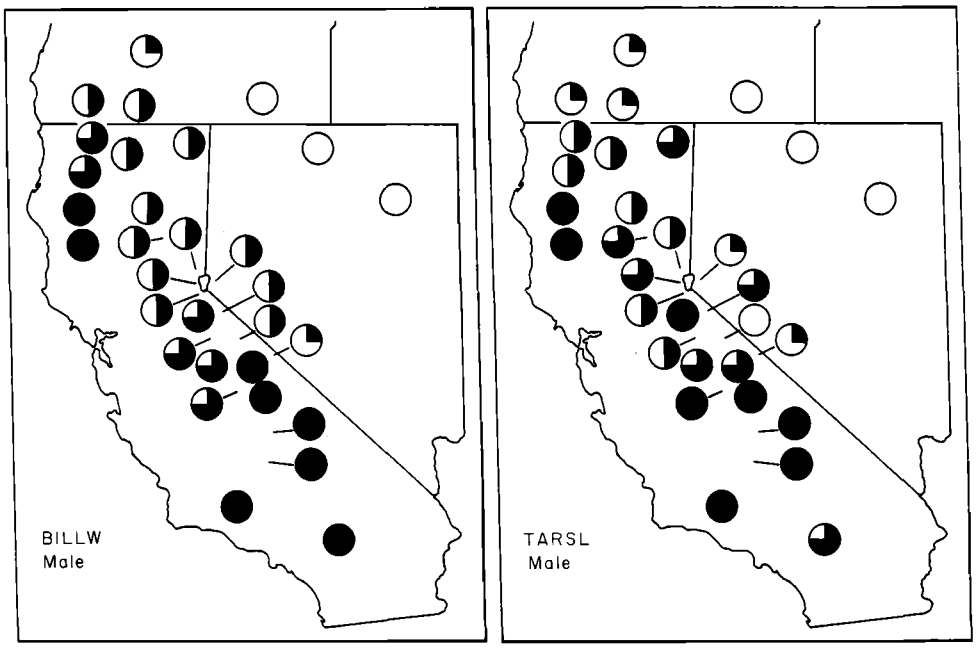

FIGURE 10. Pie diagrams depicting general pattern of variation in bill width and tarsus length for males. See Fig. 8.

highest overall CVs have the highest proportion of the variance distributed among localities (as expected). Levels of character variation, both over all individuals and within populations, are very similar in males and females. Within-population values are typical of those reported for other avian species (see Johnson 1980).

Skeletal characters.—For each character, ANOVA reveals significant geographic heterogeneity for both sexes (Table 11). The correlation coefficients between character pairs are positive and statistically significant for both sexes (Table 12). Most correlation coefficients fall in the range of 0.30 to 0.70, lower than those among bill characters. In general the geographic patterns of character variation are similar for males and females, and to those observed for skin characters; to save space only some are illustrated (Figs. 12–14). SKULW shows a north to south increase in size, with the northernmost Cascades and Great Basin samples having narrow skulls and the North Coast Range and southern California samples having wide ones. TIBOL and SYNXW show a pattern similar to SKULW, although some samples from the center of the study area are relatively small, effecting an imperfect cline aligned northeast to southwest. Nonetheless, TIBOL and SYNXW are largest in the North Coast Range and in southern California. STERL, PSYNL, and CORAL exhibit more complex patterns, but tend to be smaller (especially STERL) in the central Sierra Nevada and Great Basin, and large in the North Coast Ranges and southern Sierra Nevada (except CORAL, and PSYNL for Mt. Pinos). Although characters covary in part, as evidenced by the significant positive correlation coefficients, no simple consistent pattern emerges.

Levels of character variability are also shown in Table 11. Considering all

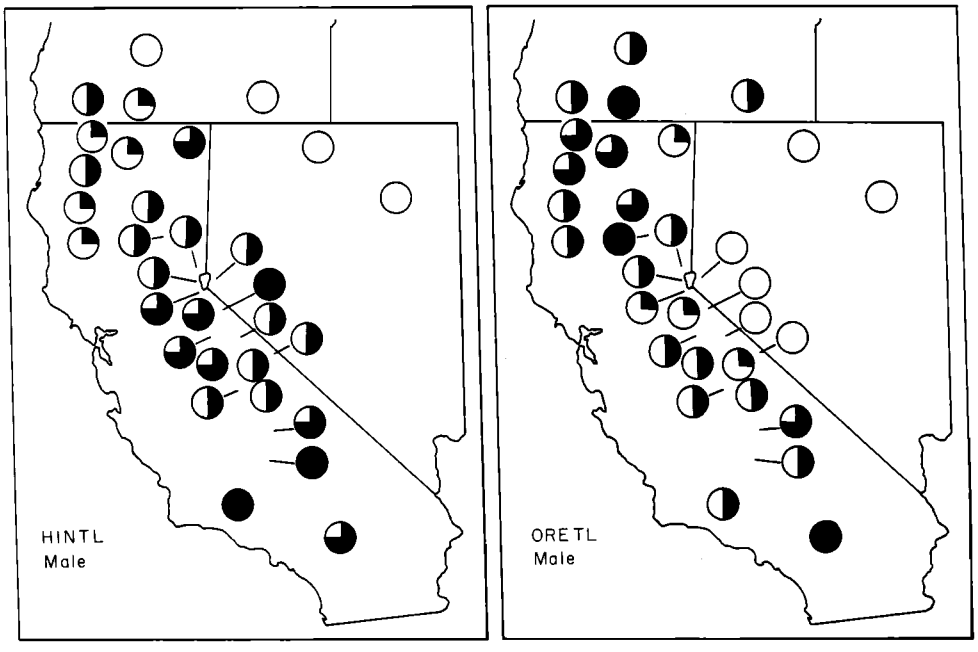

FIGURE 11. Pie diagrams depicting general pattern of variation in length of hind toe (HINTL) and outer rectrix (ORETL). See Fig. 8.

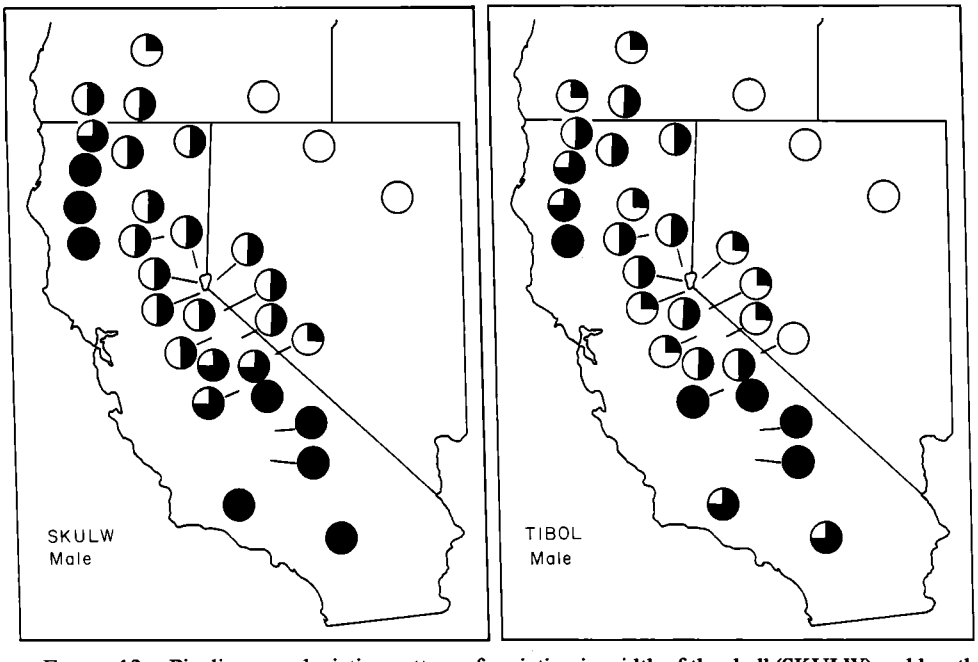

FIGURE 12. Pie diagrams depicting pattern of variation in width of the skull (SKULW) and length of the tibiotarsus (TIBOL). See Fig. 8.

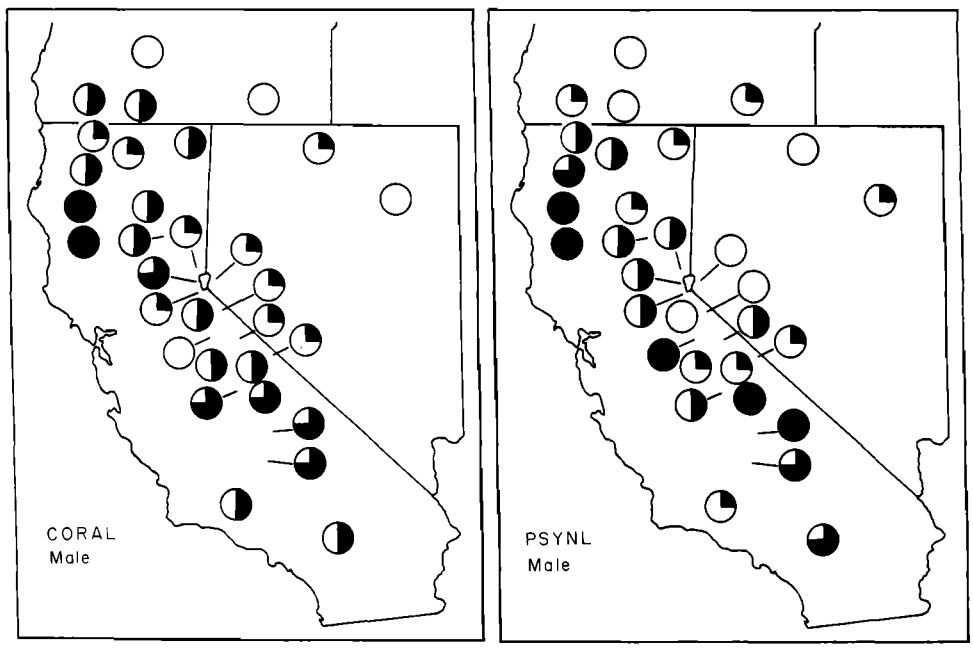

FIGURE 13. Pie diagrams showing general pattern of geographic variation in the lengths of the coracoid (CORAL) and posterior synsacrum (PSYNL). See Fig. 8.

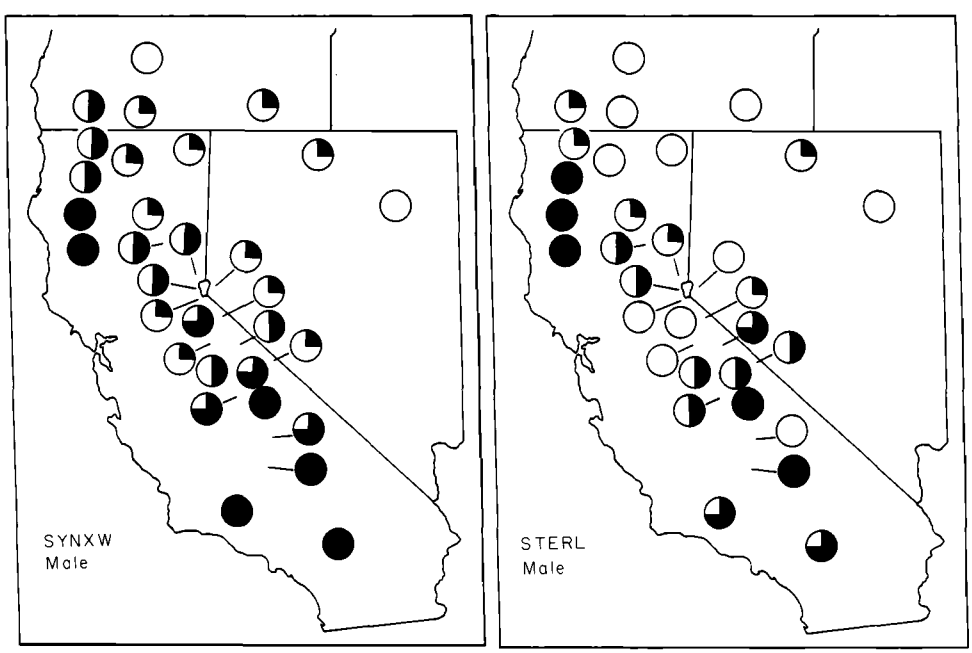

FIGURE 14. Pie diagrams depicting pattern of variation in the maximum width of the synsacrum (SYNXW) and length of the sternum (STERL). See Fig. 8.

TABLE 11

ANOVA FOR SKELETAL CHARACTERS FOR MALES AND FEMALES. CHARACTER ABBREVIATIONS DEFINED ON P. 13

	Males						Females					
Character	d.f.	SS	MS	*F*	CV[1]	CV[2]	d.f.	SS	MS	*F*	CV[1]	CV[2]
SKULW												
Between groups	30	172.7	5.76	27.7**	0.041	0.023	29	81.2	2.80	3.5**	0.040	0.026
Within groups	361	75.1	0.21				125	100.6	0.80			
SKULL												
Between groups	30	113.3	3.77	8.4**	0.067	0.042	29	45.8	1.58	7.4**	0.065	0.044
Within groups	377	170.2	0.45				127	27.3	0.21			
CORAL												
Between groups	29	55.8	1.92	7.1**	0.034	0.027	29	31.5	1.09	4.7**	0.035	0.027
Within groups	370	100.1	0.27				130	30.2	0.23			
SCPEW												
Between groups	30	4.6	0.15	4.2**	0.051	0.044	29	2.4	0.08	2.5**	0.051	0.046
Within groups	382	14.0	0.04				132	4.4	0.03			
STERL												
Between groups	30	46.1	1.54	3.0**	0.034	0.031	28	24.4	0.87	2.1**	0.033	0.030
Within groups	372	191.1	0.51				121	50.8	0.42			
PSYNL												
Between groups	29	8.8	0.30	2.2**	0.059	0.056	29	6.6	0.23	2.1**	0.056	0.051
Within groups	376	51.7	0.14				128	13.7	0.11			
SYNXW												
Between groups	30	30.5	1.02	6.5**	0.034	0.027	28	14.6	0.52	3.6**	0.033	0.027
Within groups	371	57.8	0.16				129	18.5	0.14			
FEPEW												
Between groups	30	3.8	0.13	7.9**	0.042	0.032	28	1.5	0.05	3.7**	0.040	0.033
Within groups	383	6.1	0.02				132	1.9	0.01			
FEDEW												
Between groups	30	3.1	0.10	3.2**	0.051	0.041	28	1.3	0.05	3.0**	0.038	0.033
Within groups	374	12.2	0.04				129	2.0	0.02			

TABLE 11
CONTINUED

Character	Males						Females					
	d.f.	SS	MS	*F*	CV[1]	CV[2]	d.f.	SS	MS	*F*	CV[1]	CV[2]
FEMRL												
Between groups	30	66.5	2.15	9.8**	0.029	0.022	29	25.8	0.89	3.5**	0.030	0.024
Within groups	368	80.8	0.22				121	30.9	0.26			
TIBOL												
Between groups	30	158.0	5.27	8.1**	0.029	0.023	28	53.9	1.93	2.2	0.030	0.026
Within groups	352	227.7	0.65				122	105.1	0.86			
HTROL												
Between groups	30	10.7	0.36	8.1**	0.038	0.030	28	3.0	0.11	2.0**	0.038	0.035
Within groups	381	16.9	0.04				131	7.0	0.05			
HUMRL												
Between groups	30	49.3	1.64	2.4	0.028	0.020	28	22.8	0.81	3.7**	0.029	0.024
Within groups	369	257.7	0.70				127	27.9	0.22			
ULNAL												
Between groups	30	68.5	2.28	9.2**	0.028	0.022	28	27.2	0.97	2.9**	0.030	0.026
Within groups	363	90.5	0.25				125	41.2	0.33			
ULPEW												
Between groups	30	1.5	0.05	10.4**	0.032	0.024	25	0.5	0.02	3.3**	0.032	0.028
Within groups	367	1.8	.005				131	0.8	.006			

[1] Coefficient of variation (CV) for all individuals.
[2] Average CV per sample.
* $P < 0.05$; ** $P < 0.01$.

TABLE 12

CORRELATION COEFFICIENTS BETWEEN SKELETAL CHARACTERS; FEMALES ABOVE THE DIAGONAL, MALES BELOW. ALL VALUES ARE STATISTICALLY SIGNIFICANT ($P < 0.05$). ABBREVIATIONS FOR CHARACTERS DEFINED IN TEXT ON P. 13

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	r-size[1,2]
1. SKULW	—	0.74	0.66	0.51	0.42	0.36	0.62	0.54	0.63	0.68	0.59	0.48	0.68	0.62	0.62	0.939
2. SKULL	0.78	—	0.60	0.45	0.36	0.34	0.51	0.52	0.53	0.60	0.54	0.48	0.62	0.56	0.52	0.899
3. CORAL	0.51	0.43	—	0.38	0.53	0.43	0.51	0.46	0.43	0.70	0.65	0.57	0.76	0.73	0.56	0.683
4. SCPEW	0.43	0.36	0.42	—	0.43	0.25	0.49	0.52	0.55	0.44	0.36	0.46	0.48	0.51	0.54	0.688
5. STERL	0.46	0.38	0.48	0.40	—	0.27	0.42	0.43	0.42	0.44	0.42	0.46	0.55	0.56	0.50	0.746
6. PSYNL	0.29	0.24	0.32	0.18	0.30	—	0.34	0.24	0.33	0.42	0.30	0.29	0.42	0.40	0.36	0.661
7. SYNXW	0.63	0.54	0.52	0.41	0.49	0.31	—	0.62	0.65	0.52	0.45	0.46	0.55	0.56	0.61	0.856
8. FEPEW	0.59	0.55	0.43	0.46	0.42	0.28	0.59	—	0.66	0.53	0.49	0.46	0.53	0.54	0.62	0.830
9. FEDEW	0.45	0.38	0.34	0.37	0.32	0.18	0.39	0.48	—	0.55	0.45	0.52	0.54	0.58	0.68	0.823
10. FEMRL	0.65	0.59	0.61	0.39	0.46	0.36	0.57	0.56	0.37	—	0.76	0.56	0.84	0.80	0.51	0.868
11. TIBOL	0.60	0.56	0.59	0.35	0.50	0.36	0.55	0.47	0.32	0.76	—	0.36	0.75	0.77	0.54	0.833
12. HTROL	0.57	0.54	0.49	0.39	0.47	0.34	0.54	0.52	0.41	0.57	0.50	—	0.63	0.63	0.57	0.883
13. HUMRL	0.65	0.59	0.68	0.44	0.52	0.35	0.59	0.57	0.37	0.85	0.72	0.64	—	0.89	0.61	0.903
14. ULNAL	0.64	0.58	0.64	0.46	0.54	0.36	0.61	0.56	0.40	0.80	0.76	0.60	0.87	—	0.66	0.926
15. ULPEW	0.66	0.59	0.51	0.51	0.48	0.26	0.60	0.62	0.50	0.58	0.56	0.59	0.63	0.67	—	0.891

[1] Size = cube-root of mass vs character means at each locality for males only.
[2] All values significant ($P < 0.01$).

individuals, CVs range from 2.8% (HUMRL) to 6.7% (SKULL) for males and 2.9% (HUMRL) to 6.5% (SKULL) for females, demonstrating lower levels of geographic variation than the bill characters (about 10%; see comment above regarding these "overall" CV values). Comparison of between- and within-groups SS shows that SKULW for males, and SKULL, CORAL, and SKULW for females have the highest proportion of variance distributed among localities, although all characters are significantly heterogeneous.

Average CVs within samples range from 2.0% (HUMRL) to 5.6% (PSYNL) for males and 2.4% (HUMRL and FEMRL) to 5.1% (PSYNL) for females. The sexes show very similar levels of character variation both within and among samples. In both sexes, PSYNL is nearly as variable on average within samples as it is considering all individuals, demonstrating relatively weak geographic differentiation. This general pattern was obtained for several other characters, e.g., STERL for both sexes, and TIBOL, HTROL, ULNAL, and ULPEW for females only. The CVs for skeletal characters fall in the range of those reported for morphological characteristics of other birds (Johnson 1980).

Character variation as a function of size.—To the degree that cube-root of mass depicts size, patterns of geographic variation, especially in BILLW and SKULW, appear to have a substantial size component (cf. Figs. 8, 10, 12). Significant correlation coefficients (Tables 10, 12) computed between each character mean and the mean cube-root of mass at each site, show that each character possesses a size-related component of geographic variation. However, size is not a uniform component of geographic character variation. For example, the r between size and BILLD-1, 0.928, is considerably higher than that for size and HINTL, 0.488. Similarly for skeletal characters, SKULW shows the highest r with size and PSYNL the least, 0.939 and 0.661, respectively. In general the r values tend to be lower for skeletal characters than for skin characters. Nonetheless, "size" seems to explain a large proportion of the variance in both study skin and skeletal characters, although clearly variation remains, not accounted for by size.

Geographic variation in bill characters includes a size component, evident by comparison of BILLW and cube-root of mass (Figs. 8, 10). In Figure 15, a plot of mean values per site for bill width, length, and depth vs the cube-root of mass ("size") shows that the relationship of bill characters to size is not isometric. For example, at small size, primarily in samples from the Great Basin, bill length exceeds both width and depth. However, as size increases, bill width becomes absolutely greater than bill length and depth. Hence, as size increases, bill shape changes (relatively) from long and narrow to wider and deeper, or more massive. That is, bill length/width is <1.0 at small size, and >1.0 at larger size.

Values of cube-root of mass range from 3.06 (MART) to 3.33 (BLAC), the difference (0.27) representing 8.1% of the largest value. However, bill width ranges from 8.1 to 12.1 mm, the difference being 33.1% of the largest value. Therefore, as size increases, bill width increases at a greater "rate." The other characters in the skin data set do not increase at the same rate as size.

With 15 skeletal characters, many ratios of characters are possible. Five general body regions were measured: skull, pectoral, synsacrum or pelvic, wing, and hind limb. Plots of locality means for one character from each body region vs cube-root of mass indicate shape variation (Fig. 16). For example, at small mass, STERL/ULNAL exceeds unity, whereas at larger body masses the ratio is <1.0.

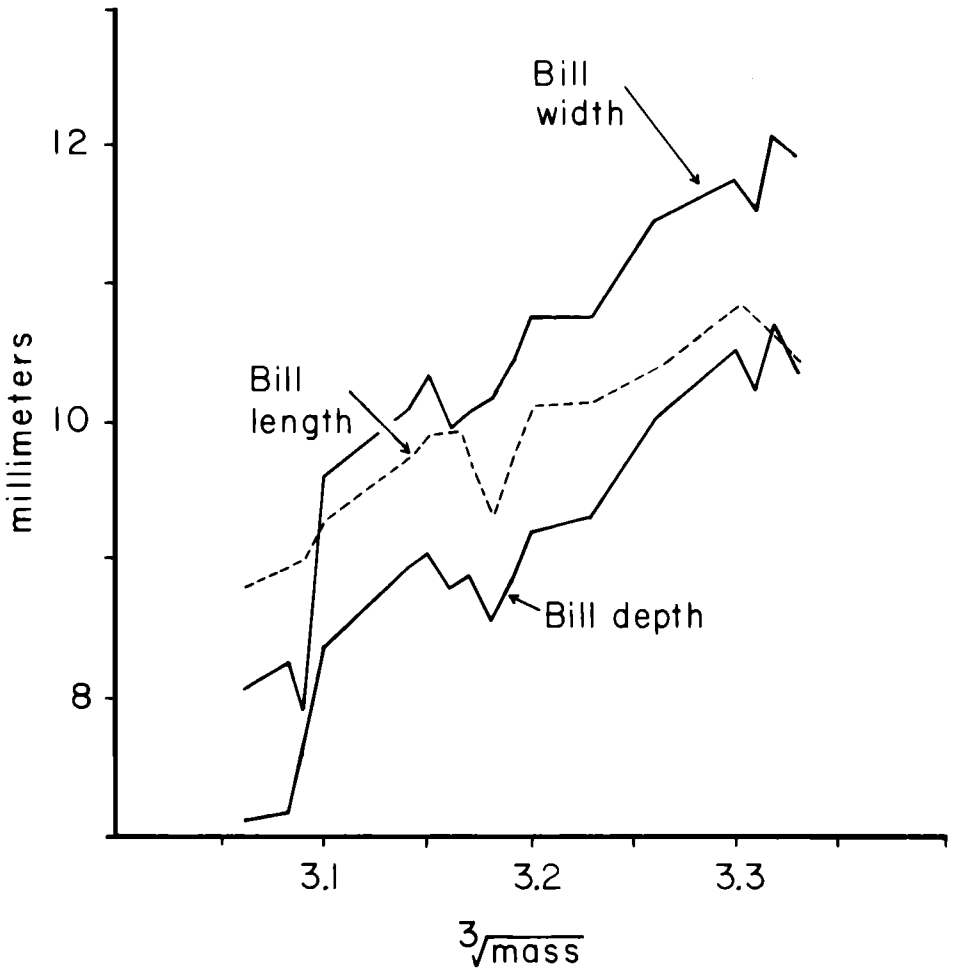

FIGURE 15. Plot of locality means for bill width, length, and depth, against locality means for cube-root of mass. Samples are ranked according to cube-root of mass, irrespective of geographic location. This plot illustrates changes in bill size and shape as a function of "size."

The SKULW/SYNXW ratio also varies with body mass, especially at low values of mass. Similar contrasts of the other characters reveal differences in shape. Of the five skeletal characters plotted, the differences between the largest and smallest values range from 5.0% of the largest value for sternum length to 13.1% for skull width, similar to the range of variation in cube-root of mass. Thus, differences in the covariation of skeletal characters and size yield geographic variation in shape, although of a lesser degree than that observed for bill characters.

Although size is a "common denominator" in observed patterns of geographic differentiation, there is non-size or shape-related variation among samples of Fox Sparrows. However, geographic patterns in shape are not deducible from this presentation because localities were ranked by mass and not geographic occurrence. Clearly, conclusions about size hinge on the degree to which mass reflects

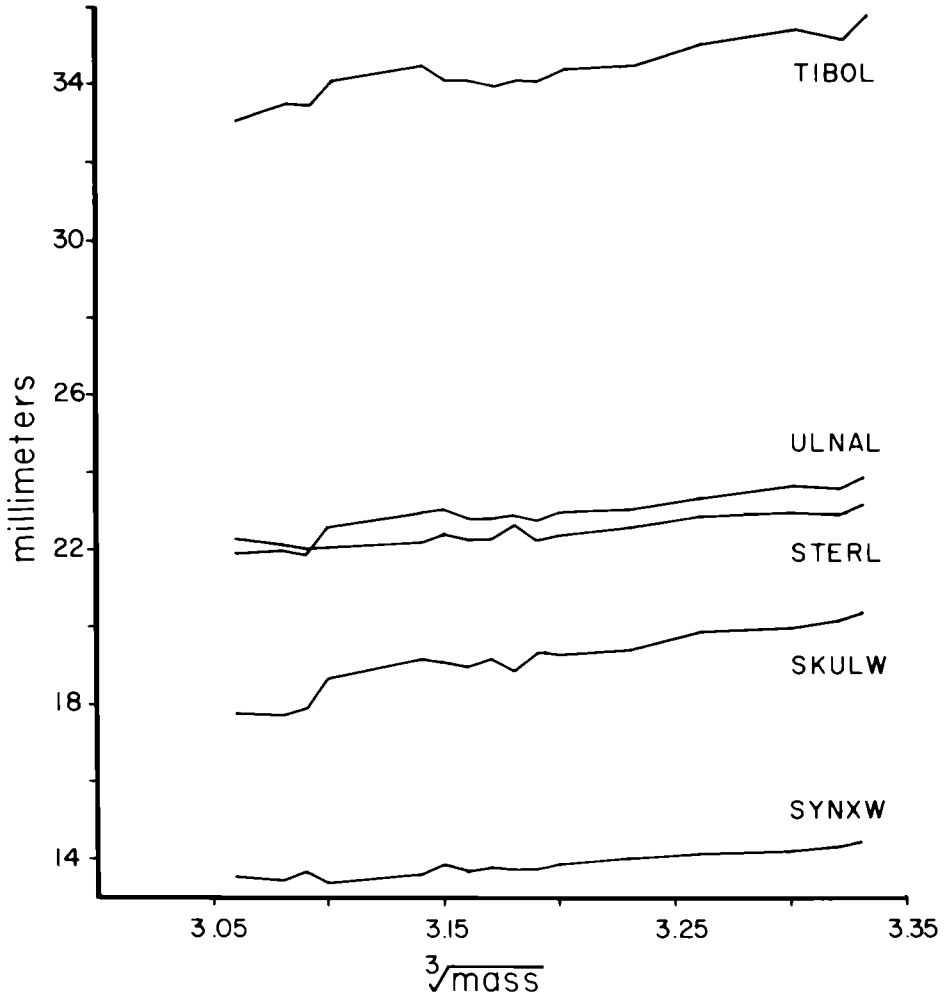

FIGURE 16. Plot of locality means for tibiotarsus length (TIBOL), ulna length (ULNAL), sternum length (STERL), skull width (SKULW), and synsacrum maximum width (SYNXW) against locality means of cube-root of mass.

size, the latter of which is an amalgam of variation. I explore below the patterns of shape variation using cluster analyses.

MULTIVARIATE ANALYSIS OF VARIANCE

For skin characters, MANOVA (BMDP4V; Dixon 1979) for both males and females produced significant values ($F = 6.53$ and 2.91, respectively, $P < 0.01$), indicating significant geographic heterogeneity among groups. Similarly, significant geographic heterogeneity for both sexes was revealed for skeletal characters ($F = 2.80$ and 1.50, $P < 0.01$).

Given the significant F-values from MANOVA, it is appropriate to use other multivariate and quantitative techniques to explore the pattern of variation among

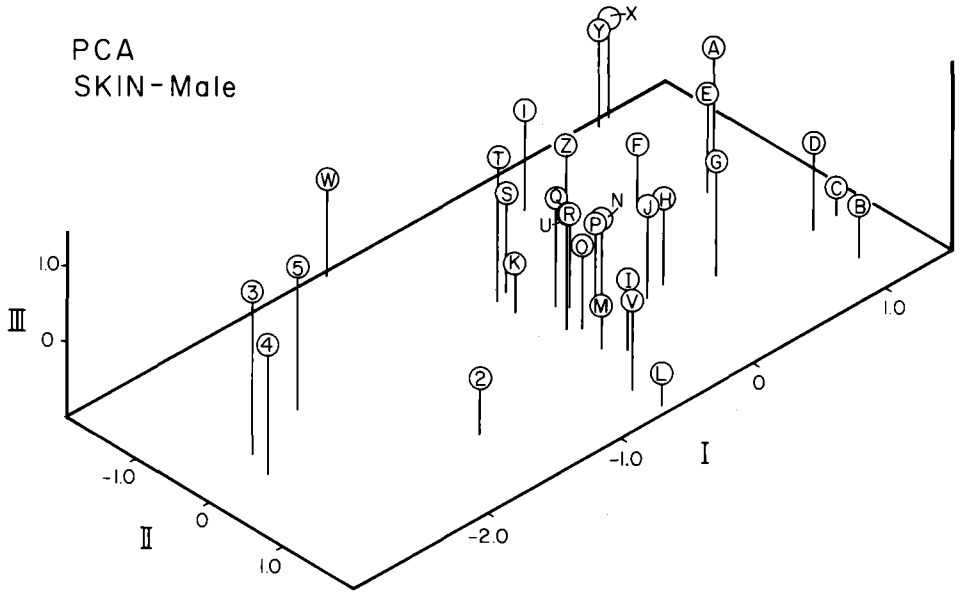

FIGURE 17. Three-dimensional model depicting results of principal components (PC) analysis of skin characters for males. The position of samples represents locality mean scores on the first three PCs. Samples are identified by letter in Table 1. The length of each vertical line denotes the average score of the sample on PC III.

sites. Multivariate methods evaluate all characters simultaneously, and allow discovery of the dominant theme of variation in morphology. To this end, cluster and principal components analysis were used. Discriminant function analysis produced results that paralleled the PCA and are not discussed here.

PRINCIPAL COMPONENTS ANALYSIS

Skin characters.—Principal components analysis of skin characters revealed (by inspection) similar patterns for males and females (Figs. 17 and 18, Table 13). Principal component I (PC I) accounts for 58.8% of the variance for males and 55.3% for females; the first three PCs account for 77.2% of the variance for males and 76.2% for females. The bill characters are highly correlated with PC I for both sexes, whereas WINGL, TARSL, and HINTL exhibited lower correlations. Both males and females have similar character correlations with PC II; HINTL influences variation among samples. On PC III, character correlations are again similar for each sex, but variation in HINTL contributes more to separation of samples on PC III for males than for females.

Three-dimensional models (Figs. 17, 18) of mean scores of samples on PC I–III document the structure of geographic variation. On PC I, locality means are dispersed between MART (4) and REDM (C) for males and MART (4) and PINO (B) for females. On PC I, the Great Basin samples are toward the left and the "large" samples, those from the southern North Coast Range and southern California, are at the opposite end. This plot represents to a large degree the geography of variation in bills, which includes both size and shape components. Along PC

TABLE 13

CHARACTER CORRELATIONS WITH PRINCIPAL COMPONENTS FOR SKIN CHARACTERS. CHARACTER ABBREVIATIONS DEFINED ON P. 12

Character	PC I		PC II		PC III	
	Males	Females	Males	Females	Males	Females
WINGL	0.367	0.179	0.228	0.319	0.021	0.145
TARSL	0.533	0.486	0.172	0.205	0.016	0.006
HINTL	0.303	0.175	0.847	0.971	−0.423	−0.071
BILL-1	0.822	0.802	0.214	0.008	0.475	0.548
BILLW	0.960	0.953	−0.073	−0.008	−0.090	−0.153
BILLD-1	0.955	0.959	−0.078	−0.088	−0.116	−0.129
BILL-2	0.879	0.868	0.173	0.022	0.361	0.426
BILLD-2	0.954	0.951	−0.120	0.013	−0.109	−0.153
Percentage of variance	58.8	55.3	11.2	13.7	7.2	7.2

II, samples are interspersed between the extremes WALK (L) and BLAC (X) for males, and STEN (5) and WARN (V) for females. The samples from the geographic center of the study area, although relatively bunched along PC I, are spread out along PC II. The rather uniform character loadings (except HINTL) do not yield a suite of traits that might constitute an adaptive explanation for the observed dispersion of samples on PC II. Samples are uniformly spread along PC III, between REDM (C) and RUBY (3) for males and BUCK (Q) and STEN (5) for females. Again, no suite of characters was indicated as comprising (potentially) an adaptive complex.

Overall, the plots define three broad groupings: Great Basin samples, southern California plus North Coast Range, and the remainder of the samples. However, overlap occurs between these groups. BLAC and YOLL (*brevicauda*) are separated from other samples, as is WHIT (*canescens*). Among southern California samples, SANB and LOOK are set somewhat apart from DOME, REDM, and PINO. ODEL and WALK are each "outliers" in the morphological space, but neither is especially disjunct geographically. The sample from Spencer Creek (SPEN), although taken in willows, is not particularly similar to samples from riparian habitats in the Great Basin. In these plots distances between samples might not reflect actual distances in multivariate space, because of distortion in this space-reducing procedure. Inspection of minimum spanning trees (Sneath and Sokal 1973) indicated that the reduced, 3-dimensional space is not overly distorted, and that relative morphometric distances among samples are accurately portrayed.

The results of the analysis of females (Fig. 18) differ from those for males in terms of the arrangement of samples within the broad groupings, which are, however, generally equivalent for both sexes. Small sample sizes for females preclude rigorous comparison of variation between the sexes.

To explore further the geographic patterns resulting from the PCA, I performed SS-STP analyses of individuals' scores on each of the first three PC axes. ANOVA of PC I scores for both sexes obtained significant F-values (Table 14), and the SS-STP analysis defined 13 maximally non-significant subsets of samples for males, and 14 for females. The plots of scores on PC I for males (Fig. 19) and

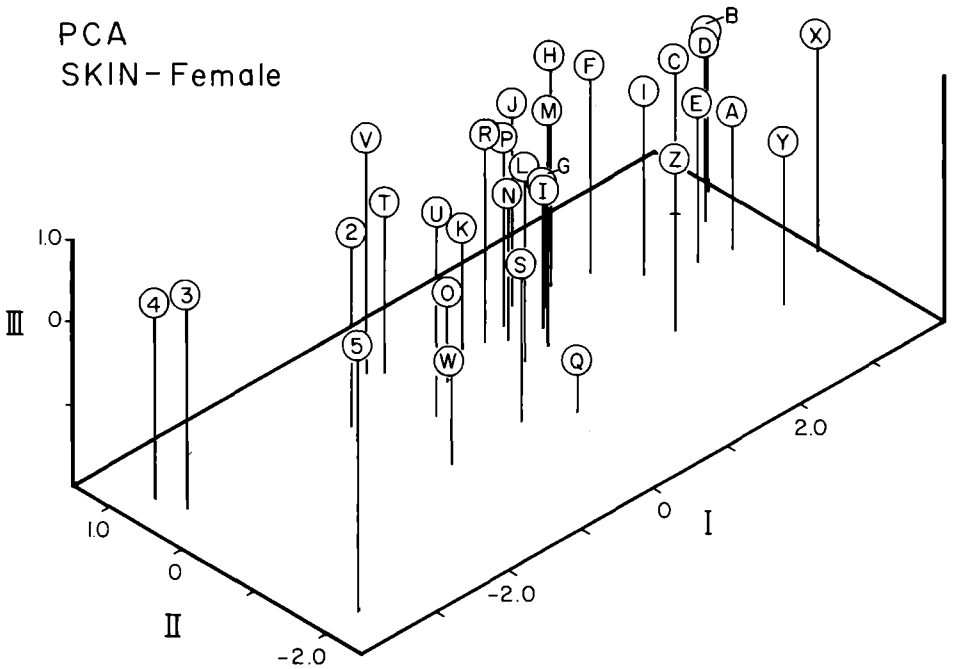

FIGURE 18. Three-dimensional model depicting results of principal components (PC) analysis of skin characters for females. See Fig. 17.

females (Fig. 20) both show a very similar clinal pattern, resembling that obtained for BILLW (Fig. 10). The Great Basin samples (RUBY, MART, STEN, WHIT) and ODEL (Cascades) have low values on PC I, and localities in the southern Sierra Nevada and North Coast Range have large values. The remaining samples show increasingly positive scores on PC I from north to south. Because PC I summarizes a maximum amount of variation in the 8-dimensional space, these plots portray the dominant theme of variation. The pattern exhibited by PC I is also similar to that shown for the cube-root of mass (Fig. 8), a character that was not included in the PCA, and therefore, PC I might indeed be highly influenced by, or be the best measure of, overall size.

ANOVA obtained significant *F*-values for PC II scores for both sexes, and the SS-STP analysis revealed seven maximally non-significant subsets of males (Fig. 21) and five for females. The five subsets of females do not show a geographic pattern and are not illustrated; the pie diagram (Fig. 22) resembles that for males. The SS-STP plot of scores on PC II for males reveals few geographic trends. Great Basin samples from STEN, MART, and RUBY have similar scores on PC II, as do samples from the North Coast Range. Although samples from south of Lake Tahoe tend to have high scores on PC II, exceptions occur, such as BERN, CHER, MONO, and LOOK. Although PC II is markedly influenced by variation in HINTL, the plots of this character (Fig. 11) and PC II (Fig. 21) are not very similar. Thus PC II contains information about characters other than HINTL, such as WINGL and TARSL. If PC II is not influenced by size to the same degree

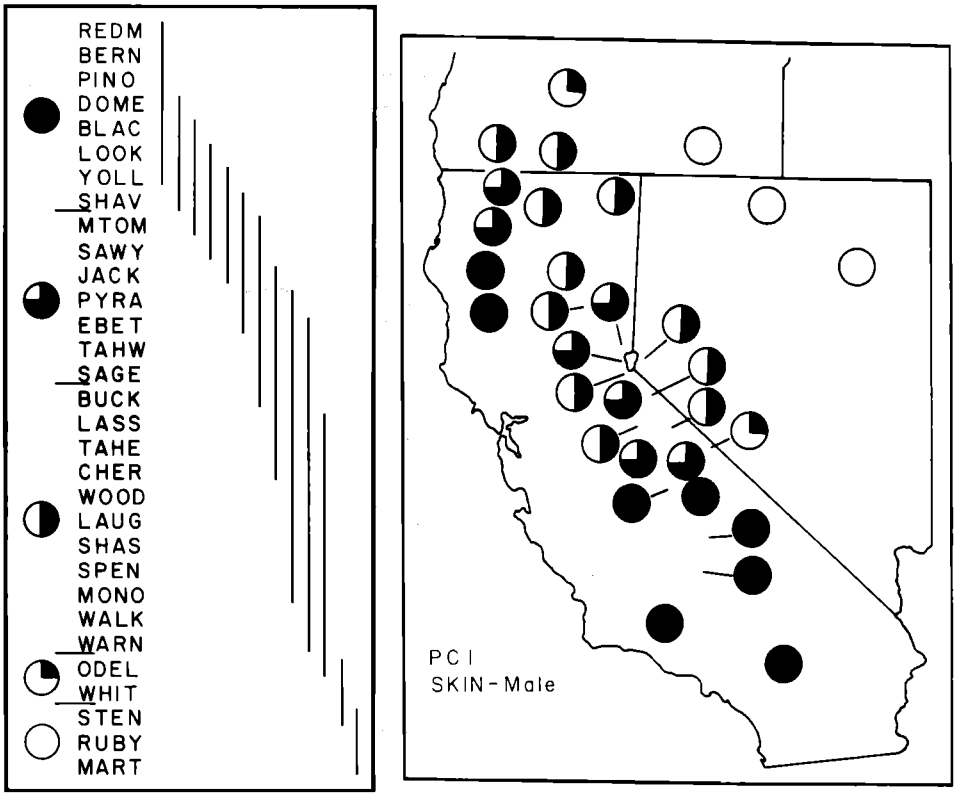

FIGURE 19. SS-STP analysis of individual males' scores on PC I for skin characters. Localities are ranked from high positive scores on PC I (blackened circles) to negative scores (open circles). The range of means was divided into five equal portions, and the pie diagrams coded as in Figure 8. On the left, each vertical line corresponds to a maximally homogeneous subset (see p. 14).

as PC I, the geography of shape has no consistent habitat, elevational, or regional correlates.

ANOVA obtained a significant *F*-value for scores on PC III for males but not for females; three maximally non-significant subsets were defined for males. These three subsets are not geographically informative (and are not shown), as can be seen from the plot of PC III scores (Fig. 22). However, localities with similar scores (half circles) tend to occur adjacently in northern California. Samples with the lowest scores on PC III occur in two groups, WOOD, WALK, and MONO (the *monoensis* samples), and PINO and REDM. Some samples from the Great Basin (STEN, RUBY, MART) have high scores on PC III, although so do samples from the Cascades (SPEN) and Sierra Nevada (LOOK and MTOM). As with PC II, if PC III portrays size-independent (bill) shape, the pattern is inconsistent with those of habitat, elevation, or geography.

Skeletal characters.—PCA of skeletal characters for both sexes reveals similar patterns of character variation (Table 15). PC I probably portrays size because most characters exhibit relatively high, positive correlations with it. An exception

TABLE 14

ANOVA RESULTS FOR INDIVIDUALS' SCORES ON THE FIRST THREE PRINCIPAL COMPONENTS

	SS-male	SS-female	MS-male	MS-female	F-male[1]	F-female[2]
			Skin characters			
PC I						
Between groups	359.51	133.40	11.98	4.45	93.41**	26.74**
Within groups	48.49	20.61	0.13	0.17		
PC II						
Between groups	99.68	64.05	3.32	2.13	4.07**	2.94**
Within groups	308.29	89.98	0.82	0.73		
PC III						
Between groups	55.37	31.68	1.85	1.06	1.98*	1.07
Within groups	352.63	122.36	0.93	0.99		
			Skeletal characters			
PC I						
Between groups	266.15	104.31	8.87	3.48	23.48**[3]	8.11**[4]
Within groups	143.59	55.73	0.38	0.43		
PC II						
Between groups	33.72	30.37	1.12	1.01	1.55*	1.01
Within groups	275.12	129.64	0.72	1.00		
PC III						
Between groups	52.25	41.61	1.74	1.39	2.81**	1.52
Within groups	235.44	118.39	0.62	0.91		

[1] d.f. = 30,378.
[2] d.f. = 30,124.
[3] d.f. = 30,380.
[4] d.f. = 30,130.
* $P < 0.005$. ** $P < 0.001$.

to this result is the low correlation for PSYNL (0.473 for males and 0.530 for females). PC I accounts for 52.7% of the variance among males and 54.9% among females; the first three PC axes account for 64.2% of the variation for males and 65.8% for females. For both sexes, PC II is influenced by PSYNL. On PC III, males and females have high correlations for SKULL and SCPEW, and FEDEW for only males. Inspection of character correlations does not indicate any obvious suites of covarying characters. For example, it is difficult to attach a biological explanation to PC III, where SKULL and SCPEW are contrasted.

On the three-dimensional plots of mean locality scores for males and females (Figs. 23, 24), samples are spread along the first axis, from REDM (C) to STEN (5) for males and REDM (C) and RUBY (3) for females. Along PC II, the samples are dispersed between PINO (B) to STEN (5) for males and MONO (K) and PINO (B) for females. Samples are dispersed along PC III from CHER (I) to MART (4) for males and STEN (5) and MTOM (G) for females. As for the PCA of skin characters, three groups were obtained: the Great Basin, southern California and the North Coast Range, and the remaining samples. For females, the southern California and North Coast Range samples are fairly well separated on PC I. However, the Great Basin samples do not form a distinct group. The PCA of

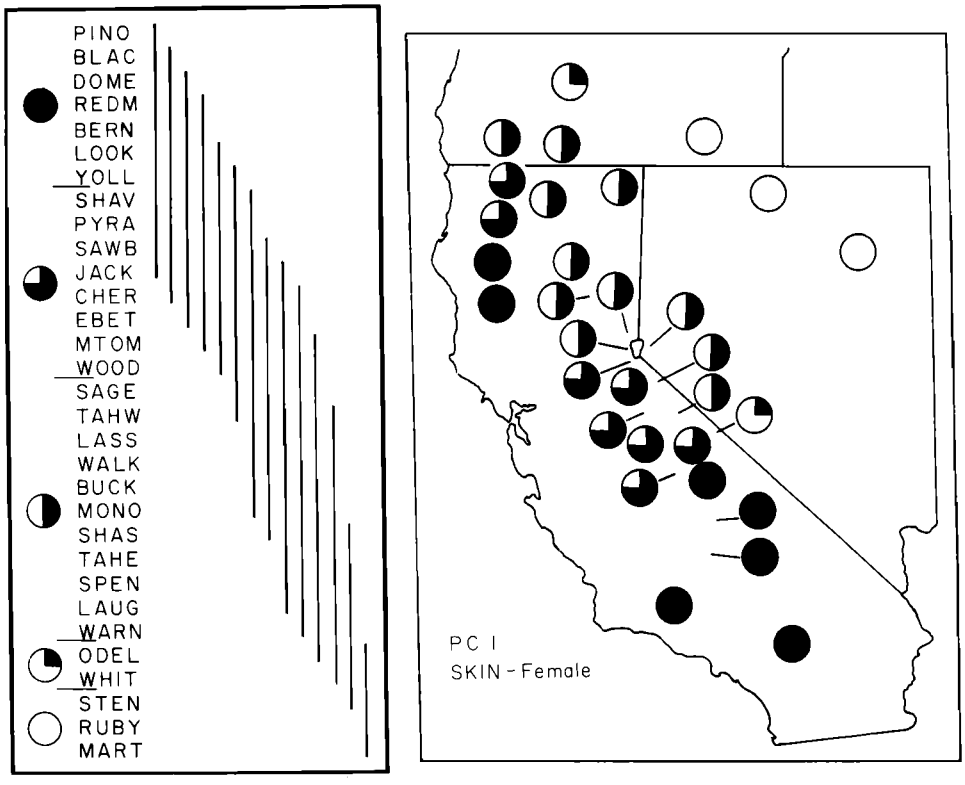

FIGURE 20. SS-STP analysis of individual females' scores on PC I for skin characters. See Fig. 19.

females and males differ, but sample sizes are small for females and I do not analyze these differences further.

Closer inspection of the plot for males reveals several noteworthy aspects. The samples from the Great Basin (STEN, RUBY, MART, WHIT, excluding WARN) all have low scores on PC I and high scores on PC III, but the samples are dispersed on PC II, suggesting that similarly-sized birds have dissimilar shapes. ODEL is similar to WHIT on PC I, but it differs from the Great Basin samples on PC II and PC III. The WARN sample is contained in the group of samples from the central Sierra Nevada, not with the other Great Basin samples, although the Warner Mountains occur on the perimeter of the Great Basin. Samples from the southern Sierra Nevada and North Coast Range have relatively high scores on PC I but are somewhat dispersed on PC II (especially PINO), possibly an indication of shape differences. These latter samples are "connected" to the remaining samples via intermediate-sized samples from the central Sierra Nevada (e.g., SHAV) and North Coast Range (SAWY).

PCA scores were subjected to SS-STP analysis as done for skin characters. On PC I for both sexes, a significant *F*-value from ANOVA was obtained, and the SS-STP analysis identified 13 maximally non-significant subsets of males and 10 of females. The patterns (Figs. 25, 26) closely resemble each other and several of

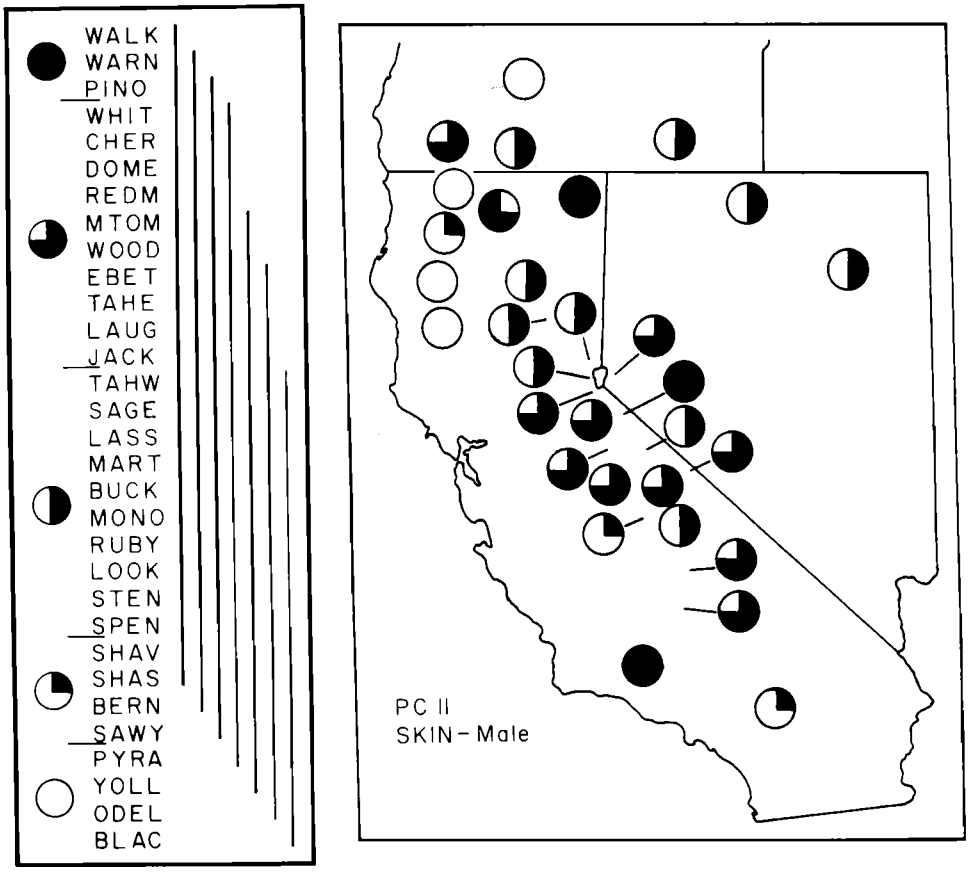

FIGURE 21. SS-STP analysis of males' scores on PC II for skin characters. See Fig. 19.

the individual character patterns; they show a clinal north to south increase on PC I, exceptions being WHIT, YOLL, and BLAC. The primary pattern of variation in the 15 characters, summarized by the first principal component, is very similar in both sexes to that obtained in the analysis of skin characters and cube-root of mass. PC I for skeletal characters seems to reflect a strong size component.

The SS-STP analyses of scores on PC II and PC III both resulted in significant *F*-values for males, but not for females, which are not discussed further because of small sample sizes. The patterns of PC II and III scores are difficult to interpret. The two maximally homogeneous subsets (not shown) of PC II scores of males do not reveal a geographic pattern (Fig. 27). That is, samples with similar scores on PC II share no obvious common habitat or elevational attributes and are often widely dispersed. As illustrations, samples with intermediate scores (half circles) occur throughout the north-south range of the transect, and samples from the Sierra Nevada exhibit nearly the full range of values.

The plot (Fig. 28) of scores on PC III and the five subsets defined by SS-STP are also difficult to interpret, although adjacent sites tend to be more similar. In summary, if PC II and III are relatively free of size-effects, then no clear geographic patterns are evident in "shape." Although not shown, similar results were obtained for females.

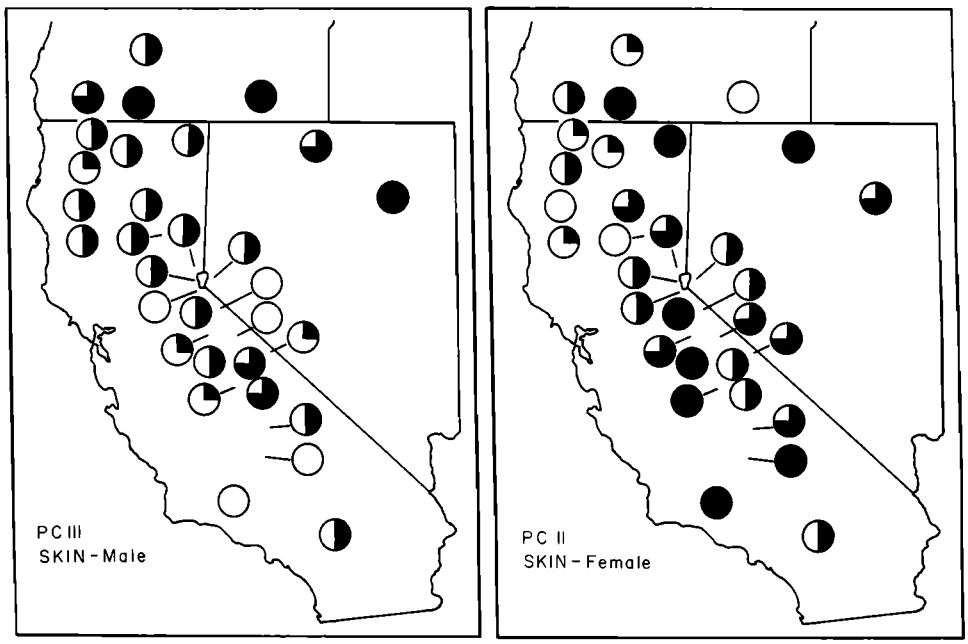

FIGURE 22. Pie diagrams depicting individuals' scores on PC III (males) and PC II (females) for skin characters.

To investigate the generality of the PCA of skeletal characters, PCAs were performed for each of 10 samples of males representing both the extremes in morphology and breeding habitat, and samples taken near one another from similar habitats and elevations. Examination of the correlation coefficients of

TABLE 15

CHARACTER CORRELATIONS WITH PRINCIPAL COMPONENTS FOR SKELETAL CHARACTERS. CHARACTER ABBREVIATIONS DEFINED ON P. 13

Character	PC I		PC II		PC III	
	Males	Females	Males	Females	Males	Females
SKULW	0.847	0.838	−0.146	−0.087	−0.200	−0.173
SKULL	0.823	0.829	−0.240	−0.126	−0.437	−0.487
CORAL	0.669	0.772	0.085	0.100	0.086	−0.097
SCPEW	0.609	0.674	−0.118	−0.236	0.492	0.476
STERL	0.612	0.590	0.084	−0.030	0.128	0.260
PSYNL	0.473	0.530	0.863	0.830	−0.027	0.065
SYNXW	0.738	0.718	−0.008	−0.056	0.004	0.176
FEPEW	0.748	0.715	−0.078	−0.200	0.118	0.203
FEDEW	0.607	0.754	−0.174	−0.109	0.508	0.225
FEMRL	0.782	0.802	0.051	0.058	−0.094	−0.045
TIBOL	0.733	0.704	0.078	−0.029	−0.120	−0.088
HTROL	0.733	0.688	0.035	−0.063	0.018	0.160
HUMRL	0.808	0.836	0.039	0.031	−0.051	0.003
ULNAL	0.811	0.818	0.043	0.012	−0.011	0.106
ULPEW	0.788	0.769	−0.114	−0.062	0.097	0.217
Percentage of variance	52.7	54.9	6.1	5.6	5.4	5.3

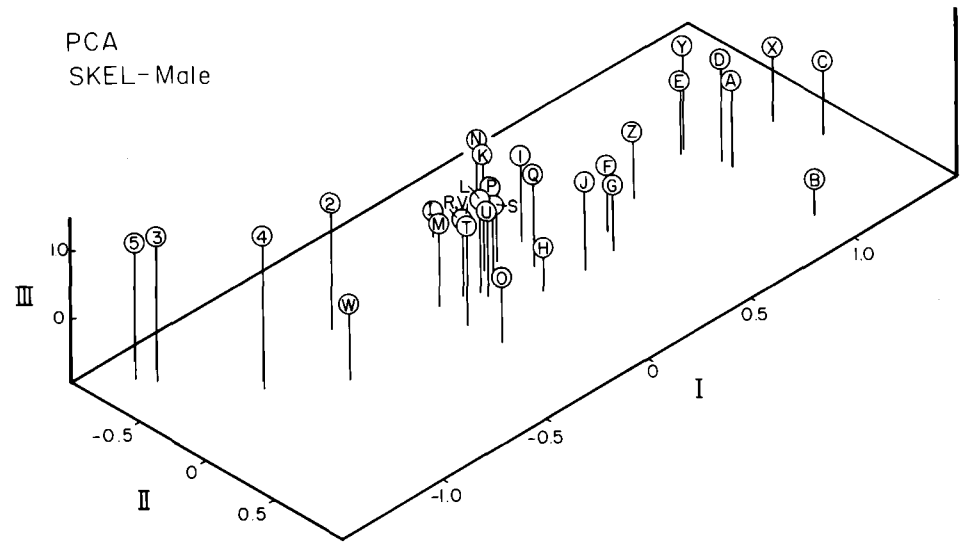

FIGURE 23. Three-dimensional model depicting results of principal components (PC) analysis of skeletal characters for males. See Fig. 17.

characters with PC I for each of the 10 samples (Table 16) shows little similarity from locality to locality. For example, correlations with PC I for SKULL range from −0.509 (BERN) to 0.796 (WHIT). These two localities represent rather extreme morphologies, and lack of concordance of character correlations might

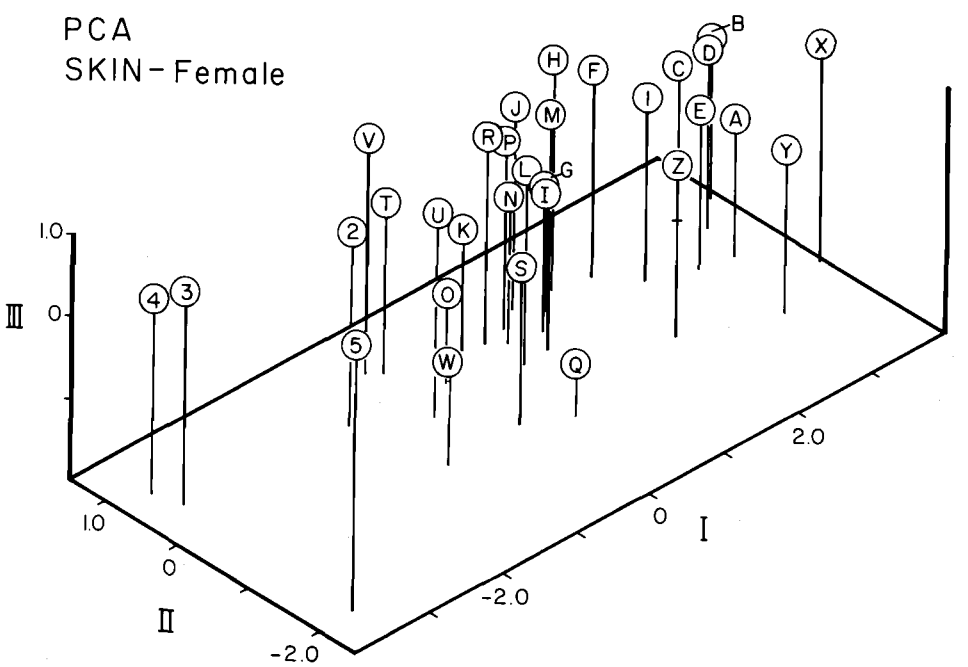

FIGURE 24. Three-dimensional model depicting results of principal components analysis of skeletal characters for females. See Fig. 17.

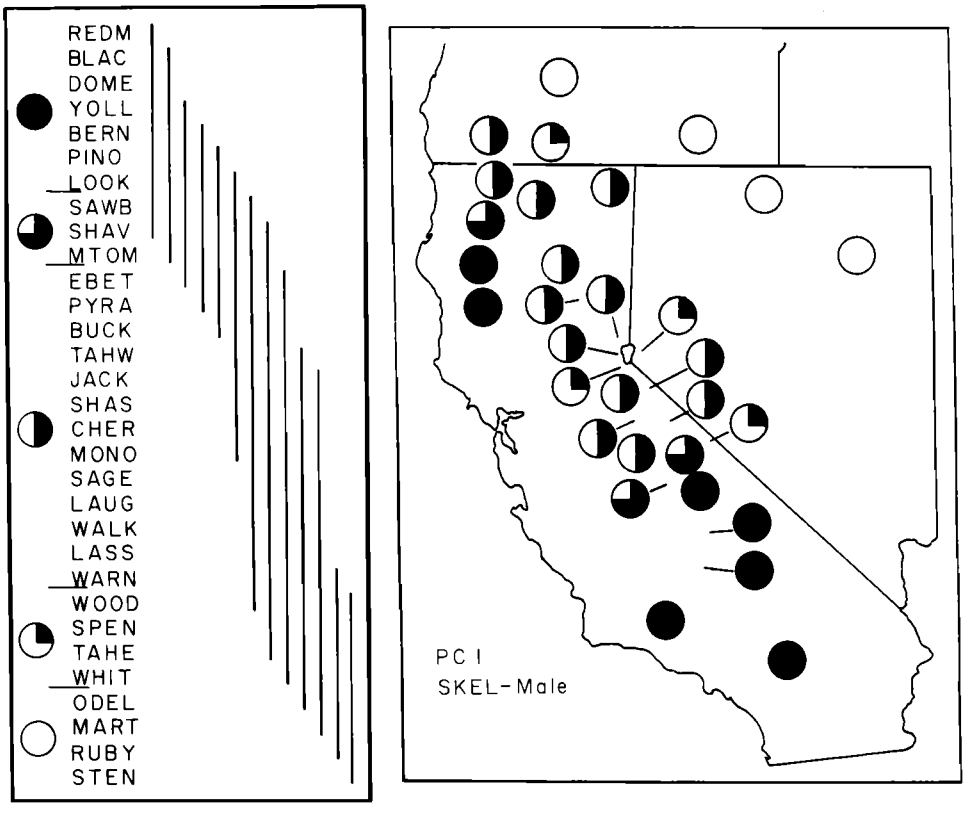

FIGURE 25. SS-STP analysis of individual males' scores on PC I for skeletal characters. See Fig. 19.

be due to geographic variation in the relative relationship of this character and the major axis of within-locality variation. Considering character correlations for three adjacent sites (DOME, REDM, SHAV), again the correlations are inconsistent, even over short geographic distances. For example, FEMRL is correlated with PC I at 0.003 in the DOME sample, and at 0.868 in the REDM sample. Similar contrasts in DOME and REDM can be seen in CORAL, PSYNL and TIBOL. Across the 10 localities, only FEPEW, FEDEW, HUMRL, and ULPEW have reasonably consistent character correlations with each PC I. The individual PCA results demonstrate that the among-site geographic pattern of character variation summarized by PC I (Fig. 17) is not a simple function of character variation within samples. That is, there is geographic variation in the way in which characters covary within samples.

The PCA of 10 separate samples was also designed to evaluate shape variation following Chernoff and Miller (1982). Their procedure involves standardizing character loadings to a mean of 1.00. Values greater than 1.02 are interpreted as showing positive allometry and less than 0.98 as negatively allometric. For example, a value of 1.08 would imply that as size increases, the character increases at a relatively greater rate. When this transformation was applied to the character loadings from the 10 individual PCAs, many values were less than 0.40 and many others were greater than 1.50. In fact, few of the 150 values were near 1.00

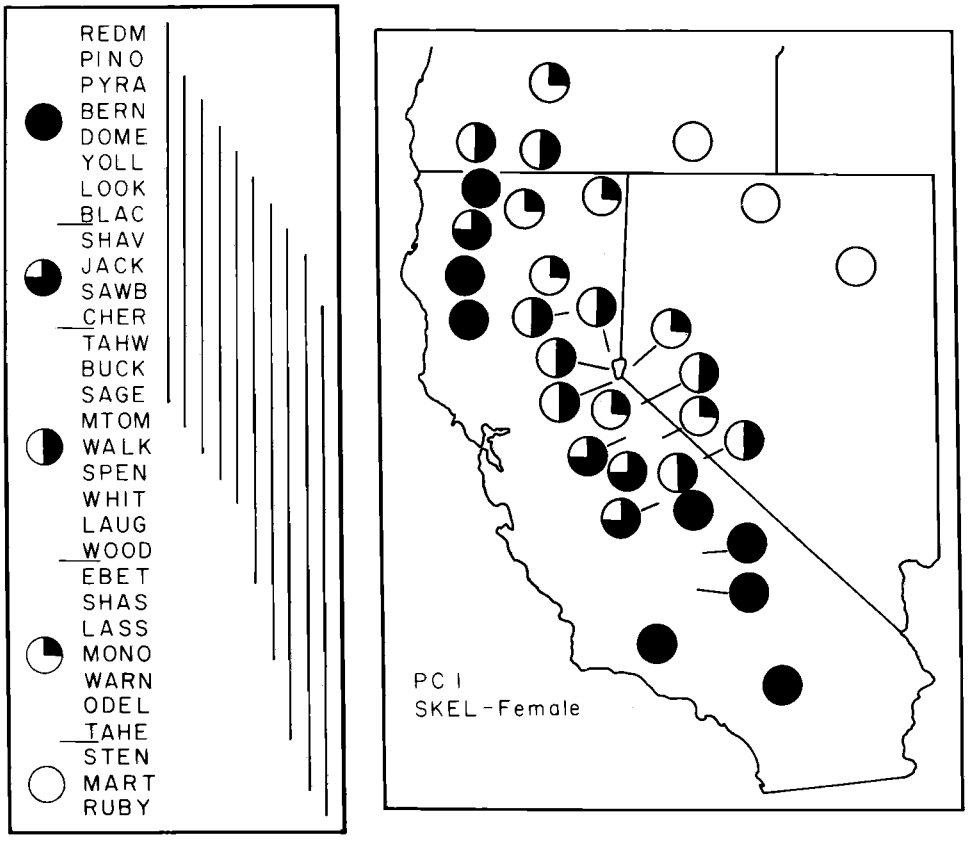

FIGURE 26. SS-STP analysis of individual females' scores on PC I for skeletal characters. See Fig. 19.

(isometry). Chernoff (pers. comm.) noted that this method of shape analysis depends on the data forming an ellipse in multivariate space, with a definite size axis. However, as discussed above, size as measured by cube-root of mass only varies 8.1% between extremes of sample means. Hence, the morphological space for these sparrows is not characterized by an ellipsoidal form with a distinct size-axis. Therefore, the method of Chernoff and Miller (1982) is probably not appropriate for these sparrows. However, it is useful to discover these attributes of Fox Sparrow morphology, and to note the lack of consistent character correlations in the individual population analyses.

CLUSTER ANALYSES

Although my aim is not specifically to examine the present subspecific framework, I discuss the subspecific affinity of samples to facilitate understanding of the geographic patterns implied by the phenograms.

Study skin characters.—The pattern of phenetic similarity among males (Fig. 29) shows four main clusters. One grouping contains all samples of *stephensi* and *brevicauda* plus some samples from the southern Sierra Nevada currently assigned

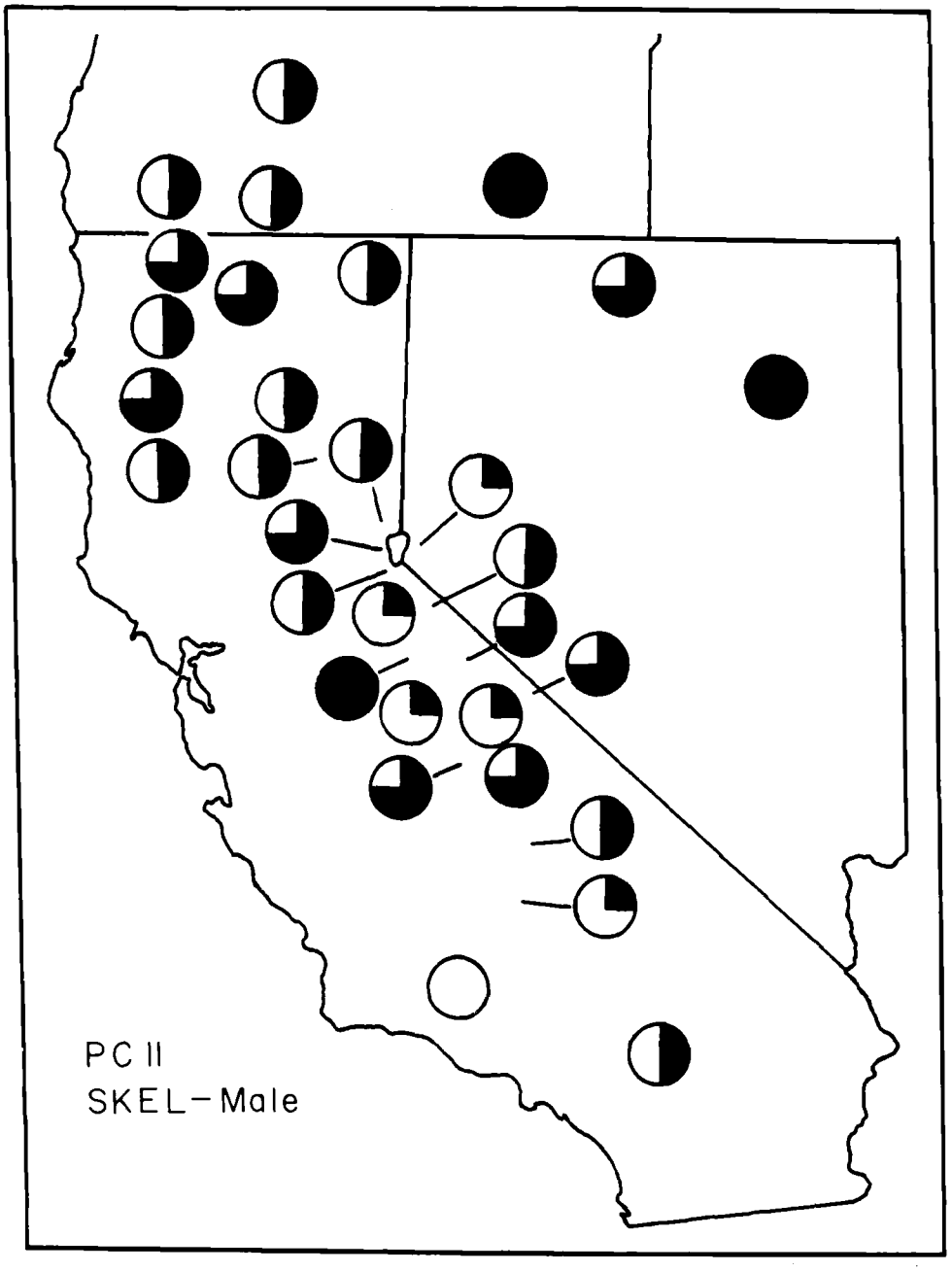

FIGURE 27. Pie diagram depicting individuals' scores on PC II for skeletal characters for males.

to *megarhyncha*. Another cluster contains the two samples of *schistacea* (RUBY-MART), the single sample of *canescens* (WHIT), and two samples from the subspecies *fulva* (ODEL and STEN, excluding WARN). The close phenetic similarity of the two samples of *schistacea* is apparent, whereas the similarity of WHIT-

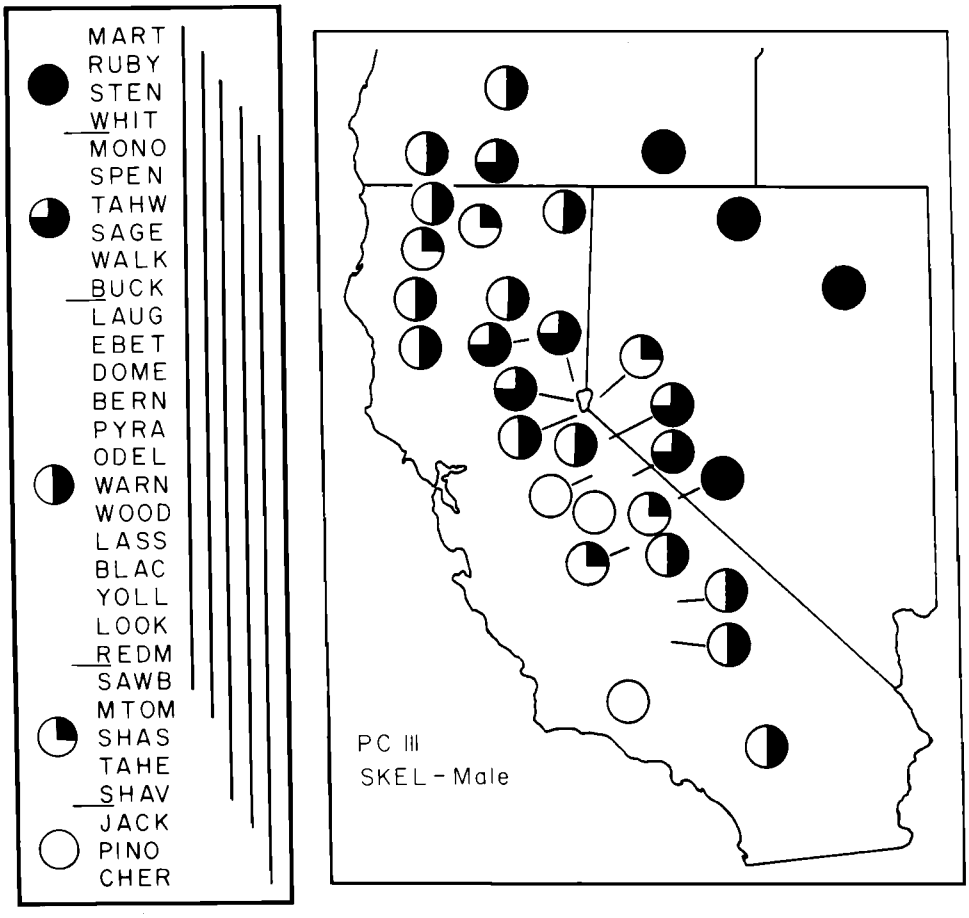

FIGURE 28. SS-STP analysis of individual males' scores on PC III for skeletal characters. See Fig. 19.

ODEL is unexpected, because of the geographic distance separating these sites, and their habitat and elevational differences. The remaining two clusters contain a geographically widespread array of samples mostly assigned to *megarhyncha,* plus the WARN sample (*fulva*) and MONO (*monoensis*). There is a sub-cluster containing MONO, TAHE, WALK, WOOD, and WARN, which are geographically proximate and south of Lake Tahoe, except for WARN. In the remaining cluster, samples are generally from north of Lake Tahoe, the northern North Coast Ranges (excluding the *brevicauda* samples), the Cascades and Sierra Nevada; these sites are relatively close geographically. SAWY and PYRA do not cluster with samples from *brevicauda* to the south, but rather with nearby sites, all of which are assigned to *megarhyncha.*

Cluster analysis of females (Fig. 30) produced results similar to those obtained in the analysis of males. A cluster emerged that contains all samples in *stephensi, brevicauda,* and some southern samples of *megarhyncha.* However, SAWY and PYRA are included in this cluster, in contrast to the males, suggesting a less

TABLE 16

CHARACTER CORRELATIONS WITH PC I FOR 10 SEPARATE PRINCIPAL COMPONENTS ANALYSES, FOR 10 LOCALITIES (SITE CODES DEFINED IN TABLE 1)

Character[1]	LASS	YOLL	PINO	DOME	REDM	WARN	SHLK	WHIT	BERN	SHAV
SKULW	0.29	0.42	0.27	0.43	0.51	0.62	0.82	0.89	0.13	0.54
SKULL	0.25	0.34	0.53	0.21	0.56	0.32	0.43	0.80	−0.51	0.17
CORAL	0.49	0.86	0.59	0.02	0.71	0.77	0.81	0.61	0.12	0.83
SCPEW	0.83	0.47	0.08	0.70	0.22	0.52	0.86	0.63	0.73	0.19
STERL	0.27	0.59	0.44	0.67	0.49	0.39	0.82	0.63	−0.16	0.59
PSYNL	0.57	0.66	0.70	−0.35	0.77	0.67	0.35	0.05	−0.25	−0.25
SYNXW	0.08	0.76	0.56	0.64	0.56	0.65	0.48	0.64	0.10	0.72
FEPEW	0.55	0.72	0.74	0.79	0.81	0.84	0.27	0.81	0.28	0.62
FEDEW	0.51	0.74	0.34	0.91	0.64	0.67	0.19	0.59	0.95	0.49
FEMRL	0.55	0.80	0.39	0.01	0.87	0.52	0.61	0.45	0.17	0.83
TIBOL	0.37	0.78	0.46	0.12	0.83	0.26	0.44	0.18	0.07	0.75
HTROL	0.30	0.05	0.50	0.64	0.54	0.79	0.77	0.68	0.30	0.37
HUMRL	0.55	0.80	0.67	0.27	0.78	0.66	0.73	0.32	0.49	0.79
ULNAL	0.65	0.84	0.63	0.52	0.70	0.62	0.78	0.68	0.08	0.84
ULPEW	0.49	0.50	0.63	0.85	0.63	0.62	0.81	0.54	0.54	0.69

[1] Character abbreviations defined on p. 13.

marked distinction between *brevicauda* and *megarhyncha* and the *stephensi*-type morphology. Except for a BLAC-YOLL cluster, adjacent samples are not most similar to one another, as found generally for males. The remaining clusters reflect general geographic proximity. STEN, MART, and RUBY, samples from the Great Basin, form a distinct cluster. Within the two clusters of samples assigned mostly to *megarhyncha,* there was less of a tendency for samples north and south of Lake Tahoe to fall in opposing groups, as found for males. For example, the clustering of MONO and STEN conflicts with their geographic arrangement and habitats. The WHIT and WARN samples, both from the periphery of the Great Basin, clustered together, despite the fact that the WARN sample was obtained from chaparral (unlike Linsdale's [1928] sample, which was taken in riparian habitat).

Cluster analyses are useful for detecting patterns in the levels of phenetic similarity among sites. The above analyses, based on the taxonomic distance (d_{jk}) measure, might be affected by size differences, in spite of standardization of data (see Sneath and Sokal 1973; Lemen 1983), because of the sensitivity of distance measures to size variation. Many methods of shape, or size-independent analyses, exist (Humphries et al. 1981; Mosimann and James 1979; Lemen 1983; Wood 1983; Bookstein et al. 1985), but without a consensus as to which method is best for comparing shape independent of size. As a preliminary investigation of size-independent variation among samples of Fox Sparrows, I constructed phenograms based on character means which were first divided by the mean cube-root of mass for each site and then transformed to $\log_{10}$. The product-moment correlation coefficient and taxonomic distance measures were both used as measures of association, to produce a matrix of pairwise similarity values comparing "shape." This analysis groups samples of similar shape.

The phenogram (Fig. 31) contains two major clusters. The top cluster resembles that obtained in the distance phenogram because it contains samples from *stephensi, brevicauda,* and some *megarhyncha*; outliers to the main clusters in this

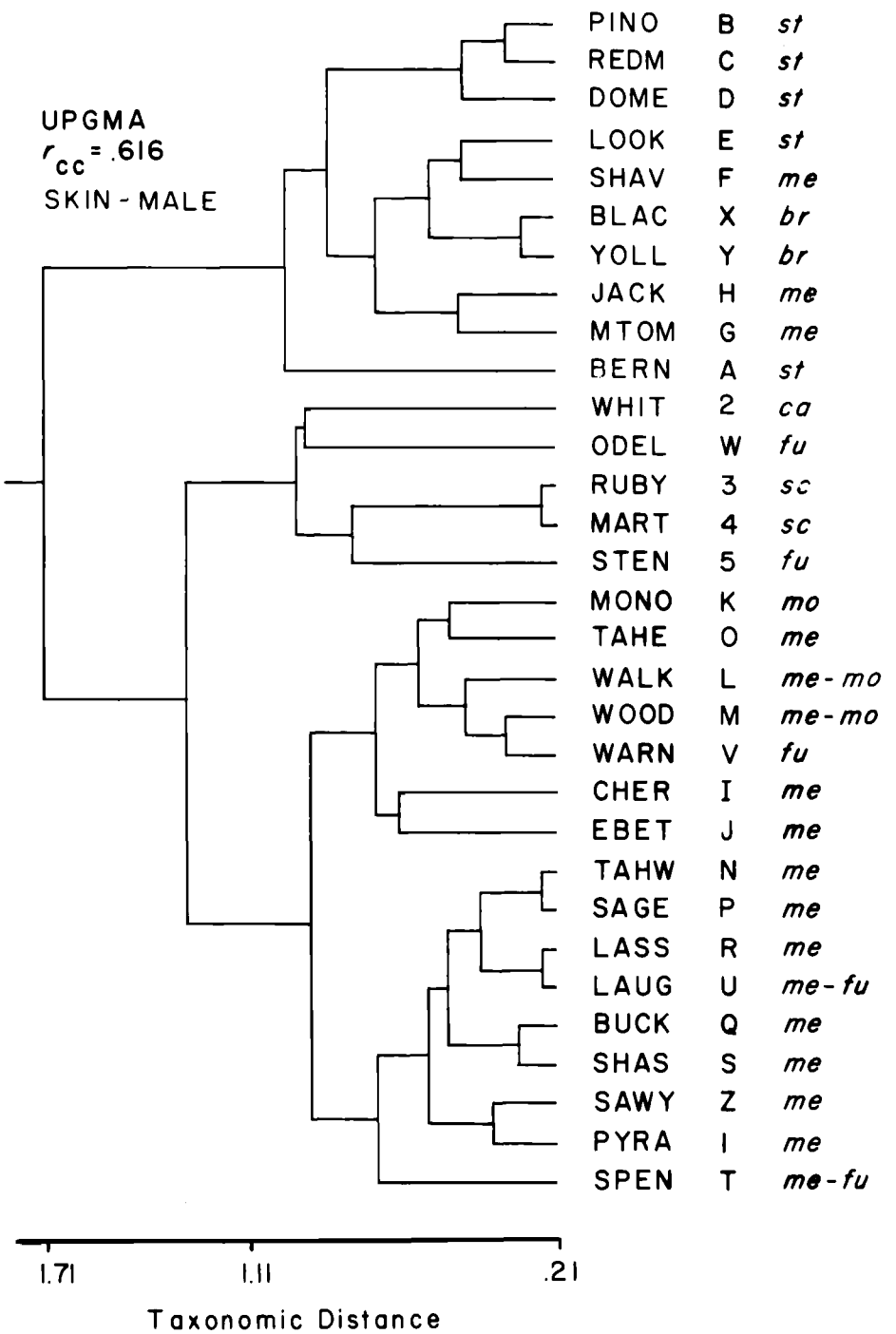

FIGURE 29. UPGMA phenogram based on the matrix of pairwise taxonomic distances between localities, derived from locality means for skin characters for males. Two-letter abbreviations are the first two letters of the subspecies name (Table 1).

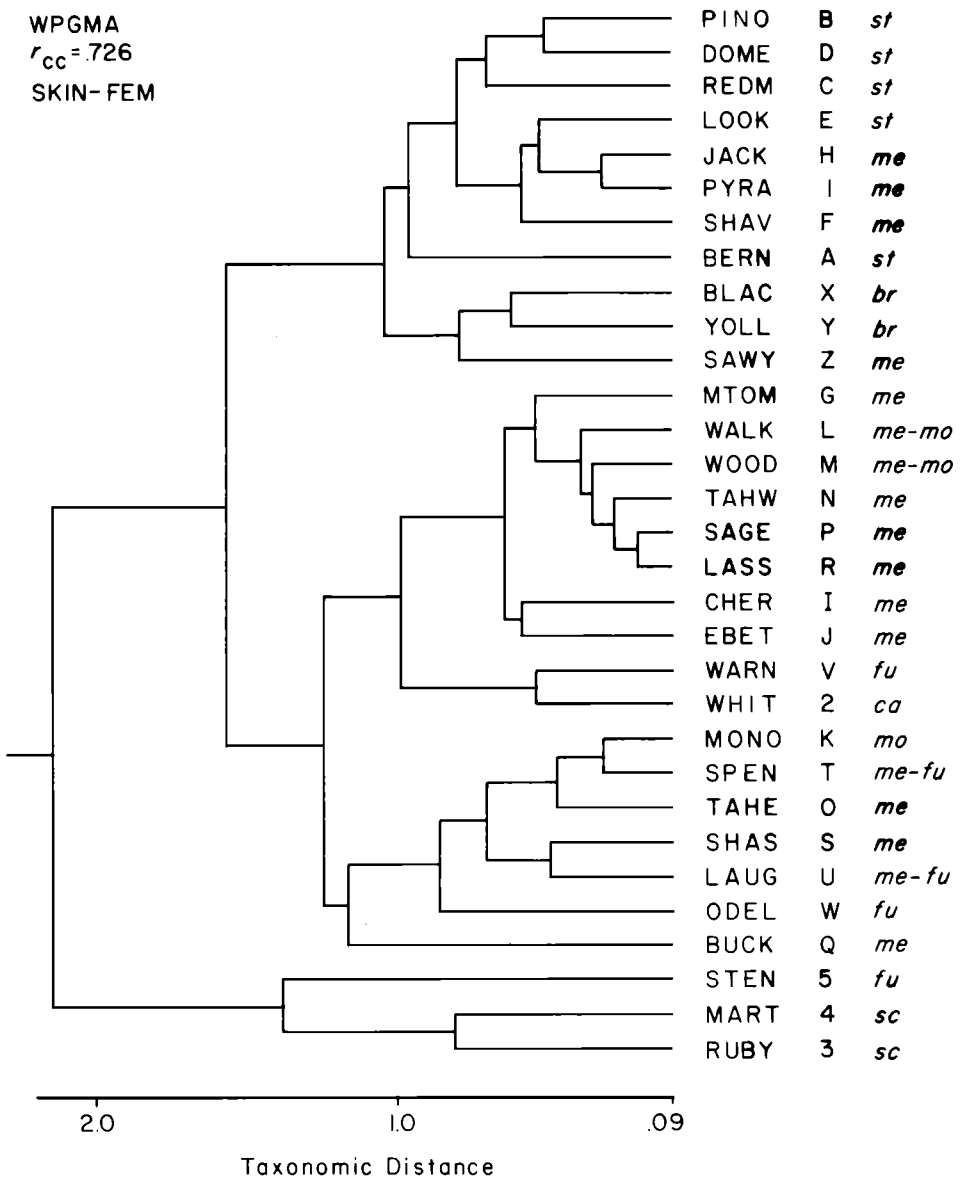

FIGURE 30. WPGMA phenogram based on the matrix of pairwise taxonomic distances constructed from locality means for skin characters for females. See Fig. 29.

major section include TAHE, SPEN, MONO, and LASS. Importantly, the samples of *brevicauda* are similar to those from *stephensi* in both size and shape. Several points of interest are evident in the remaining cluster. Some of the Great Basin samples, RUBY, MART, and STEN, have phenetically similar shapes (and sizes), whereas the WARN and WHIT samples, taken on the perimeter of the Great Basin, are relatively different. In the remaining instances, geographically proxi-

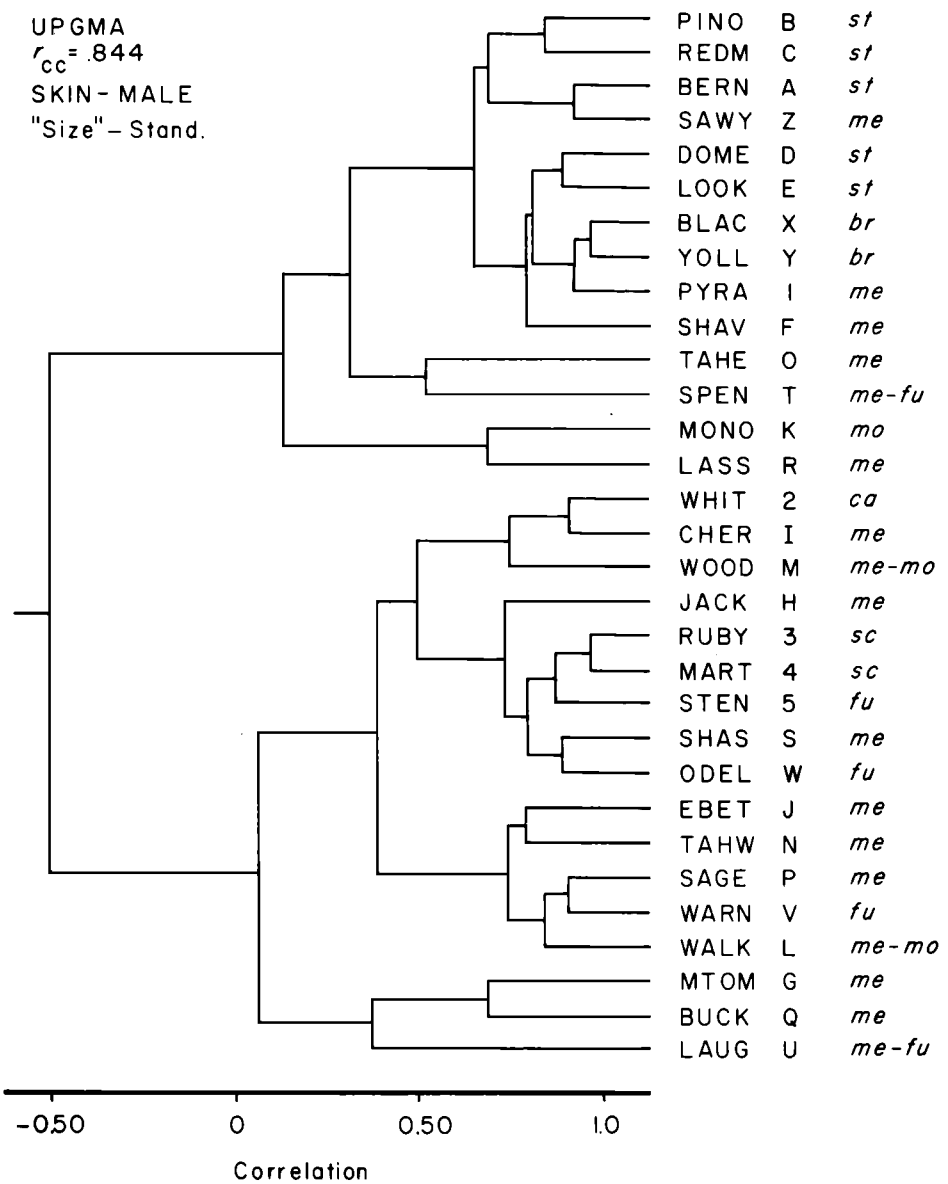

FIGURE 31. UPGMA phenogram based on the matrix of pairwise taxonomic distances constructed from locality means that were first divided with the mean cube-root of mass for each site, and then transformed to $\log_{10}$. Data were skin characters for males.

mate samples tend to be most similar. However, there are not discrete clusters of phenetically similar "shapes" which might be predicted based on geographic or ecological considerations, if discrete evolutionary units existed in "phenotype space." For example, three samples taken close together, SHAV, MTOM, and JACK, are dispersed throughout the phenogram. Although these latter three sam-

ples were taken at different elevations (Table 1), inspection of the phenogram shows that elevation does not produce a consistent shape across geography. In summary, there is clear geographic heterogeneity in this rough estimate of shape, but it has no obvious geographic patterns, a result also obtained in the SS-STP analysis of variation of individuals' scores on PC II and PC III. An alternative analysis, based on a distance Wagner analysis, could be used to infer if present patterns are the result of current ecology, or phylogenetic history of populations (Thorpe 1984).

Skeletal characters.—The analysis of males (Fig. 32) produced four general clusters. In agreement with the analysis of skin characters, a cluster emerged that contains samples in *stephensi* and *brevicauda,* but only one sample from *megarhyncha.* Within this cluster, no pair of samples includes geographic neighbors (e.g., LOOK-YOLL, REDM-BLAC); instead, the cluster represents only a regional grouping of samples. STEN, RUBY, and MART again form a group, one which is most similar to ODEL and WHIT. WARN is most similar to samples from the Sierra Nevada. The remaining samples form roughly two clusters, consisting of *megarhyncha, fulva,* and *monoensis.* In general, this diagram reflects geography. For example, SHAV, JACK, and MTOM are clustered together. In the two central clusters, samples from north and south of Lake Tahoe tend to segregate into different clusters, although exceptions occur (e.g., MONO). The divergent position of CHER is unexplained; however, it was taken from a low density, recently-colonized site.

The phenogram of females has three basic clusters and resembles that for males generally, but not in detail (Fig. 33). As in prior analyses, samples from *stephensi* and *brevicauda* cluster together, in this instance joined by SHAV and PYRA. Within this cluster, the phenetically most similar samples are not geographically adjacent. STEN, MART, and RUBY form a cluster, most similar to one containing MONO, ODEL, and TAHE, three geographically dispersed samples. WHIT and WARN are similar to each other, and are more similar to Sierran than to Great Basin samples. Several geographic anomalies are evident, such as the phenetic groupings of MONO-ODEL, CHER-SAWY, and TAHW-LAUG. The remaining samples, in the third cluster, are from *megarhyncha, fulva,* and *canescens.*

Following the procedure outlined for the "size-independent" analysis of skin characters, a phenogram was constructed for transformed data for skeletal characters (Fig. 34). The most striking feature of this branching diagram is the extent of shape differentiation among sites. Although many clusters are identifiable, they are not necessarily distinct. That is, the clusters originate at low levels of association. However, a number of clusters contain samples that are geographically or ecologically related. The Great Basin samples, excluding WARN, form one of the most distinct clusters, in agreement with the analysis of skin characters. WALK, EBET, and TAHE have similar shapes; yet they are relatively distant from neighboring samples (e.g., MONO, WOOD, CHER). The samples from *stephensi* are fairly similar, except for LOOK. The two samples of *brevicauda* (YOLL and BLAC) are relatively divergent, yet within the same major grouping, which contains the *stephensi* samples. SHAV, JACK, and MTOM are separated by short geographic distances, and share a relatively similar, yet apparently unique shape.

Thus, to the extent that this analysis summarizes size-independent variation, a complex pattern of shape variation exists with no obvious correlates to common

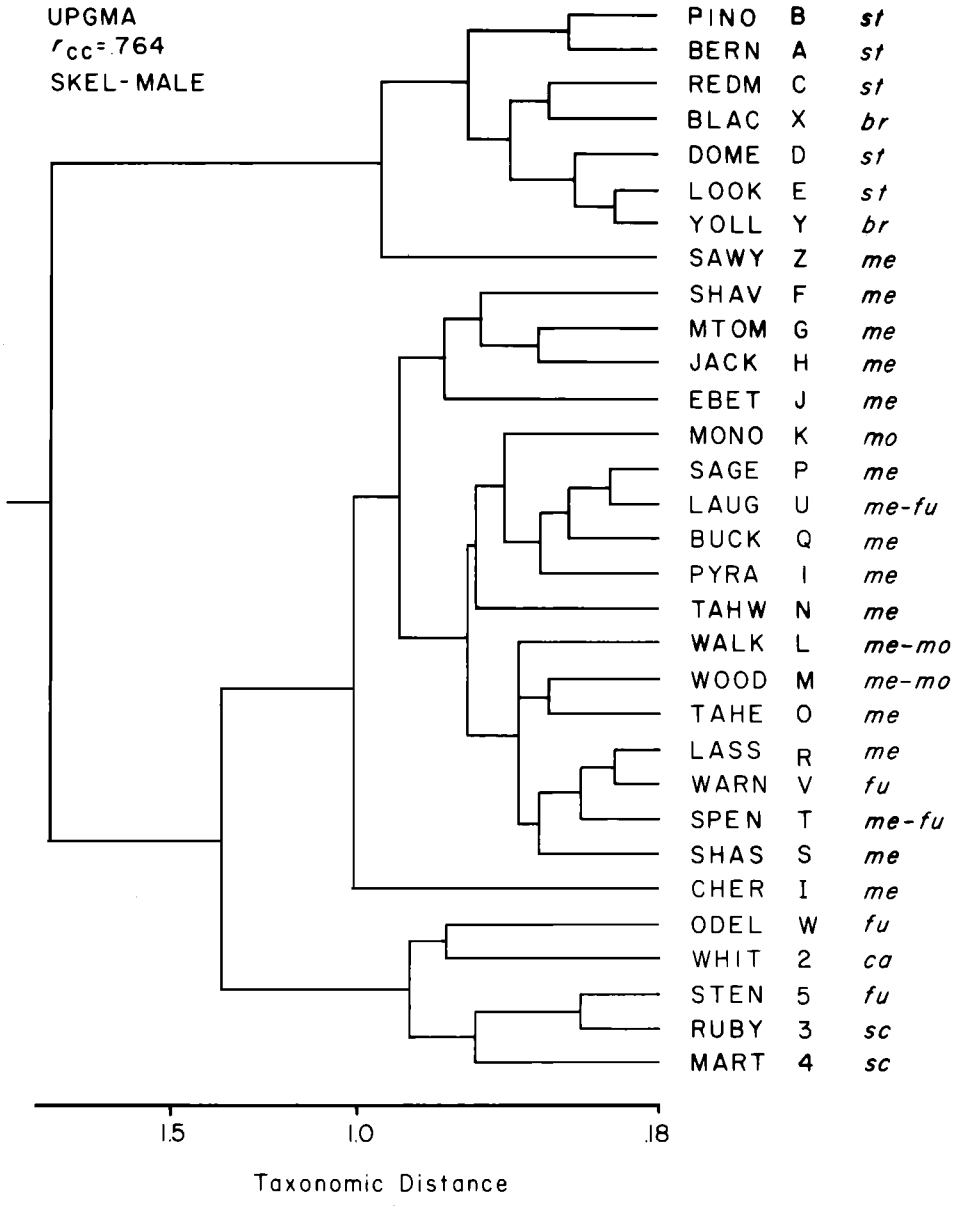

FIGURE 32. UPGMA phenogram based on matrix of taxonomic distances between samples calculated from locality means for skeletal characters for males. See Fig. 29.

habitat features and, in some instances, geographic proximity. Although shape variation exists, it does not parallel results of the analysis of skin characters, implying a degree of independence of these external and internal character suites.

MANTEL TESTS

The results of Mantel tests are given in Table 17. The matrix of Rogers' genetic distances yielded insignificant *t*-values when tested against both the GEOG and

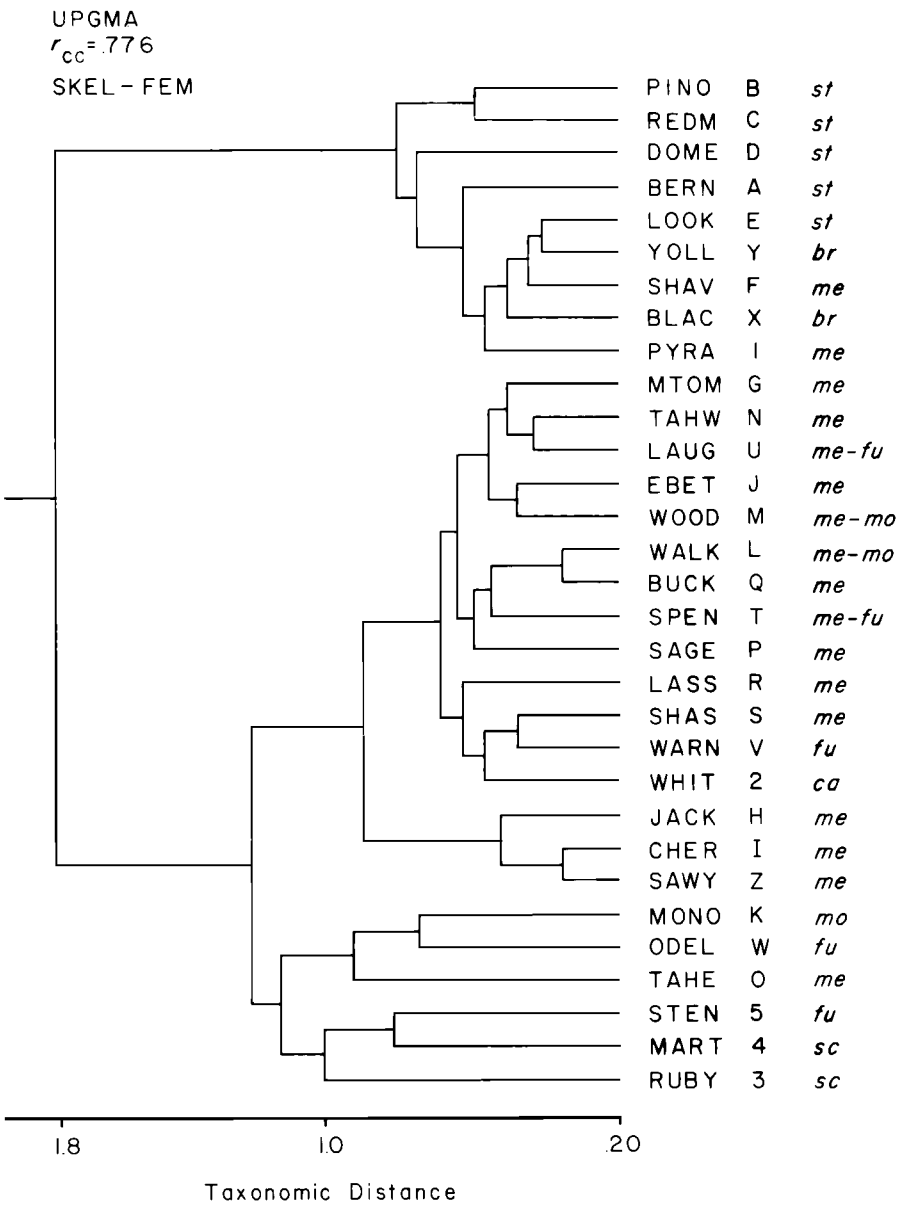

FIGURE 33. UPGMA phenogram based on the matrix of taxonomic distances calculated from locality means for skeletal characters for females. See Fig. 29.

REGE matrices, lending support to the conclusion that there is no simple geographic structure in the genetic distance data. A similar result, albeit qualitative, was obtained from inspection of the phenogram (Fig. 4). Furthermore, the matrix correlation coefficients, both <0.10, indicate little in common between matrices. Thus, genetic variation is not "explained" by the GEOG or REGE hypothesis matrices, which essentially test for an isolation by distance effect. Although I have

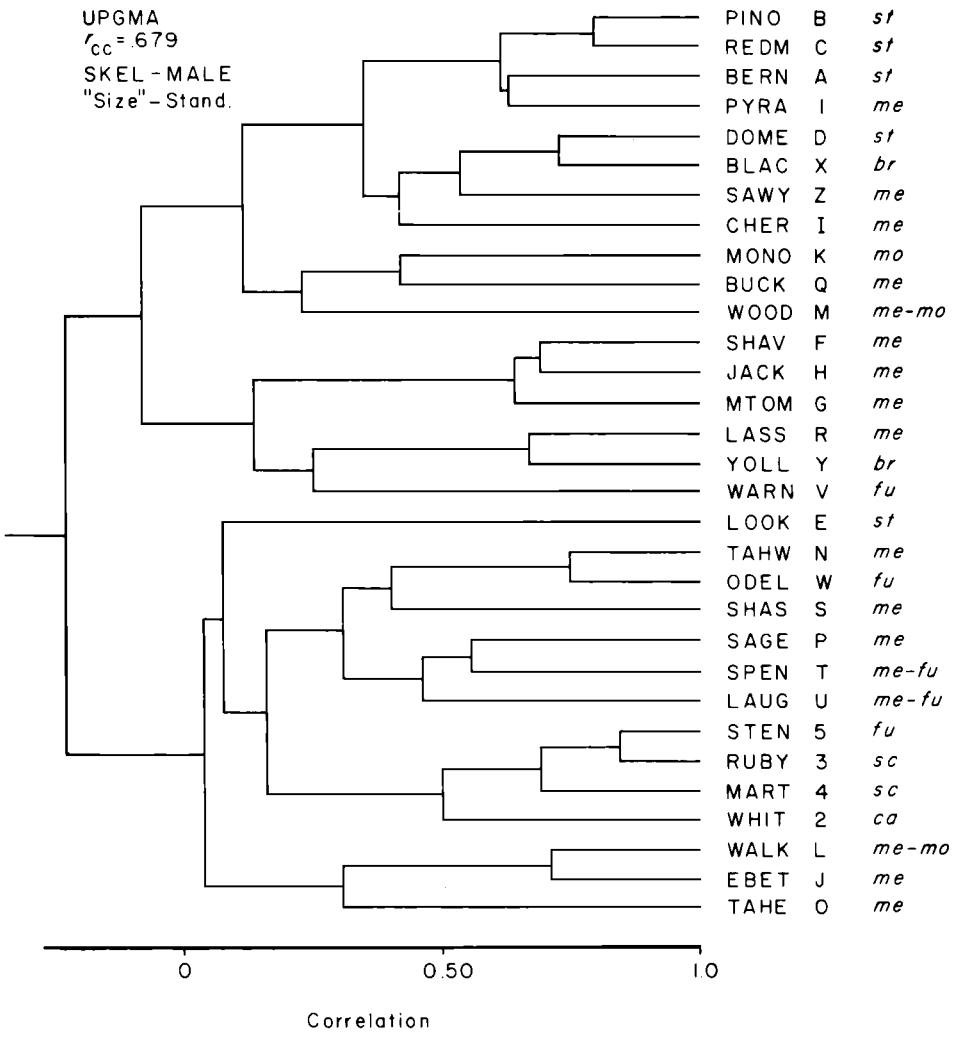

FIGURE 34. UPGMA phenogram based on the matrix of pairwise taxonomic distances constructed from locality means which were first divided with the mean cube-root of mass for each site, and then transformed to $\log_{10}$. Data were skeletal characters for males.

not tested other hypotheses, I think that there is no meaningful (e.g., historical or ecological) geographic pattern of genetic distances.

The taxonomic distance matrices, representing both skin and skeletal characters, are significantly concordant with geographic distances, a result consistent with both an isolation by distance effect, or "regional" geographic patterning (Jones et al. 1980), and clinally varying environmental factors. The matrix correlation coefficients are 0.43 (skin data) and 0.34 (skeletal data). The taxonomic distance matrices, however, are not significantly related to the reciprocal of geographic distances (REGE); this suggests a lack of "local" geographic structure, a result obtained qualitatively in the foregoing discussion of phenograms. Jones et al. (1980) noted that local patterning would result in positive correlation coefficients,

TABLE 17

T-VALUES RESULTING FROM MANTEL TESTS BETWEEN MATRICES OF GEOGRAPHIC DISTANCES, RECIPROCAL OF GEOGRAPHIC DISTANCES, ROGERS' GENETIC DISTANCES, AND TAXONOMIC DISTANCES FOR SKIN AND SKELETAL DATA. VALUES IN PARENTHESES ARE CORRELATION COEFFICIENTS BETWEEN EACH MATRIX

	1	2	3	4
1. Geographic distance	—			
2. Reciprocal of geographic distance	—	—		
3. Rogers' genetic distance	0.41 (0.07)	−0.80 (−0.06)	—	
4. Taxonomic distance-skins[1]	4.81* (0.43)	−2.59 (−0.16)	3.02* (0.34)	—
5. Taxonomic distance-skeletons[1]	4.12* (0.34)	−2.74 (−0.16)	2.10 (0.21)	9.36* (0.85)

[1] Males only.
* $P < 0.0055$.

whereas the skin and skeletal data for Fox Sparrows both show negative *r*-values. Hence, on a fine scale, distances tend to be greater between geographically adjacent samples than expected from a linear distance model.

The pattern of Rogers' genetic distances is significantly concordant with the taxonomic distances based on skin characters, but not with those calculated from the skeletal data. The significant relationship between genetic and taxonomic distances for skins is somewhat surprising, because the genetic distances are random with respect to GEOG and REGE. Therefore, the low but significant correlation coefficient (0.34) between genetic and morphological data is not attributable simply to the geographic distance between sites (an isolation by distance effect). The correlation implies that some samples are phenotypically and genetically more similar than expected (random), although this correspondence does not make geographic or ecological "sense."

The skin and skeletal distance matrices were concordant; a highly significant *t*-value was obtained as well as a high matrix correlation coefficient, 0.85. Therefore, although the phenograms produced from these matrices differ (Figs. 29, 32), a highly significant pattern is common to both. There might not be a fundamental difference between these two suites of characters, which otherwise might be expected if external morphological traits are influenced by natural or sexual selection differently than aspects of skeletal anatomy. Additional comparisons of variation in external and skeletal traits are warranted.

ENVIRONMENTAL AND MORPHOLOGICAL VARIATION

Results of canonical correlation analysis for skin and skeletal characters are given in Tables 18 and 19. In all four analyses (both sexes for skin and skeletal characters), one canonical variable was sufficient to express the dependency between the two sets of variables (i.e., the sets of variables are not independent). That is, the variation in the morphological data is "explained" by the environmental variables, and only one axis is necessary. It is then appropriate to examine character loadings to discern which variables are most important in each data set;

TABLE 18

CANONICAL VARIABLE LOADINGS OF SKIN AND ENVIRONMENTAL CHARACTERS (ABBREVIATIONS DEFINED ON P. 14. THE SIGNIFICANCE OF THE CANONICAL CORRELATION IS ASSESSED WITH BARTLETT'S TEST (DIXON 1979)

Character	Canonical variable I	
	Males	Females
	Morphology	
WINGL	0.716	0.187
TARSL	0.803	0.739
HINTL	0.738	0.325
BILL-1	0.851	0.875
BILLW	0.873	0.958
BILLD-1	0.892	0.945
BILL-2	0.889	0.891
BILLD-2	0.890	0.976
	Environmental	
ELEV	0.166	−0.142
LONG	0.052	−0.302
LATI	−0.787	−0.579
MAYT	0.033	0.122
MAYX	−0.303	−0.156
MAYM	0.462	0.381
JUNT	0.250	0.259
JUNX	0.051	0.277
JUNM	0.346	0.298
JULT	0.034	0.046
JULX	−0.253	−0.063
JULM	0.252	0.147
APRE	−0.040	0.073
ANPR	−0.011	0.394
Correlation	0.984***	0.990**

*** $P < 0.001$, ** $P < 0.01$.

the absolute values of the character correlation coefficients are examined. In the analysis of skin characters for males, latitude is the most important factor among the "environmental" variables. This result indicates that as latitude decreases, the skin characters tend to get larger, as reflected by their high positive loadings on CV I. For males, MAYX, MAYM, and JUNM have the next highest loadings (−0.303, 0.462, and 0.346, respectively); this suggests that as average maximum May temperature decreases, and average minimum May and June temperatures increase, Fox Sparrows tend to be larger. Growth of nestling Fox Sparrows occurs primarily in May and June (Linsdale 1928); and these temperatures might exert strong influences on morphology. No simple association emerges from the environmental-skeletal comparison (Table 19).

DISCUSSION

POPULATION GENETICS OF FOX SPARROWS: EMPIRICAL RESULTS AND PATTERNS

Tabulation of allelic and genotypic frequencies provides an estimate of genetic population structure, which allows analyses of evolutionary factors that influence the origin and maintenance of genetic variation within and among populations.

TABLE 19

CANONICAL VARIABLE LOADINGS OF SKELETAL AND ENVIRONMENTAL CHARACTERS; MEAN VALUES FOR EACH CHARACTER WERE USED FOR EACH SITE. FOR BOTH MALES AND FEMALES, THE CANONICAL CORRELATION BETWEEN MORPHOLOGICAL AND ENVIRONMENTAL DATA SETS IS 0.999 ($P < 0.001$); THE SIGNIFICANCE OF CANONICAL CORRELATIONS IS ASSESSED WITH BARTLETT'S TEST (DIXON 1979)

	Canonical variable I			Canonical variable I	
Morphology	Males	Females	Environmental	Males	Females
SKULW	0.834	0.429	ELEV	−0.114	0.152
SKULL	0.758	0.500	LONG	−0.285	0.252
CORAL	0.569	0.314	LATI	−0.435	−0.707
SCPEW	0.514	0.272	MAYT	0.054	0.048
STERL	0.720	0.067	MAYX	−0.100	−0.079
PSYNL	0.733	0.464	MAYM	0.191	0.180
SYNXW	0.606	0.495	JUNT	0.350	0.115
FEPEW	0.669	0.120	JUNX	0.464	0.079
FEDEW	0.591	0.480	JUNM	0.396	0.270
FEMRL	0.753	0.538	JULT	−0.105	0.120
TIBOL	0.732	0.446	JULX	−0.089	−0.166
HTROL	0.724	0.361	JULM	0.089	0.191
HUMRL	0.770	0.404	APRE	−0.063	−0.214
ULNAL	0.796	0.405	ANPR	0.312	−0.200
ULPEW	0.731	0.430			

Because of the advantages of electrophoretic analysis, an extensive literature exists on the empirical genetic structure of vertebrate populations (see reviews in Powell 1975; Selander 1976; Nevo 1978; Avise and Aquadro 1982; Smith et al. 1982). The few published intraspecific surveys of allozyme variation in birds have generally considered restricted geographic areas and few population samples and loci (Barrowclough 1983). The present study contributes baseline data on genetic variation of natural avian populations, as well as providing a molecular perspective on the evolution of the Fox Sparrow.

LEVELS AND THE NATURE OF PROTEIN VARIATION WITHIN POPULATIONS

In the Fox Sparrow levels of polymorphism vary among loci (Table 4). Selander (1976) and Johnson (1976) summarized data suggesting that enzymes acting on multiple substrates tend to be more polymorphic than substrate-specific enzymes. Selander (1976) cautioned, however, that attempts to classify enzymes by this criterion (Group I, single physiological substrate, and Group II, multiple substrates [see Gillespie and Langley 1974]) were hampered by numerous exceptions. Thorpe (1982) cited an unpublished study by Ward showing that variation among loci was approximately normally distributed but not bimodally distributed, as predicted if molecular evolution at enzyme loci proceeds fast or slow as postulated by Sarich (1977).

Inspection of levels of polymorphism at individual loci (Table 4) does not reveal two discrete classes of enzyme loci in the Fox Sparrow. Many Group I enzymes (e.g., MDH-1,2; G-6-PDH; 6-PGD; ICD-1,2; GPI; PGM-1,2; and GOT-1,2) are

only slightly polymorphic, possibly in accord with the Group I-II dichotomy. However, enzymes from both classes I and II are not consistently either monomorphic or highly polymorphic, respectively. Johnson, Zink, and Marten (unpubl. data) have found considerable variation among bird species as to which loci are polymorphic and to what extent. Although protein polymorphism in birds does not appear restricted to a few loci, some loci appear generally to be monomorphic: MDH-1,2; ICD-2; CK-1,2; SOD-2; G-6-PDH; GDH; GDA; and general proteins. Needed is a synthesis of information about levels of polymorphism at enzyme loci in birds, and how these levels compare for the same loci in other groups of organisms.

Average individual heterozygosity in Fox Sparrows, 3.85%, is similar to that found for other vertebrates (Selander 1976; Nevo 1978; Avise and Aquadro 1982; Baccus et al. 1983), and documents genetic variability. Relative to some small mammals (Patton and Feder 1981) and salamanders (e.g., Nevo 1978; Larson 1980), heterozygosity is low in Fox Sparrows, but it is greater than that observed in some large mammals (Ryman et al. 1980), and a few small mammal (Hafner et al. 1983) and avian populations (Johnson and Zink 1983). Relative to most birds, Fox Sparrows possess average levels of genetic variability (Barrowclough 1983).

The nature of within-population genetic variability is of importance (Lewontin 1974). If the distribution of alleles at enzyme loci is influenced by non-random mating or natural selection, the potential to infer some aspects of evolutionary history from patterns of allozyme variation will be reduced. Showing no significant departures from Hardy-Weinberg equilibrium predictions are population samples of: Fox Sparrows (present study); Yellow-rumped Warblers, *Dendroica coronata* (Barrowclough 1980a); Dark-eyed Juncos, *Junco hyemalis* (Barrowclough, pers. comm.); sapsuckers (*Sphyrapicus,* Johnson and Zink 1983); several species of *Empidonax* flycatchers (Zink and Johnson 1984); California Gulls, *Larus californicus* (Zink and Winkler 1983); and several species of quail (Gutiérrez et al. 1983). Baker et al. (1982), however, reported that a few samples of White-crowned Sparrows (*Zonotrichia leucophrys*) showed significant departures from Hardy-Weinberg equilibrium. Corbin (1981) reported that genotypic proportions in his samples of *Z. leucophrys* were not in equilibrium, but he did not present supporting evidence. Thus, in a diverse array of avian taxa, possibly excluding the White-crowned Sparrow, there is little evidence that genetic variation in avian populations is affected by inbreeding (see also Greenwood et al. 1978; Koenig and Pitelka 1979), genetic drift, non-random mating, and natural selection.

Barrowclough et al. (1985), Zink and Winkler (1983), and the present study have documented, for a wide variety of avian taxa, that the nature of genetic variation within populations is consistent with expectations of the Infinite allele-Constant mutation rate (IC) model, the simplest of the mutation-random genetic drift models of neutral theory (Chakraborty et al. 1980; Kimura 1982). Confirmation of predictions of the IC model demonstrate that certain classes of selection models, such as balancing selection, are clearly implausible mechanisms for the maintenance of genic polymorphisms within avian populations. For example, heterozygote superiority (heterosis or overdominance) would yield a bell-shaped distribution, rather than the J-shaped one observed in the avian data (e.g., Fig. 7). Nei (1983) reached similar conclusions. The consistency with neutral expectations implies that evolutionary processes might be deduced from allozyme re-

sults. For example, reconstructing the historical pattern of population fragmentation could be compromised if natural selection influenced allele frequencies.

I point out, as have others (Barrowclough et al. 1985; Kimura 1982; Chakraborty et al. 1980), that not all alleles are selectively neutral (e.g., Koehn et al. 1983). Instead, the majority of alleles found segregating in natural populations are considered, based on the tests of the IC model, to be selectively neutral. That is, the differences between the selection coefficients of alternative alleles at a locus are negligible relative to the inverse of the effective population size. Therefore, the fate of these alleles will be governed by stochastic processes. Certainly, some deleterious alleles arise via mutation (or possibly gene flow) and are removed from the gene pool by purifying selection. The present discussion refers to alleles detected by electrophoresis, and which *segregate* in populations of Fox Sparrows.

Environmental and Phenotypic Correlates of Protein Variation

Many authors (e.g., Ayala 1982) have searched for correlations between variation at individual loci and environmental factors (e.g., Redfield 1974; Kahler et al. 1980; Smith et al. 1983; Schwartz and Armitage 1981; Graves and Somero 1982; review in Koehn et al. 1983). It would be surprising if one could not find some environmental factor that covaried (significantly) with a polymorphic locus; Schnell and Selander (1981) make a similar point. For example, I found a significant correlation between elevation and the frequency of the LGG^c allele. The relationship might even be a cause and effect one, mediated by natural selection on protein products produced by the Lgg locus or a locus (loci) linked to it. Also, elevation and H are significantly negatively correlated, which might lead one to predict that less genetic variation is tolerated at higher elevations. However, variation at Lgg contributes significantly to H, and in effect, the number of significant correlation coefficients is approximately what one would expect by chance alone. Also, the results over all loci are essentially indistinguishable from selective neutrality. Therefore, I conclude that these significant associations between elevation and H (and Lgg) might be spurious.

Fleischer et al. (1983) reported a significant relationship between enzyme heterozygosity and morphological variance, and Baker and Fox (1978) reported an association between enzyme genotype and behavior (dominance) in the Dark-eyed Junco. Thus, natural selection on the phenotype could influence enzyme loci whose products contribute directly to behavior or morphological structures or are linked to such loci. However, Handford (1980) and Zink et al. (1985) failed to find significant associations between variation at enzyme loci and morphological traits in birds (including the Fox Sparrow) and Zink and Watt (1987) failed to document a heterozygosity-behavior association in several species of emberizid sparrows. Future studies of associations between enzyme heterozygosity and phenotypic traits should consider the possibility of obtaining spurious results because of multiple comparisons. I suggest that, in general, relatively few alleles found at enzyme loci are maintained directly or indirectly by natural selection.

Relationships among Genetic Characteristics of Populations

The analysis (Table 7) of correlations and partial correlations among estimates of genetic variation allows evaluation of some predictions. For example, as more

individuals in a breeding population are sampled, the number of polymorphic loci and alleles per locus should increase (Crow and Kimura 1970) and they do (Table 7). Of the significant partial correlation coefficients obtained between heterozygosity and ADA ("d" allele), LGG ("c" allele), POLY95, and NALL, the latter two are expected to be significantly correlated with heterozygosity because they contribute directly to its magnitude. The analysis revealed that variation at ADA and LGG contributes most to interlocality differences in heterozygosity (approximately 2–5%), not the most highly polymorphic locus (LA-2). However, there were no apparent adaptive explanations for the nature of geographic variation in levels of polymorphism at ADA and LGG. Variation among samples in the number of loci polymorphic at the 99% criterion is mainly attributable to the occurrence of rare alleles, a phenomenon dependent on sample size, and consequently the insignificant partial correlation coefficient between POLY99 and H ($r = 0.44$) is expected. Most of the other significant correlation or partial correlation coefficients are in accord with population genetic expectations (e.g., Crow and Kimura 1970). Somewhat unexpectedly, the significant negative correlation and partial correlation coefficients for LGG with H, POLY99, POLY95, and NALL imply that variation at LGG is an important determinant of among-site variation in these composite measures of genetic variation. Inspection of the geographic pattern of variation at LGG reveals no simple pattern of variation, however.

The purpose of the preceding exercise is to compare the observed and expected patterns of genetic variation within and among population samples (see also Smith et al. 1983). Such an analysis has not been previously performed for data on protein variation in avian populations. The finding of conformance of electromorph patterns to population genetic predictions lends confidence to the genetic interpretation of these data and their suitability for evolutionary analysis.

Genetic Variation and its Relationship to Population Demography and Subspecies Distributions

Many aspects of population demography might influence genetic variation. Avise and Selander (1972), Soulé (1976), Schmitt (1978), Yeh and Layton (1979), Shumaker and Babble (1980), Kilpatrick (1981), and McClenaghan and Gaines (1981) proposed that insular or isolated continental populations should show reduced levels of variability and potentially be genetically divergent because of drift in small populations and inbreeding. Isolated Fox Sparrow breeding sites, and those of low density (Table 1), show no reduction in H nor are they genetically divergent. This suggests that current conditions of population size and fragmentation have not prevailed historically (Nei et al. 1975).

Corbin (1981) postulated that boundaries between subspecies might be coincident with zones of increased heterozygosity. However, this hypothesis is plausible only if subspecies are genetically differentiated prior to secondary contact, an improbable condition for Fox Sparrows of the Schistacea group. Nonetheless, if subspecies have independent evolutionary histories and have differentiated genetically at loci not surveyed here, secondary contact between them might cause increased heterozygosity because of, for example, differential response to habitat ecotones, selection for new allelic combinations, or disassociation of coadapted multi-locus genotypes. It is apparent from Table 5 and Figure 2 that H neither

tends to increase nor decrease at subspecies boundaries. Even if subspecific boundaries are ignored, there are no apparent zones of increased heterozygosity that might signify a boundary between previously unrecognized evolutionary units or subspecies.

Levels and Patterns of Genetic Variation among Populations

Given that populations of Fox Sparrows possess genetic variation, an item of evolutionary interest is the amount of genetic variance distributed among samples. Typically, differentiation is measured by computing genetic distances or *F*-statistics (Wright 1965, 1978), both measures of an among-locality component of genetic variation. The amount of genetic variation among sites due to subdivision and drift (F_{ST}; assuming neutrality of alleles) is 1.35%. This value is typical of those observed for other avian populations (generally <5%), but lower than those found for many other vertebrates (see reviews in Selander and Kaufman 1975 and Barrowclough 1983). However, few F_{ST} values exist for avian populations (reviewed in Barrowclough 1983). Recent surveys, not included in Barrowclough's summary, by Fleischer (1983), Zink and Winkler (1983), Johnson and Zink (1983), Johnson, Zink and Marten (unpubl. data), and Zink et al. (1987) corroborate the generally low values of F_{ST}.

Baker et al. (1982) reported significant genetic heterogeneity in the White-crowned Sparrow along a linear series of song dialects spanning only 30 km in coastal California. They (Baker et al. 1982, 1984) argued that song dialects acted as barriers to gene flow and promoted genetic divergence among dialect groups. This is an important claim, as it implies a locally highly subdivided population structure (Zink 1985a), an atypical result of surveys of genetic population structure in birds. Zink and Barrowclough (1984) concluded that the allozyme data of Baker et al. (1982) yielded an equally plausible fit with an isolation by distance model, and that dialect populations are not discrete, genetically defined entities whose geographical limits correspond to dialect boundaries. However, over a short geographical span, these samples of White-crowned Sparrows exhibit more genetic heterogeneity (F_{ST} = 4.2%) than do Fox Sparrows over a much broader region (e.g., F_{ST} = 1.35%). More surveys of avian species with and without song dialects, and over broad geographic regions, are required to evaluate the evolutionary consequences of song dialects (see also Hafner and Petersen 1985). At present, it is not possible to conclude that song dialects cause or maintain genetic differentiation among populations (Zink 1985a).

Because the genetic structure of populations is related to evolutionary processes (Wright 1978), considerable attention has focused on estimating F_{ST} values in non-avian vertebrates; some studies are mentioned here to provide a perspective on the avian results. Larson (1980) reported an F_{ST} value of 0.47 for population samples (including geographic isolates) of *Aneides flavipunctatus* taken in the northern and western halves of California. Larson and Highton (1978) reported an F_{ST} of 0.74 in another salamander (*Plethodon dorsalis*). Studies of mammals have shown both high (e.g., Johnson and Selander 1971; Kilpatrick and Zimmerman 1975; Patton and Feder 1981; Zimmerman and Gayden 1981) and low (e.g., Nozawa et al. 1975; Dew and Kennedy 1980; Ryman et al. 1980; Honeycutt et al. 1981; Chesser 1983) values of F_{ST}. Sites and Greenbaum (1983) reported what

they considered to be one of the lowest F_{ST} values observed for a vertebrate (a lizard), 0.099. However, Avise and Aquadro (1982) and Barrowclough (1983) summarized several lower values. These few examples illustrate the levels of population subdivision observed in some terrestrial vertebrates (excluding bats). Of greater importance is the fact that for most vertebrate groups a range of population subdivision is known. Rarely are the values for a given taxonomic group consistently less than 0.05 (Barrowclough 1983). Birds as a *group* seem typified by possessing a low among-deme component of genetic variation. However, more avian populations need to be surveyed.

Avise and Aquadro (1982) and Aquadro and Avise (1982) have shown that biases because of different loci surveyed, and different laboratory conditions, such as sequential electrophoresis, do not account for the different levels of variation found in vertebrates in general, and the low level in birds in particular. Thus, the low degree of population subdivision in birds is not artifactual.

In general, comparisons of genetic distances among taxa agree with F_{ST} analyses. Low genetic distances were found among Fox Sparrow populations, the average being less than 0.002. The largest genetic distance observed between any pair of taxa is <0.004. Typically genetic distances between conspecific avian populations are <0.02 (Barrowclough 1980a), in spite of distances of hundreds of kilometers separating some samples. Values for comparisons among populations of non-avian taxa usually are an order of magnitude greater (Powell 1975; Nevo 1978; Avise and Aquadro 1982; but see Winans 1980; Dew and Kennedy 1980; Guries and Ledig 1982) than those observed for birds (Avise 1983; Barrowclough 1980a; Barrowclough et al. 1981).

Low genetic distances among taxa might result from a low level of genetic variation in the ancestral population. If it possessed low heterozygosity, then the descendant population would inherit much the same heterozygosity (Soulé 1976) and variation necessary for rapid genetic divergence would be lacking. If heterozygosity is moderate or high, and bottlenecks accompany divergence (or speciation), genetic distance between sister taxa could increase rapidly because of fixation of different alleles that were segregating in the ancestral population (Chakraborty and Nei 1977). Because of reasonable levels of H and low genetic distances among populations of Fox Sparrows, severe bottlenecks in population size have probably not been historically commonplace (Nei et al. 1975). Also, because other vertebrate groups with H values similar to birds exhibit higher genetic distances (Avise and Aquadro 1982), it seems unlikely that low levels of heterozygosity would account for the lack of differentiation among avian conspecific populations.

In the Fox Sparrow, the absence of geographic patterns of variation either at single loci or over all loci is not necessarily unexpected. First, surveys of intraspecific genetic variation in birds often detect only weak patterns (e.g., Johnson and Zink 1983). I caution, however, that this conclusion is based on surveys of mostly temperate oscines. Preliminary results from surveys of neotropical lowland forest birds indicate higher levels of differentiation (A. Capparella, unpubl. data). The low level of genetic variance partitioned among populations does not seem restricted to passerines, however. Zink and Winkler (1983) and Zink et al. (1987) found low levels of genetic variation among population samples of California Gulls and California Quail (*Callipepla californica*), respectively. Second, the average genetic distance between most avian congeneric species is very low; there-

fore, one should not expect substantial differences within species, such as those often observed in mammals and salamanders (Barrowclough 1983).

In summary, significant geographic variation was detected at at least one locus (SOD-1), although patterns of variation at individual loci were not concordant. One could not discover the geographic location of the breeding deme of an individual Fox Sparrow solely from genetic characterization of its enzyme loci. Examination of F_{ST} values and genetic distances further reveals either an absence or very low level of differentiation. Discriminating among the potential causes of this among-population homogeneity is a high priority for future study (Avise 1983); some possible explanations are considered below.

Population Genetics of Fox Sparrows: Inference of Processes

Patterns of allozyme variation can be used to infer the pattern of evolutionary history of populations or species (Wilson et al. 1977; Felsenstein 1982). In general, genetic similarity decays as a function of time since two populations last shared a common gene pool. Thus, a matrix of intertaxon genetic distances could be used to reconstruct both the spatial and temporal history of populations or species. Considerable debate continues over the existence and properties of a molecular clock (Radinsky 1978; Sarich and Cronin 1980; Vawter et al. 1980; Korey 1981; Lessios 1981; Avise and Aquadro 1982; Thorpe 1982). These debates mostly concern the empirical calibration of the clock for individual groups and whether one must calibrate each part of the genome separately (Britten 1986). For example, several different electrophoretic clocks have been used for vertebrates (Avise and Aquadro 1982) and caution must be used in their interpretation. Nonetheless, most molecular evolutionists would agree that genetic similarity decays with time. Therefore, taxa with no or few genetic differences must be, on average, relatively recently diverged from a common ancestor.

At first glance, the near absence of genetic differences among Fox Sparrow samples could be interpreted to mean that the allozyme data set cannot aid in understanding the spatial and temporal history of populations. Here I evaluate four hypotheses that are consistent with a lack of genetic differences among morphologically and ecologically differentiated populations of the Fox Sparrow. It is my contention that although few genetic differences were detected, the data nevertheless contribute to understanding aspects of the evolution of the Fox Sparrow.

Recency of Common Ancestry

An earlier analysis showed that the Fox Sparrow has probably been evolving independently since the late Pliocene (Zink 1982). Nonetheless, extant subspecies of Fox Sparrows might have been recently a part of an undifferentiated taxon, and sufficient time might not have elapsed to allow for genetic differentiation (see also Guries and Ledig 1982); that is, rates of genetic and morphologic change might differ (see Lewontin 1984). Chaparral, possibly suitable for Fox Sparrows, was present in the Great Basin, Arizona, and southern California in the Pliocene (Axelrod 1977, 1979). These habitat conditions might have allowed, relative to the current situation, a more extensive, less fragmented distribution of Fox Sparrows. The chaparral environments in the Great Basin were probably eliminated by the uplift of the Sierra Nevada in the late Pliocene, resulting in a lowering of

winter temperatures (Axelrod 1958). By the late Pliocene much of central and southern California was covered by sea (Smith 1979), with isolated land areas in southern California, such as the Transverse Range, possibly serving as a refugium. Thus, it is possible that the Pliocene distribution of the Fox Sparrow was not highly fragmented, albeit of reduced extent in southern California. If populations were isolated in the Great Basin and more westerly regions, no traces of genetic differentiation were detected that might be attributed to such isolation.

Climatic fluctuations doubtless altered the breeding distribution of Fox Sparrows or their ancestors during glacial periods. As recently as 20,000 years ago, much of the present breeding range of *megarhyncha* south of Lassen Peak was ice-covered (Hill 1975). The ice cap, more than 160 km long and 65 km wide, reached a thickness of 1,200 m in some valleys, and the firn line extended to 600 m on the west slope of the Sierra Nevada foothills along river drainages. Breeding habitats were presumably displaced to lower elevations in the southern Central Valley, probably at several points in time during the Pleistocene, concomitant with the advance and retreat of glaciers (Hill 1975). As a result, populations might have existed in a few, relatively uniform patches of habitat from which colonists emigrated as the glaciers melted, resulting in the modern distribution and the observed genetic homogeneity. Perhaps there was a single large "refugium."

In the Great Basin, numerous large lakes occurred at the height of Pleistocene glacial run-off (Snyder et al. 1964), and it is likely that riparian habitats were considerably more widespread and at lower elevations than at present, in association with these lakes and drainage systems. The current Great Basin breeding distribution of Fox Sparrows is probably a relict one, resulting from an altitudinal retreat to high-elevation riparian habitats as the Great Basin dried out. Thus, a recent, more widespread gene pool seems likely for Fox Sparrows from the Great Basin.

In summary, homogeneity of allelic frequencies could be a result of Fox Sparrows occupying a less fragmented range in the near past, with insufficient time for selection to sort out alternative alleles or genetic drift to operate (Nei et al. 1975).

Gene Flow and Effective Population Size

Gene flow in the White-crowned Sparrow appears to be high (Petrinovich et al. 1981; Payne 1981; Zink 1985a), as it does for birds in general (Barrowclough 1980b; Zink and Remsen, in press). Slatkin's (1981) method applied to allelic frequency data for Fox Sparrows suggests substantial gene flow. However, Slatkin's model assumes that the populations are in genetic and demographic equilibrium, which might not be the case for the Fox Sparrow, if it only recently underwent range expansion. Because of the important implications of a high level of gene flow, the assumptions of Slatkin's method will be considered briefly. An obvious alternative to high levels of gene flow is retention of ancestral allelic states (Slatkin terms this the "radiation model"). If Fox Sparrows only recently colonized the present range (see above), high gene flow would not be necessary to explain current genetic homogeneity.

The Fox Sparrow is a "weedy" species that invades new patches of chaparral probably as soon as suitable. A high rate of gene flow is a potential cause of geographic homogeneity of allelic frequencies, as suggested from analysis of the

spatial distribution of rare alleles. However, a hypothesis of recency of common ancestry is difficult to eliminate and might not be mutually exclusive. Slatkin (1981) considered unlikely the hypothesis of recent ancestry in situations in which the same, low frequency alleles occur in several demes. Unless populations were only recently isolated (and not in demographic and genetic equilibrium), homologous, low frequency alleles should be lost by genetic drift unless they are transmitted among sites by gene flow. That is, when populations reach equilibrium, segregating low-frequency alleles are those that arose *in situ,* subsequent to the fragmentation of the ancestral population.

Slatkin (1981) also considered if a balance between selection and mutation, operating independently in each deme, could produce a curve mimicking a specific pattern of gene flow, when in fact gene flow was very low or non-existent. Slatkin showed that this model is also improbable, because if the demes are independent, it would be unlikely to find the same allele in low frequency in many demes. Yet this is found in the Fox Sparrow and other species with high apparent rates of gene flow. Thus, apart from a very recent colonization episode effecting current distributions and genetic patterns (i.e., genetic and demographic non-equilibrium; Slatkin 1985a, b), gene flow appears high in the Fox Sparrow. As conditions of high gene flow, (a) gene flow must be high enough to ensure the dispersal of individuals carrying rare alleles, and (b) there cannot be a bias in dispersal tendency of individuals with rare alleles, and (c) the assumptions of Slatkin's (1981) model must be met.

Using a different method of analysis, Barrowclough (1980b) concluded that avian populations had relatively high rates of gene flow and high effective population sizes. For example, Barrowclough (1980b) estimated a value of $N_e = 7{,}679$ for the House Wren (*Troglodytes aedon*). Based on my field experience, I believe that Fox Sparrows can occur in population densities equal to those of House Wrens, and might have a similar population structure and effective population size. Kimura (1982) noted that at steady state (equilibrium), the origin of neutral alleles via mutation is balanced by random extinction, allowing prediction of the average heterozygosity per gene locus as $H_e = 1 - 1/(1 + 8N_e v)^{1/2}$, where v is the mutation rate and N_e the effective population size. This formula, called the "stepwise mutation model" (Ohta and Kimura 1973) is considered most appropriate for allelic variants detected by electrophoresis. Of course, estimates of N_e and v are rarely empirically determined, and I used a value of 8,000 for N_e (Barrowclough 1980b) and 10^{-6} for v (Kimura 1982). The predicted heterozygosity using these parameters, 3.05%, is very similar to that obtained in the electrophoretic estimates. The robustness of this estimate is dependent on values of N_e and v. If $v = 10^{-7}$, $H_e = 0.003$, a value differing by an order of magnitude from the observed heterozygosity. However, it is possible that the above estimates of N_e and v are of the correct magnitude. Thus, both high rates of gene flow and large effective population sizes could inhibit genetic differentiation among populations.

Rates of Molecular Evolution

Many authors have noted the reduced level of genetic differentiation among avian taxa (Barrowclough 1980a; Barrowclough and Corbin 1978; Avise et al. 1980a, b, c; Barrowclough et al. 1981; Zink 1982; Gutiérrez et al. 1983), relative to comparable taxonomic ranks in other vertebrates. Avise and Aquadro (1982)

suggested that the relatively high avian body temperature might prevent incorporation of new alleles. Another explanation advanced to account for this observation is that the avian molecular clock "ticks" at a relatively slow rate (Prager et al. 1974; Prager and Wilson 1975; Avise et al. 1980c). Sibley and Ahlquist (1982) criticized this view and suggested that the apparent slowdown in avian molecular evolution was attributable to the "oversplit" nature of avian taxa. Avise et al. (1980c), Avise and Aquadro (1982), Zink (1982), and Gutiérrez et al. (1983) point out that the phenomenon of reduced genetic variation is apparent at the species level. Because species limits seem well defined for birds, Sibley and Ahlquist's (1982) point of taxonomic inequality across vertebrates might be true in comparisons of genera and families, but not at the level of species and, as shown here, in local populations.

Avise and Aquadro (1982) and Avise (1983) examined the distribution of genetic distances in vertebrates and advanced several hypotheses to account for the wide variability in genetic distances. They focused on avian results but could find no compelling evidence for low avian inter-taxon distances other than a slowdown in rate of molecular divergence. However, the actual ages of avian taxa are usually unknown. Few independent geological criteria have been used to calibrate an electrophoretic clock and a variety of calibrations have been employed. Concerning the New World wood-warblers (Parulinae), Avise et al. (1980c) and Avise and Aquadro (1982) noted that if Mengel's (1964) scenario were correct, wood-warbler species would be on the average two million years old. Given the low average genetic distance among wood-warblers (Avise et al. 1980c), this would indicate a slow rate of change, namely that 1 unit of Nei's D would require 25 million years to accrue. Gutiérrez et al. (1983) calibrated an electrophoretic clock for some galliform birds, and they reported that 1 unit of Nei's $D = 26.3$ million years. These values are among the slowest reported for vertebrates. Therefore, the avian molecular clock might indeed "tick" at a slow rate (see also Thorpe 1982). However, these calibrations are subject to considerable error, because of uncertainty of timing of cladogenetic events, and are only rough estimates. Also, because of problems in calibrating genetic distances in situations of recent evolutionary divergence (Corruccini et al. 1980; Korey 1981), I do not convert genetic distances for Fox Sparrows into estimates of absolute time.

Slow molecular change, via lower mutation rates, could account for the low genetic distances among Fox Sparrow populations. However, a valid test of rates of molecular evolution would require comparison of genetic differentiation in taxa separated by the same geological (vicariant) events. Factors such as gene flow across barriers and effective population sizes must be equivalent. For example, a relict salamander in the Inyo Mountains of California has undergone considerable genetic differentiation (Marlow et al. 1981; Yanev and Wake 1981), whereas isolated populations of Fox Sparrows on similar mountaintops are not genetically distinct. Disjunct populations of gophers are also genetically divergent (Zimmerman and Gayden 1981). However, gophers and salamanders are far less vagile than Fox Sparrows, and probably have different population sizes and histories of population bottlenecks. These contrasts illustrate the types of factors that would need to be controlled for if one were testing the molecular slowdown hypothesis. Hence, a hypothesis of slower rates of avian molecular evolution is tenable but unproven. At the molecular level it will be informative to compare rates of

substitutions in coding and noncoding regions of DNA. The slowdown should be apparent in both regions. Such comparisons would clarify if the avian molecular conservatism is only in functional regions of DNA; if so, it might support the body-temperature hypothesis of Avise and Aquadro (1982).

Natural Selection

Uniform stabilizing selection could prevent genetic divergence among populations. Although at each locus the same allele was most frequent in all samples, tests of the IC model suggested that alleles segregating at enzyme loci are selectively neutral in two of three samples examined (Fig. 7; Barrowclough et al. 1985). Because of a lack of complete correspondence with selective neutrality in the Fox Sparrow (the only exception in 24 avian demes tested by Barrowclough et al. [1985]), natural selection might influence the geography of genetic variation in the Fox Sparrow. Ohta's (1976, 1977) mutation-slightly deleterious model does predict a J- or U-shaped distribution, but with a constant excess of rare alleles. This phenomenon deserves further study because rare alleles might be more common in birds, including the Fox Sparrow, than predicted by neutral theory (Barrowclough et al. 1985). However, even Ohta's model would not necessarily predict intense purifying selection needed to maintain the same allele in Fox Sparrow populations separated by 1,000 km and different habitats. As discussed above, I think it most likely that natural selection does not influence the maintenance of genetic polymorphisms in Fox Sparrow populations.

Implied under the hypothesis of selective neutrality of alleles at enzyme loci is that these loci might not be those most responsible for evolutionary change (e.g., Lewontin 1974; Wilson 1976). Dover (1982), Rose and Doolittle (1982), and Kidwell (1983) suggest that the genetic changes important in adaptation and in speciation and evolutionary divergence might not occur at structural gene loci. Instead, regulatory genes and/or structural genes under strong selection might drive organismal evolution. Thus, the set of genetic loci surveyed here might be biased in the sense that they do not include the genes important in determining variation in morphological dimensions and adaptation to different ecological environments (Fleischer et al. 1983; Handford 1980; Zink et al. 1985). It is important to recall that a goal of my electrophoretic analysis is to estimate the history of the fragmentation of populations. Estimation of this history is facilitated by access to characters that are not under selection. That is, the goal is not to study the genetic basis of bill size variation (itself an interesting problem); instead one desires a genealogical, or genetic framework upon which to examine patterns of morphological variation. Thus, the lack of differentiation observed among population samples of Fox Sparrows does provide information about their evolutionary history.

Summary

Little or no protein differentiation was detected among ecologically, morphologically, and geographically diverse samples of Fox Sparrows. I believe that the analyses of this "nondivergence" indicate that either populations are recently derived from a common ancestral gene pool or gene flow is currently high, or both. The genetic basis of phenotypic differences might not be reflected at enzyme loci, the alleles at which are selectively neutral. Nonetheless, the observed genetic

similarity provides an important perspective on Fox Sparrow evolutionary history—phenotypic differences might not have a genetic basis, might have only a minor genetic basis, and/or their rate of evolution might be very rapid. Whether they are right or wrong, investigation of these ideas stands to contribute information about evolutionary factors that influence geographic variation in birds.

Morphological Variation

As Johnson (1980) noted, analyses of intraspecific morphological variation in birds have contributed information about hybridization, reproductive isolating mechanisms, rapid adaptive evolution, and speciation. The objectives of the present morphometric analysis of geographic variation are to document (1) levels of character variation, (2) the nature and patterns of character variation, (3) patterns of phenetic similarity among population samples, (4) patterns of size and shape, and (5) ecological and environmental correlates of variation. A primary goal of (3) was to determine if discrete groups of samples existed, morphologically uniform *intra se,* for which an estimate of evolutionary history could be formulated. Such groups might correspond to evolutionary units (Cracraft 1983; Zink and Remsen, in press).

Levels of Character Variation: Systematic and Ecological Considerations

Several studies have examined levels of character variation (e.g., Sokal and Brauman 1980; Bird et al. 1981). Variability is necessary before natural selection (or drift) can produce change, in the classical, microevolutionary sense (Mayr 1963, 1970). Of course, other mechanisms, such as developmental shifts, allow evolutionary change in morphology without pre-existing, normally distributed character variation (e.g., Gould 1977; West-Eberhard 1986). Simpson (1944) suggested that a character with low variability within a population might yield relatively high fitness, which implies that stabilizing selection constrains or canalizes the range of phenotypic expression of the character (Via and Lande 1985). Bird et al. (1981) noted that variation in character CVs could reflect differences in fitness.

Because Fox Sparrows exhibit extreme inter-locality variation, it is of interest to determine if intra-populational levels differ from birds which both do and do not exhibit geographic variation. In addition, identification of characters or suites of characters with low variability might indicate important fitness traits. Table 20 provides CVs for samples of birds taken in continental portions of their distributions. Johnson (1980) provided further data, and Grant (1979a, b) and Power (1983) contrasted levels of character variability in island and mainland populations of birds.

CVs for skin and skeletal characters are usually $<10\%$. In my brief review of the literature, there is some indication that bill and leg/foot characters show more variability than wing and tail characters, basically the same pattern noted by Rothstein (1973) and Johnson (1980). However, beyond these generalities, few consistent patterns emerge. In Table 20, CVs are compared for skin measurements for my sample of all male Fox Sparrows (combined), and from seven relatively large samples from geographically and ecologically different sites (WHIT, BERN, SHAV, SHAS, TAHW, ODEL, BLAC). In general, bill characters and length of

TABLE 20

SUMMARY OF COEFFICIENTS OF VARIATION FOR SEVERAL SPECIES OF PASSERINE BIRDS, AND FOR SEVEN SAMPLES (ROWS 12–18 BELOW) OF FOX SPARROWS; THE OVERALL MEAN INTRA-POPULATIONAL CV FOR FOX SPARROWS IS ALSO GIVEN (ROW 11). VALUES FROM THE FIRST 10 STUDIES WERE CALCULATED FROM THE LARGEST SAMPLES REPORTED IN THE ORIGINAL PAPER

Species	Bill length	Bill width	Bill depth	Wing length	Tarsus length	Toe length
Acridotheres tristus[1]	4.91	4.04	4.34	2.59	3.30	4.86
Icterus galbula[2]	4.77	—	—	2.16	3.68	—
Melospiza melodia[3]	4.25	3.58	2.84	2.14	2.77	—
Melospiza melodia[4]	4.38	—	3.61	3.10	2.81	—
Agelaius phoeniceus[5]	3.40	—	4.60	2.76	4.25	—
Parus caerulescens[6]	5.00	3.77	4.86	3.70	3.70	—
P. gambeli[7]	5.56	7.28	7.64	3.59	—	—
Campylorhynchus gularis[8]	5.13	4.60	3.60	1.97	3.19	4.64
Carpodacus mexicanus[9]	4.32	3.21	3.97	2.28	3.53	4.32
Passer domesticus[10]	3.79	3.43	—	1.88	3.62	—
Passerella iliaca[11]	4.90	3.70	4.40	3.20	3.00	4.60
P. iliaca[12]	6.52	5.84	5.85	3.18	3.33	5.83
P. iliaca[13]	4.74	3.42	3.11	3.23	2.33	4.98
P. iliaca[14]	3.83	3.19	4.51	2.85	2.87	5.68
P. iliaca[15]	3.33	3.74	3.13	4.24	2.37	3.73
P. iliaca[16]	3.19	3.21	3.70	2.82	3.46	4.49
P. iliaca[17]	5.35	5.14	5.57	3.06	3.62	4.70
P. iliaca[18]	4.68	2.45	3.24	3.35	2.75	5.09

[1] Baker and Moeed (1979). [2] Rising (1970). [3] Smith and Zach (1979). [4] Dickerman (1961). [5] Howe et al. (1977). [6] Grant (1979a). [7] Behle (1956). [8] Selander (1964). [9] Power (1983). [10] Selander and Johnston (1967). [11] Present study, means. [12] White Mountains. [13] Black Butte. [14] Odel Butte. [15] Mt. Shasta. [16] Lake Tahoe. [17] Shaver Lake. [18] San Bernardino Mountains.

the hind toe plus claw are more variable than wing and tarsus lengths, although levels of variability differ between sites. For example, the CV for bill length ranges from 6.52% (WHIT) to 3.19% (TAHW). The other bill characters show similar variation among sites, whereas levels of variability in wing and tarsus lengths are fairly uniform among sites. No consistent geographic patterns, such as a cline in CV-values, are apparent in character variability; this parallels the results obtained by Selander and Johnston (1967) for House Sparrows.

CVs for the skeletal characters (Table 21) are <5%. There is no compelling evidence that any particular body region is relatively more variable, with the possible exception of wing characters (HUMRL, ULNAL, ULPEW). As found for skin characters, differences exist in levels of variability among samples. For example, CV-values computed for PSYNL, FEDEW, SCPEW, and SKULL each differ by up to 2.5% among sites. Geographically isolated samples, such as BERN, do not show either more or less variability (e.g., compare value for characters at BERN to overall means). The WHIT sample, from the Great Basin, similarly shows no consistent departures from the overall means. Thus, there is no consistent pattern of variation in CVs for skeletal characters that might correspond to ecological (e.g., chaparral versus riparian) or environmental factors; no clines in CVs are evident.

Few avian studies have examined intra- and inter-populational variation in skeletal characters, so a detailed comparison of Fox Sparrows and other species is not possible. In Table 21, a few CVs from a study of House Sparrows are provided, and these are in the range of those found for Fox Sparrows.

TABLE 21

COEFFICIENTS OF VARIATION COMPUTED FOR ALL INDIVIDUAL FOX SPARROWS, AND SEVEN INDIVIDUAL SAMPLES. ALSO SHOWN ARE VALUES FOR NORTH AMERICAN HOUSE SPARROWS. CHARACTER AND LOCALITY CODES ARE DEFINED ON P. 13 AND APPENDIX I

Character	WHIT	BLAC	ODEL	SHAS	TAHW	SHAV	BERN	Mean	*Passer domesticus*[1]
SKULW	3.39	2.65	1.73	2.19	2.64	2.11	2.00	2.30	—
SKULL	5.34	4.05	4.76	3.27	2.93	4.11	4.30	4.20	1.80
CORAL	2.69	2.63	3.26	2.85	3.31	3.37	2.53	2.70	—
SCPEW	5.02	4.88	4.15	3.28	4.42	5.62	5.00	4.40	—
STERL	2.43	3.29	3.17	2.97	4.27	4.98	3.06	3.10	2.84
PSYNL	5.55	5.21	7.44	3.85	5.14	4.90	4.36	5.60	—
SYNXW	2.97	3.53	2.88	3.19	3.93	3.06	2.32	2.70	—
FEPEW	3.12	3.87	3.02	2.70	3.42	3.08	2.98	3.20	—
FEDEW	3.95	2.47	6.63	3.41	6.40	5.73	3.99	4.10	—
FEMRL	2.29	2.10	2.08	1.95	1.71	2.57	1.97	2.20	2.93
TIBOL	2.08	2.32	2.10	2.55	2.39	2.55	2.37	2.30	2.88
HTROL	4.38	2.80	2.13	2.92	2.66	3.00	3.40	3.00	—
HUMRL	1.89	2.06	2.03	2.32	1.54	2.94	1.64	2.00	2.46
ULNAL	1.65	1.94	1.95	2.29	2.24	3.18	1.77	2.20	2.46
ULPEW	2.51	3.12	2.09	2.87	1.86	2.66	1.88	2.44	—

[1] Johnston and Selander (1971).

Three aspects of intra-populational character variability are emphasized here. First, character variability in Fox Sparrows is consistently neither more nor less than that found in a variety of birds (Table 20). Second, CVs are <10% for all characters, with bill characters showing the most variation relative to wing and tarsus length. Third, variation in levels of variability among sites might be relatively great in Fox Sparrows; that is, differences among sites can exceed interspecific differences (Table 20). Because the mean CV-value (over all individuals) might be misleading, analysis of patterns in populational CV-values should be pursued.

Numerous authors have examined morphological variability and searched for adaptive explanations for among-site differences (e.g., Van Valen 1965; Soulé and Stewart 1970; Rothstein 1973; Hamilton and Johnston 1978; Grant 1979a; Power 1983). Some of these studies have correlated increased character variability with increasing niche breadth within populations, whereas others (e.g., Schoener 1970) have proposed that morphological variability is attributable to interspecific competition. Grant (1979a) evaluated character variability in Blue Tits (*Parus caerulescens*) taken from islands and mainlands and in the presence or absence of a congener. He concluded both that morphological variability increased in the absence of a congener (presumed competitor) and that phenotypic trends were also a part of broad-scale clinal variation, which he attributed as response to environmental factors.

Both within and among Fox Sparrow populations, bill characters tend to be more variable than skeletal and other external characteristics, excluding the length of the hind toe plus claw. Both bill and hind toe plus claw are probably subject to the effects of abrasion, and, therefore, some of the increased variance could be nongenetic and simply attributable to wear. Another interpretation of increased

bill variability is that within the observed range of bill sizes and shapes, bills do not differ in selective value. An alternative, food-related hypothesis is tenable. Diets show annual variation, from primarily insects in the breeding season to vegetable matter in winter (Linsdale 1928; pers. obs.). Winter densities of Fox Sparrows are high because birds (including young) from several distinct breeding areas winter syntopically, in an area of lesser extent than the combined sum of their breeding areas. Morphological structures associated with foraging might be subjected to selective pressures for minimizing competitive interactions and exploiting a variable set of resources over the annual cycle, hence, greater intrapopulational variability in bill dimensions. Of course, it is unclear why other characters require less variability to cope with annual habitat and diet variation. Simpson (1944) suggested that increased variation is evident in traits that are less important for fitness. Study of the association between prey size and type and bill size in the Fox Sparrow is needed for the annual cycle. Bill characteristics are heritable in Song Sparrows (Schluter and Smith 1986), indicating the potential to respond adaptively by natural selection. It would be of value to document heritability and fitness consequences of bill size variation in the Fox Sparrow, because this would clarify if bill size variation has an adaptive basis.

As alluded to by Grant (1979a), levels of variability might be influenced by the presence of other species that might be competitors for resources. For example, Song Sparrows breed sympatrically (and syntopically) with Fox Sparrows in the White Mountains, but not in chaparral. If these two species compete for resources, Fox Sparrows might be expected to show lower CVs for bill characters, or character displacement, because part of the foraging niche is occupied by Song Sparrows. The species have somewhat overlapping bill morphologies (Linsdale 1928; Zink 1982). Examination of CVs for WHIT and SHAV, geographically proximate but ecologically different samples, reveals that differences do exist, but the WHIT sample is *more* variable for all characters except tarsus length (and especially for length of bill and hind toe). Thus, the presence of Song Sparrows might "cause" Fox Sparrows to exploit a relatively broader range of foods in the White Mountains. Alternatively, one might argue that the generally smaller bills of Fox Sparrows in the Great Basin represent a shift because of the presence of Song Sparrows. However, it is not possible to control for habitat differences affecting bills of Fox Sparrows independently of competing species. Unfortunately, sample sizes from the Great Basin are small, and it is inappropriate to speculate further about patterns of variation in Great Basin Fox Sparrows. Considerable variation in level of character variability exists among the chaparral samples (Table 21), which implies that chaparral *per se* (relative to riparian habitats) is not an important determinant of levels of character variation; there are no systematic patterns to the variation.

I suggest that differences in character CV-values are difficult to interpret in an adaptive context (Gould and Lewontin 1979). Characters, or suites of them, might be relatively more or less variable because of differences in heritability and number of genes contributing additive genetic variance to their expression (Lerner 1954; Falconer 1981; Lewontin 1984). Quantitative genetic analyses are required to determine the evolutionary importance (fitness) of differing levels of variation in polygenic traits such as bill dimensions, measured in populations where the environmental contribution to phenotypic expression might vary. That is, from only

correlation analyses, it would be difficult to be certain of an ecological (adaptive) cause-and-effect relationship for characters differing in CV-value among populations. Studies of marked individuals over several generations will begin to unravel the nature of natural selection on external phenotypic characters (Boag and Grant 1981; Price et al. 1984a, b; Schluter and Smith 1986).

In conclusion, there are some differences among populations of Fox Sparrows in levels of character variability, much as for heterozygosity. Certainly such differences might have a genetic basis and be a result of differing selection pressures. I detected no obvious ecological or environmental correlates of interpopulation differences in CVs; perhaps further analysis would detect some.

Levels and Patterns of Character Variation among Populations

The relative amount of inter-locality character variation can be ascertained by examining the between-locality sums of squares from ANOVA (Tables 9 and 11). Some characters exhibit higher levels of geographic divergence relative to others, a result consistent with most studies of avian geographic variation (e.g., Handford 1983). ANOVA on PC scores (Table 14) also indicates that a significant portion of the phenotypic variance is partitioned among sites, especially for size (PC I). Although to a lesser degree than PC I, a significant amount of variation is distributed among samples for most analyses of scores on PC II and PC III. These quantitative summaries confirm the existence of geographic heterogeneity in morphometric traits.

In morphometric studies of avian populations, patterns of character variation are not always concordant (Rising 1970; Power 1970; Baker 1980; Johnson 1980). Some studies have documented similar patterns of variation between the sexes (Johnson 1980) whereas others have not (Baker and Moeed 1980). In the Fox Sparrow, characters that exhibit a definite pattern of variation tend to show a common one for both sexes, namely that found for cube-root of mass (Fig. 8); the differences between the sexes are apparent but relatively minor. If cube-root of mass reflects size, then geographic patterns of character variation are strongly influenced by size, a result also consistent with many studies of avian geographic variation (Zink and Remsen, in press).

Character variation in Fox Sparrows has several features. Birds from the Great Basin are nearly always smallest in size, resulting in a rather sharp break (possibly a step-cline) between the Great Basin and regions to the west. However, too few samples were available to determine if clinal patterns exist in the Great Basin. Many characters exhibit a north–south clinal pattern in the Cascades and Sierra Nevada. This clinal pattern does not have a plateau at the north end, but values increase steadily from ODEL to LOOK where they tend to stabilize at a uniform value in the southern Sierra Nevada and Transverse Range (e.g., *stephensi*). That is, many characters vary along a north–south cline which bifurcates and results in large character means in the North Coast Range and across southern California (e.g., *stephensi*).

Regions of phenotypic uniformity connected by clines do not exist. Thus, character clines are probably a result of primary intergradation (see Endler 1977). It is difficult to determine if the stepped nature of character variation at the Great

Basin-Sierra Nevada interface is primary or secondary intergradation between two previously allopatric and differentiated units. I think that primary intergradation is the most parsimonious hypothesis, because the environmental changes are also abrupt.

Potential Environmental Determinants of Morphological Divergence

Patterns of character variation might arise and be maintained in response to environmental features. Johnston and Selander (1964, 1971), James (1970), Power (1970), Rising (1970), Niles (1973), and Baker (1980) found that character variation in some bird species seemed to parallel variation in environmental characteristics (see review in Johnston 1972). Alternatively, Ross and Baker (1982) were unable to identify phenotype-environmental correlations over a fairly local scale. Few weather stations were located near my sampling sites. Furthermore, data were unavailable for wet-bulb temperature, vapor pressure, and absolute humidity, important variables to compare with morphological patterns (F. James, pers. comm.). Thus the environmental (temperature, rainfall) data are relatively weak, inhibiting detection of precise, quantitative associations with phenotypic variation.

The canonical correlation analysis identified latitude and May minimum temperature (MAYM) as environmental features that account for variation in study skin characters for both sexes, plus annual precipitation for females. Obviously, latitude *per se* is uninformative, and, therefore, characteristics associated with latitude must be important (see James 1970; Mosimann and James 1979; James 1983). Patterns of morphological variation were less related to elevation and longitude, although these vary to a lesser extent than latitude. Most monthly minimum temperatures are only weakly associated with morphological patterns, conflicting with both Bergmann's and Allen's rules (see James 1970; Zink and Remsen, in press). For example, tarsus length is correlated with MAYM at a relatively low value of 0.326, the highest correlation coefficient found for this character and an environmental parameter.

The canonical correlation analysis suggests that morphological variation in females could be attributable to latitude, annual precipitation, and MAYM. However, in contrast to the analysis of males, the lengths of the wing and hind toe are not strongly represented on Canonical Variable I, and latitude and MAYM are not as highly associated with morphological variation. Thus, it appears that morphology "responds" to environmental factors differently in males and females. The sexes differ somewhat in their pattern of geographic variation, and this analysis (Table 18) identified potential causative agents in need of future analysis.

The trend of decreasing size toward the north conflicts with Bergmann's Rule. James (1970) refined the "rule" as "Small size is associated with hot humid conditions, larger size with cooler or drier conditions." Because mean temperatures decrease with increasing latitude and elevation, high elevations in low latitudes should mimic the conditions at higher latitudes. In the Fox Sparrow, character means generally are not significantly associated with elevation. In contrast to many other species of birds (Johnston 1972; Aldrich 1984), morphological variation in the Fox Sparrow does not seem to vary with latitude and elevation

in the ways predicted by either Bergmann's or Allen's rules. Zink and Remsen (in press) reviewed evidence for these rules and found weak support for them; Gloger's Rule, however, received strong support.

The relationship between skeletal characters and the environmental data is similar to that obtained for skin characters. Again, elevation and longitude are not strongly associated with character means. That is, phenotypic variation is influenced to a lesser degree by elevation and longitude than factors associated with latitude. Bergmann's Rule predicts that the body core should be larger in colder environments. However, most mean temperatures and precipitation values are not significantly associated with character means. With regard to Allen's Rule, as in the analysis of skin characters, "extremities," such as lengths of the tibiotarsus, femur, ulna, and humerus, are not significantly correlated with temperature; the highest correlation of one of these characters with a minimum temperature is 0.144 (STERL). Thus, variation in skeletal characters also seems at odds with Bergmann's and Allen's ecogeographic rules.

Inspection of the results presented in Table 19 shows that for males, June temperatures (a period of nestling growth), latitude, and annual precipitation are correlated with patterns of variation in skeletal characters. A considerably different picture emerges for females, because June temperatures seem unrelated to morphological variation, and only latitude seems to represent an underlying determinant of phenotypic patterns. Also, the loadings (Table 19) for female morphological traits are consistently lower than males, and considerably more variable, ranging from 0.067 (STERL) to 0.538 (FEMRL). Therefore, the analysis does not identify any suites of environmental characters potentially responsible for trends in morphological variation in females. As in the analysis of skin characters, the sexes seem to vary in different ways with respect to the environmental factors considered here. A comparison of male and female growth rates would be useful (for any type of data).

The analyses of Fox Sparrows (Tables 18, 19) did not expose consistent correlations between morphological and environmental factors. However, besides the lack of weather stations near collecting sites and potentially less informative climatic variables, the limited geographic scale used here (relative to continent-wide surveys, e.g., James 1970) might obscure environmental correlates of morphological variation. To summarize the canonical analysis, I suggest that factors correlated with latitude, but not measured here, could influence the clinal patterns observed. For example, day length, nest microenvironments, or the range of temperature fluctuations (Murphy 1985), might be important. Also, geographic variation in foods fed to nestlings could influence growth patterns, and as a consequence, adult morphology. Factors affecting size need study.

Morphological variation might be "determined" by natural selection occurring on the winter grounds. For this hypothesis to be valid, philopatry to breeding sites must be well developed. That is, if winter conditions vary in a clinal fashion, breeding demes must have (1) developed precise migratory patterns prior to morphological differentiation, and (2) show extreme site fidelity to both breeding and wintering sites. Because of Swarth's (1920) seemingly plausible adaptive explanation for the matching of plumage color and winter humidity conditions (leapfrog migration), the above hypothesis merits consideration. However, I doubt that variation in winter conditions influences morphological patterns among

breeding populations. Up to 10 subspecies of the Fox Sparrow regularly winter syntopically in California (Linsdale 1928; pers. obs.), and it seems questionable if the same winter environment affects differentially the survival of Fox Sparrows from different breeding sites.

Fox Sparrows begin migration prior to completion of growth of most body parts including the bill (Swarth 1920), but the degree of completion of growth prior to departure for the winter grounds is unknown. Therefore, young birds might complete growth in a different environment from that in which they were hatched and fledged. Environmental conditions encountered during early migration during the first year of life could influence patterns of growth. However, it seems unlikely that conditions encountered on fall migration could cause the observed clinal variation among breeding demes, because often young of several phenotypically distinct subspecies co-occur syntopically in migration (Linsdale 1928; Zink, pers. obs.). In my opinion, the primary determinants of morphological patterns of variation act during the nestling period. Nevertheless, documentation of morphological development that occurs after departure from the breeding grounds is needed.

Historical Patterns and Temporal Stability of Phenetic Relationships among Populations

Because no two characters exhibit the same pattern of variation, multivariate analyses were used because they simultaneously incorporate variation in all characters. The objectives are to account for character correlations (redundancy), estimate the principal geographic "theme" of morphological variation, and to search for historical patterns.

The Mantel tests (Table 17) revealed that patterns of geographic variation in morphology, as summarized by the taxonomic distances, reflect geographic proximity. The taxonomic distances among samples vary as a function of the linear geographic distance between sites. However, the rather low matrix correlation coefficients between geographic and taxonomic distances (0.43 for skins, 0.34 for skeletons) indicate that geographic isolation, or among-site distance, might not be the only factor responsible for morphological differentiation. In other words, populations, or groups of them, might share a common evolutionary history not strongly associated with the linear geographic proximity of samples. However, a significant component of the low matrix correlations involves the samples of *brevicauda,* which are morphologically very similar to samples from southern California, yet are geographically rather distant. If these samples were removed, the matrix correlation coefficients would undoubtedly increase. Thus, an isolation-by-distance effect is present. The phenetic resemblance of BLAC and YOLL to samples from southern California is meaningful and should not be ignored. Discovery of environmental similarities or historical routes of gene flow between these two regions might clarify if the phenotypic similarity is ecological or historical.

The significant association between taxonomic and geographic distances is consistent with several interpretations: the rate of gene flow decreases as a function of geographic distance, local selection overcomes gene flow, or environmental gradients affecting expression of phenotypic variation are themselves clinal (and the traits influenced by nongenetic factors). Determining the relative magnitudes

of these factors would clarify the ecological and historical components of the observed phenotypic variation (Endler 1982).

The cluster analyses defined groups of samples that generally correspond to three regions: Great Basin, southern California plus North Coast Ranges, and the remaining samples. Certain samples, such as WARN, WHIT, ODEL, PYRA, SAWY, and SHAV are morphometrically intermediate. In the PCAs (Figs. 17, 18, 23, 24) groups of samples were identified that generally correspond to those identified in the phenograms. (Although one might expect congruence because both analytical techniques used the same data, each analysis operates under different assumptions and has somewhat different goals.) The SS-STP analysis of individuals' PC scores (Table 14) illustrated more precisely the pattern of geographic variation. Patterns of variation for both sexes and for both character sets exhibited concordant clinal patterns on PC I, namely a north to south increase, strikingly similar to that obtained for cube-root of mass, or size. No discrete sets of characters emerged as especially influential in the north–south clines or the three groups of samples; instead, all characters seem influenced by size. Inspection of patterns of variation of PC II and PC III scores reveals a less structured pattern, and most of the variance is contained within samples (Table 14). Therefore, shape does not vary in a geographically ordered fashion, a result corroborated by the size-standardized phenograms.

Numerous workers have investigated the relationship between size and shape (Mosimann and James 1979; Humphries et al. 1981; Lemen 1983; Wood 1983; Bookstein et al. 1985). The usual assumption is that geographic patterns in shape are likely to have a more complex genetic basis than size-related factors, which can affect many characters in a similar way (Humphries et al. 1981). Whether this is true is open to debate, as size *per se* might be an important characteristic (James 1970; Garnett 1981; Atchley 1983) because it is often heritable. In the Fox Sparrow, increasing size results in differing shapes because of allometry of different body regions (Figs. 15, 16). Nonetheless, if variation in size can be effected by relatively few genes, then patterns strongly influenced by size might arise rapidly. That is, it might take longer for a consistent geographic pattern of shape to arise when it requires a more extensive genetic reorganization (Lemen and Freeman 1984). Because there is no consistent pattern to shape variation in the Fox Sparrow, one could hypothesize a lack of extensive genetic differences among samples. Mosimann and James (1979), Power (1970), James (1970), and Abbott et al. (1977) documented patterns of shape variation in birds, whereas Ross and Baker (1982) did not. Further studies are needed on patterns of shape variation and its covariation with size.

Earlier I (Zink 1983) examined the temporal stability of morphological patterns in Fox Sparrows using samples from seven sites included in this study. At certain levels of organization, patterns of variation were stable over 50 years, but at some sites, some character means differed statistically. As a result of temporal change, the patterns of phenetic similarity among sites differ between the two sampling periods. Temporal variation has at least two implications. First, chronological variation can bias analyses of variation that use samples of individuals pooled across time (Pizzimenti 1981). Second, some of the among-site variation in size might be labile. A future analysis should examine patterns of character covariation across years to determine if "shape" or character correlations remain constant.

Temporal variation might mean that phenotypic variation among populations is a result of current (or very recent) ecological pressures instead of a reflection of population genealogy or history.

A goal of the analysis of phenotypic variation is to determine the existence of groupings of samples that might represent independently evolving units. For example, within the Yellow-bellied Sapsucker (*Sphyrapicus varius*), Johnson and Zink (1983) suggested that three (biological) species exist. In the Fox Sparrow in western North America, three somewhat phenotypically distinct groups of samples were identified. In the majority of the phenograms, the large specimens from southern California and the North Coast Ranges stood apart, implying that the other two groups were phenetically most similar to one another. If phenetic similarity is related to historical patterns of phenetic divergence, then these samples are most closely related. However, the distinctiveness of the three groups is blurred by phenotypically intermediate samples, temporal variation exists, and a dominant component of intergroup differences is size. Therefore, in spite of the very great differences between extreme phenotypes in these groups, there is no definitive evidence of groups of samples with independent evolutionary histories.

Morphological and Protein Covariation

Numerous authors have examined the relationship between protein and morphological variation in organisms other than birds (Smith et al. 1982). Previous studies have suggested that these character sets are probably subject to different evolutionary pressures and often evolve independently (Schnell and Selander 1981). However, nonconcordance might be an expected result of the statistical limitations involved in detecting differences in quantitative (e.g., morphological) traits as opposed to those with simple genetic bases such as allozymes (Lewontin 1984, 1986). In Fox Sparrows of the Schistacea group, the F_{ST} analysis revealed that most (over 98.5%) of the allozymic variation resides within populations, in stark contrast to morphological characteristics (Table 14), especially size. The phenogram summarizing levels of genetic similarity produced no geographically ordered pattern, whereas morphological variation is geographically structured. Extirpation of Fox Sparrows from a major portion of the range would not markedly reduce levels of genetic variation, either qualitatively or quantitatively. However, such an extirpation event could drastically alter the geography of phenotypic variation. Whether or not allozymes and morphology evolve(d) independently in the Fox Sparrow cannot be known without data on the heritability and number of loci contributing genetic variance to morphological traits (Lewontin 1984). Nonetheless, the decoupling of evolutionary processes acting on allozymes and morphology remains a viable hypothesis.

Only Handford and Nottebohm (1976) and Johnston (1975) examined quantitatively inter-populational concordance of allozymes and morphology in birds. Both studies found generally low congruence. Between species, Zink (1982) and Barrowclough (1983) identified lineages of birds that have seemingly undergone differential amounts of protein and morphological divergence. Although no other quantitative comparisons of protein and morphological variation are available for birds, some studies of allozymes in birds have detected patterns of variation that are consistent with traditional morphological limits. Johnson and Zink (1983) identified patterns of protein variation that matched morphological patterns in

sapsuckers. Additional quantitative studies of protein and morphological variation in birds are required before a basis will exist for determining the degree of congruence of different data sets.

A Molecular Perspective on the Origin of Morphological Variation

Several workers believe that passerine bird species originated in the Pleistocene (Mengel 1964; Brodkorb 1971; Hubbard 1973; Sibley and Ahlquist 1982). Many species-specific characters in birds are plumage traits, traits that might be subject to rapid evolution (Avise et al. 1980c; Sibley and Ahlquist 1982). Importantly, however, geographic variation is usually most evident in plumage coloration, and not species specific plumage patterns (usually debates over subspecies or species status involve plumage patterns). Other traits, such as bill characteristics, are thought to be evolutionarily "plastic" and able to change rapidly. Many birds, especially passerines, differ in traits potentially capable of rapid evolution. The low degree of allozymic divergence measured for many avian populations and congeneric species is consistent with a hypothesis of rapid phenotypic evolution, in both species-specific plumage traits and other characteristics (e.g., bills, plumage coloration). A lack of allozyme differences is also consistent with an interpretation that intraspecific differentiation has a large nongenetic component.

The potential rate and magnitude of phenotypic change is not directly assessable for most birds. Documented cases of rapid (i.e., hundreds of years) changes in morphology (Johnston and Selander 1964; Zink 1983) might not include species-specific morphological characteristics. For example, after 100 years since the introduction of House Sparrows into North America, they have differentiated but are still clearly recognizable as House Sparrows; their species-specific features have not changed. Also, allozymic differentiation is weak (Fleischer 1983). Wake et al. (1983) noted phenotypic stasis in species-specific characteristics over tens of millions of years in salamanders, which they attributed to developmental canalization. The fossil record of birds has not been studied sufficiently to allow such generalizations for many birds. However, Steadman (1981) described a fossil sparrow from the Miocene of Kansas that was very similar to the extant Grasshopper Sparrow (*Ammodramus savannarum*), indicating substantial phenotypic stasis in some, apparently species-specific, skeletal features. Steadman's important report seems to conflict with the general impression of rapid evolution in passerine birds. The Grasshopper Sparrow is allozymically differentiated from a variety of apparently closely related sparrows (Avise et al. 1980b), possibly indicating a long period of independent evolution. However, the origin of species-specific characteristics of the Grasshopper Sparrow might have been rapid or slow.

Analyses of genetic data strongly indicate that populations of Fox Sparrows have not been isolated and evolving independently for a long period of time (as might be predicted from patterns of morphological variation). Even aspects of morphological differentiation are consistent with (but not proof of) rapid change, such as a strong size component and random shape differences. Although the lack of allozyme differences is not evidence of genome-wide genetic similarity, it suggests that hypotheses of phenotypic evolution that require either no or little genetic differentiation and selection should be explored. Even if there is an extensive genetic reorganization underlying morphologically differentiated populations, the

allozyme perspective yields a picture of rapid phenotypic differentiation (for which a model was presented by Lande [1985]). It is a viable hypothesis that the phenotypic differences among extant populations of Fox Sparrows have arisen since occupation of the current range, less than or equal to 20,000 years ago. The discussion (above) of Pliocene and Pleistocene climatic events in California and the Great Basin addresses this idea.

A Hypothesis for the Origin and Maintenance of Morphological Differences among Fox Sparrow Populations

If natural selection affects loci not measured by electrophoresis, alleles at selectively neutral loci (allozymes) might flow through areas that contain selection barriers to alleles at loci under selection, such as those that encode morphological traits. This process could result in genetic homogeneity of electromorphs and yet there could be genetically mediated local adaptation in morphological traits. Of relevance to the local adaptation argument is the heritability of traits under study. Several authors have documented significant heritability of morphological characters *within* populations of birds (e.g., Boag and Grant 1978; Smith and Zach 1979; Smith and Dhondt 1980; Garnett 1981; Dhondt 1982). James (1983) transplanted eggs of Red-winged Blackbirds among Florida, Colorado, and Minnesota, monitored the growth and development of young, and compared phenotypes of young birds to those of the foster and parental populations. She found that young birds resembled the phenotypic conditions typical of the foster population to a greater-than-expected degree. As Gould and Johnston (1972) noted, even if morphological traits are significantly heritable *within* populations, their expression *among* localities might be primarily influenced by environmental factors and not necessarily indicate underlying genetic differences.

The type of analysis performed by James is a crucial step in evaluating the causal factors and ultimately the evolutionary significance of geographic variation. Many students of avian geographic variation have assumed that geographic variation represents differing genotypes yielding specific morphologies in different areas (e.g., Aldrich 1984; Zink 1985b). The origin of geographic variation is thought to be a more-or-less gradual adaptation of populations to local conditions via the action of natural selection working on individual genetic variation within populations. An equally viable hypothesis is that morphological variation, excluding plumage characteristics which seem under direct genetic control (see, however, Slagsvold and Lifjeld 1985), is environmentally induced. The phenomenon of nongenetic geographic variation is well known in plants (e.g., Wheeler and Guries 1982), and has been acknowledged by zoologists for decades (e.g., Mayr 1963). Therefore, a polytypic species should not be assumed to be also genetically substructured. Other hypotheses should be developed to explain morphological patterns of variation.

By what mechanism(s) could morphological differentiation in Fox Sparrows arise rapidly and be maintained over geography in the face of high gene flow? Might more than just selectively neutral genes flow? One explanation arises from Gould (1977), Alberch et al. (1979), and Alberch (1980). These authors have developed the idea that morphological differences among taxa arise via alteration of the timing of developmental events and growth rate of different body regions

during the ontogeny of an individual. The genetic basis of such developmental shifts, and therefore the resultant phenotypic consequences, might be slight and uncorrelated with overall genomic trends (and patterns in other characteristics). Also, the geography of variation might result entirely from gene-environment interactions, in which case genotypes need not vary geographically. That is, the same genotype has a range of potential phenotypes (Via and Lande 1985), and differing local environments might induce particular phenotypes, and geographic variation. The phenotypic consequences of seemingly minor shifts in developmental pathways can be rather great (e.g., Alberch 1980). Grant (1981) examined interspecific morphological differences among some Galapagos finches, and concluded that relatively simple changes (undoubtedly genetic) occurring during ontogeny could explain many interspecific phenotypic differences; few such analyses exist for other avian taxa (Engles 1940). I develop this idea briefly because it applies to population differences in the Fox Sparrow.

Allometry exists among characters. A 10% difference in mass is generally correlated with a 10% (±5%) increase in other body proportions, with the major exception of the bill. Hence, as size increases, body parts scale in an isometric fashion (e.g., Fig. 15) exclusive of the bill. Characters, or suites of characters, have particular ontogenetic trajectories. If conditions in southern California and the southern North Coast Range permit either a faster development or longer growth period, larger bills could result. That is, if bill characters grow at a faster rate relative to other body regions (and to bills in other populations) and growth simply occurs over a longer interval, bill size will increase proportionately more. The major point here, as emphasized by Alberch et al. (1979), is that substantial differences in morphology can be mediated by changes in the timing of onset and offset, and the rate at which particular body regions grow. Thus, long periods of microevolution might not be required for geographic differentiation to originate, and more importantly, it can be maintained in spite of gene exchange with neighboring demes.

Few data are available on Fox Sparrow growth rates (but many on passerines, e.g., Ricklefs 1973, 1979), and none that can be used to compare growth rates in populations with different morphologies. However, Threlfall and Blacquiere (1982) provide data on a few characters for a population of Fox Sparrows in Newfoundland which are relevant to this discussion. They show that body parts grow at different rates, and that adult size for each character is reached at different times in the growth cycle. For example, tarsus length reached adult size by day 10, but culmen length was about two-thirds of adult length by this time, when young fledge. These few data suggest that alterations in the onset or offset of growth of body regions (e.g., bills), or rate of growth among sites could produce rather different overall shapes and sizes. Therefore, the extreme morphological differences in Fox Sparrows might be attributable to developmental shifts mediated by site-specific environmental factors during the nestling period, factors which are correlated with latitude. This hypothesis could be tested with reciprocal transplant, or "common garden" experiments, in which eggs from different sites are brought under controlled experimental conditions and allowed to hatch and develop.

In summary, my goal has been to reconcile the lack of allozyme differences, the inference of high gene flow and recency of common ancestry, and the extensive levels of phenotypic differentiation. Clearly, such a reconciliation can take several

forms. Many would favor a hypothesis that envisions flow of neutral genes, but local adaptation as the process operating on intrapopulation genetic variation to produce geographic patterns in morphology. In fact, I have spent considerable space in the preceding pages examining the nature of morphological variation and possible environmental influences on such variation. This traditional microevolutionary approach might well explain patterns of phenotypic variation. The allozymic perspective I have invoked might be incorrect or only partially relevant, but I believe that the genetic data provide an accurate picture of gene flow and population structure. However, environmental induction or alteration of developmental programs, either with or without (minor) genetic changes, are consistent with my observations of genetic and morphological covariation. Studies are needed to establish the genetic basis of geographic variation in polygenic traits and the fitness consequences of such variation (Zink and Remsen, in press; Schluter and Smith 1986). No doubt some geographic differences will be genetically based and represent local adaptations. The possibility of stochastic forces on phenotypic evolution (Lande 1980, 1985) and the consequences of "tinkering" with developmental programs (Alberch et al. 1979) need to be explored with avian examples.

Evolutionary Significance of Geographic Variation

General Considerations

The analysis of "traditional" skin and skeletal features revealed rather marked geographic variation over a fairly short geographic distance. A traditional interpretation would involve an adaptive explanation for phenotypic patterns of variation: genetic variation for morphological traits was the raw material for phenotypic change, and each local population became adapted to prevailing ecological/environmental conditions. Secondly, a traditional interpretation of patterns of variation in the Fox Sparrow might (note the hedge) be that we can see, in our narrow cross-section of the Fox Sparrow lineage, speciation in progress. If this were true (and it might be), then speciation might be in the early stages because of the lack of differences at allozyme loci. I could conclude, therefore, that the initial stages of speciation involve differentiation in size, bill shape, plumage coloration, but not at enzyme loci. Frankly, such interpretations about adaptation and speciation "make sense" and might in fact be adequate, if not accurate, assessments. However, as I have discussed throughout, explanations about nonadaptation and a lack of speciation potential are also consistent with my data. In any one study of geographic variation, it is difficult to determine which patterns of variation represent adaptation, and whether the prospect of speciation is great or nil. Therefore, I attempt below to evaluate the significance of geographic variation in the Fox Sparrow in an evolutionary context.

Geographic Variation and Adaptation: An Indirect Assessment

Although geographic variation might represent the (after)effects of adaptation of populations to different local environments (Miller 1956; Mayr 1970), is it likely that geographically invariant species are less well adapted, or that their environments do not vary? Degree of geographic variation is potentially related to (1) degree of fragmentation of a species range and the nature of gene flow (e.g.,

island versus stepping-stone models; Slatkin 1985b), (2) among-site variation in intensity of natural selection, (3) population history, demographic structure and mating system, (4) tendency to occupy a greater variety of microhabitats across the range (Miller and McCabe 1935), and (5) species-specific degree of phenotypic plasticity (Via and Lande 1985). Discriminating among these alternatives is problematic because tests are mostly indirect and the alternatives are not mutually exclusive. For example, a geographically uniform species might have recently occupied its current range, and/or have high levels of gene flow. Also, a species might not exhibit geographic differentiation simply because it has a low potential for phenotypic variation in spite of geographic fragmentation, small effective population size, reduced gene flow, and geographically differing selective pressures. In any case, the phenotype expressed throughout the range would be a compromise one, sufficiently buffered against the range of environmental conditions encountered (Lerner 1954). A geographically uniform species could be as adapted to local conditions as members of a polytypic species. Study of the developmental constraints on geographic variation should receive high future priority (Smith et al. 1985).

Geographic variation can be caused by a series of interacting genetic and nongenetic factors. This multi-faceted interpretation of geographic variation derives from consideration of species that differ in their degree of geographic variability. In contrast with the Fox Sparrow is the Green-tailed Towhee (*Pipilo chlorurus*), a similarly sized, confamilial species which breeds in the western United States and is syntopic with the Fox Sparrow in many places. Based on their genetic distance (Zink 1982) I predict that they have been evolving independently for at least 5 million years. The two species have similar vocalizations, a fact which implies sufficient time in syntopy to allow either convergence of vocalizations because of habitat acoustics or interspecific competition (Cody 1974). It is possible that the same environmental factors that affected Fox Sparrows over the past one million years have also affected Green-tailed Towhees. However, this towhee is morphologically uniform over its range (A.O.U. 1957) in contrast to the striking degree of character variation in the Fox Sparrow. These two species might simply have intrinsically different degrees of phenotypic canalization. Thus, the Fox Sparrow might not be locally adapted, but instead, it might only be locally "influenced."

In the Fox Sparrow, one would want to cross-transplant series of eggs from ODEL, PINO, BLAC, and RUBY (the four corners of the sampling area) and follow growth and development and, most importantly, the success of cross-fostered young at finding mates and raising young (i.e., fitness). Because of the difficulties of such tests, it is unclear whether geographically uniform species (1) are not "as adapted" as they could be because of genetic constraints on morphology (Smith et al. 1985), (2) are not as adapted as they could be because they have not had sufficient time in the current range, (3) persist less well in evolutionary time, or (4) have reduced probabilities of speciation.

Geographic Variation and Speciation

Although the process of geographic differentiation might illustrate the manner in which differences among species arise, Goldschmidt (1940) and Eldredge and Cracraft (1980) proposed that intra- and interspecific evolution is decoupled. That

is, geographic variation is envisioned to be an adaptive, within-species phenomenon whereas adaptation *per se* need not be the cause of speciation. Factors that might cause speciation, such as population bottlenecks, are not necessarily also processes of adaptation. A basis for interpreting the geographic variation–speciation link obtains from Mayr (1942: 155), "Geographic variation is thinkable only, if subspecies are incipient species. This, of course, does not mean that every subspecies will eventually develop into a good species. Far from it! All this statement implies is that every species that developed through geographic speciation had to pass through the subspecies stage." Mayr's statement can be interpreted to mean that geographic isolation produces geographic variation, which becomes the raw material of species differences. That is, the probability of speciation is believed to increase with increasing degrees of geographic differentiation.

Speciation is ultimately a genetic phenomenon, the cessation of gene flow between descendants of a once common gene pool. Traditionally, it has been assumed that geographic variation in some phenotypic feature signifies a genetically subdivided population structure, a necessary stage in the speciation process. The environmental modification hypothesis discussed above allows for geographic patterns of morphological variation to originate and be maintained without an underlying genetic basis. Also, relatively minor genetic changes in developmental pathways might have rather marked phenotypic effects. Phenotypic change with little or no genetic differentiation would compromise the interpretation that avian polytypic species represent, necessarily, various stages in the speciation process. Because the probability of speciation is related to the degree of genetic differentiation among populations (Templeton 1980a, b), inferences about the avian speciation process could be biased if phenotypic patterns of variation do not reflect genetic variation.

It seems clear that morphological differentiation can occur among populations independent of speciation (by anyone's definition). What then is the significance of geographic variation in the process of speciation and the evolution of species differences? Under what conditions is a study of geographic variation also a study of speciation? Although geographic isolation is surely required for differentiation and speciation, can we ascertain if particular subspecies of the Fox Sparrow are "closer" to speciation than populations of a geographically uniform species such as the Green-tailed Towhee?

Speciation, if marked by the origin of reproductive isolation, might occur without morphological or protein changes, and it might occur rapidly. Powell (1975) documented the origin of reproductive isolation in a small number of generations in fruit flies, and others have investigated the degree of reproductive isolation of conspecific populations (Dobzhansky 1970; Frost and Platz 1983). These studies suggest that reproductive isolation could coevolve with geographic differentiation in a relatively short period of time. This process might be enhanced in peripheral or island populations (Power 1983). Unfortunately, species are not all consistently defined—some differ in morphology, some in vocal traits, and others in biochemical characteristics. There are no consistent phenotypic correlates of reproductive isolation with which to measure the biological significance of the differences of allopatric populations of birds (Zink and Remsen, in press), including the Fox Sparrow. In practice one must judge whether or not geographic differences among (allopatric) populations are of a magnitude similar to those found between species

known to be reproductively isolated (Selander 1971). This method of speciation analysis is an unsatisfying aspect of the biological species concept (McKitrick and Zink unpubl. data). Dangers also arise by assuming that the lack of reproductive isolation is an indication of conspecificity (Cracraft 1983).

I think that most biologists would agree that morphological differences arise before, concomitant with, and after speciation, if speciation is defined as the origin of reproductive isolation. However, if a geographically uniform species underwent speciation, the same mechanism that kept the ancestral species morphologically uniform might operate on descendant species, and result in sibling species. Sibling species, however, are rather rare in birds (Mayr 1963; Zink and Johnson 1984). It is possible, but not proven, that geographically variable species, such as the Fox Sparrow, are more "fertile" grounds for speciation. Such reasoning led me initially to predict that understanding the nature of geographic variation in the Fox Sparrow would necessarily lead to a better understanding of the avian speciation process. Discerning how observed differences relate to the evolution of biological species turned out to be, however, a more complex exercise. It is difficult to know *a priori* what characteristics Fox Sparrows use to choose mates. Traditionally, if differences do not exist in plumage patterns or song, otherwise divergent populations are assumed to be potentially capable of interbreeding (and conspecific). It is difficult, however, to evaluate this traditional method because no one, to my knowledge, has been able to test the importance of, for example, song while holding behavior and morphology "constant." Thus, I do not know which, if any, of the characteristics of extant Fox Sparrow populations that I studied would function as reproductive isolating mechansims. Genetic distance at enzyme loci is not generally correlated with reproductive isolation (Pashley et al. 1985). Perhaps none of the differences among populations of Fox Sparrows contain information about speciation.

Cracraft's view (1983) of species and speciation analysis does not center on reproductive isolation, and identifies the origin of groups of individuals with at least one species-specific characteristic as the fundamental process in the origin of evolutionary units or species. A species-specific, or diagnostic, trait can be biochemical, morphological, ecological, or behavioral; it need not be associated with reproductive isolation. I will not discuss the merits of alternative species concepts here (see section on subspecies below), but no matter what species concept is employed, the details of speciation are not well understood (Zink and Remsen, in press).

Most if not all species concepts have in common the process of differentiation among populations. Therefore, comparison of characteristics of populations and species at least sets the limits of possibilities for the events and processes involved in speciation, irrespective I think, of the particular species concept in use. The works of Templeton (1980a, b) provide a theoretical framework for examining genetic and morphological correlates of speciation without undue adherence to the geography of speciation (see Bush 1975 for a review of the latter topic). Templeton (1980b) provided a conceptual model, or mechanistic taxonomy, for predicting the nature of speciation given data on species differences in proteins, degree of geographic isolation that occurred during the fragmentation of the ancestral range, and most importantly the ancestral population structure. For example, if a population was highly subdivided and a founder event occurred,

speciation would be most likely to occur via chromosomal transilience, and the initial genetic distance between immediately descendant, or sister, taxa would be large. A difficulty in applying Templeton's model arises in estimating the ancestral population structure. Extrapolation of current population structure is possible but might often be incorrect, especially for species that have lived in areas subjected to Pleistocene glaciations. Alternatively, Templeton's model might be used to predict the relative likelihood of a future speciation event, given knowledge of the current population structure.

The approach I take here is to compare and contrast patterns of morphological and protein variation among populations of Fox Sparrows and among species of sparrows related to the Fox Sparrow. This scheme documents the extent of differences occurring between the time of origin of population differentiation and the evolution of (nonsibling) congeners. This perspective could elucidate processes associated with divergence and speciation in these sparrows and provide a framework for evaluating whether interspecific differences seem to be an extension of geographic differentiation.

Here I employ Templeton's model in a historical sense. Genetic distances (Nei 1978) between congeneric species in the genera *Zonotrichia* and *Melospiza* average <0.10, low by most vertebrate standards but typical of those found for other avian congeners (Zink 1982). Parenthetically I note that there is no evidence for a genetic revolution (Mayr 1963) at the level of enzyme loci in birds. Work on avian population structure has revealed that populations differ by D-values of approximately 0.002 (Barrowclough 1980b, 1983; this study), values considerably lower than interspecific ones. The population structures of the ancestors of *Zonotrichia* and *Melospiza* are unknown. However, we can posit that these ancestors had panmictic and not subdivided populations based on measures of several avian species (Barrowclough 1983). Note that this characterization of population structure is not based on morphological patterns of variation, which might be interpreted in the Fox Sparrow, for example, to indicate a genetically highly differentiated species. Also, we might assume that a chromosomal mode of speciation is improbable in birds because of the lack of differences among most congeneric species (Shields 1982).

According to Templeton (1980b; his Fig. 1), only three conditions and two modes seem likely to explain speciation in these emberizid sparrows. If a founder event occurred, speciation would most likely occur through a genetic transilience (Templeton 1980a) or less likely through adaptive divergence. A vicariance biogeography approach applied to many species could rule out founder events (dispersal) in many cases (Cracraft 1983), but this is presently empirically unknown for many species. If an ancestral, panmictic population were fragmented into large subdivisions, speciation would occur only through adaptive divergence. Only these three possibilities are consistent with the low level of protein differences among species of sparrows. Note that I assume that all would agree that the species of sparrows analyzed by Zink (1982) are "good species." Also, I assume that Templeton's model has applicability irrespective of the particular concept of species invoked. Hence, the model helps to eliminate some possible modes of population differentiation and speciation, but without information on the nature of the geographic fragmentation of the ancestral ranges, further inference is not possible. Identifying phenotypic and genetic correlates of speciation via adaptive divergence

should receive future attention. For example, given that Fox Sparrow populations appear genetically very similar, what attributes of their external morphology would falsify a hypothesis of adaptive divergence? If one could falsify adaptive divergence, then the observed geographic differences might not have relevance to a speciation process. Can additional information be gained from contrasts of intra- and interspecific differences?

Geographic differences sometimes grade into species differences. This is especially true for superspecies, which are presumed to be a recently evolved monophyletic group, the allopatric units of which show characteristics of both species and of local populations. For illustration, if the Fox Sparrow was considered to consist of separate species based on morphological criteria, such as the Great Basin vs western samples, would the genetic and morphological differences resemble interspecific ones? The geographic differences in morphology among populations exceed, at least quantitatively, the level of differences between sparrow species (Zink 1982). That is, they have reached species distinction in level of skeletal distance and could be incipient species. However, as noted above, populations separated in morphometric space are not genetically differentiated (at enzyme loci). Of what consequence are the genetic data? Genetic distance increases on average an order of magnitude or more as one proceeds from comparisons of local populations to congeneric species. Genetic distance should not be used as an absolute taxonomic yardstick, however. Some avian species are barely differentiated at enzyme loci (Johnson and Zink 1983). Thus, although there might be consistent, significant changes occurring at enzyme loci during avian speciation, they are limited to the fixation of different alleles at probably $<10\%$ of the loci. Also, it is possible that interspecific exceeds intraspecific genetic differentiation simply because of the longer time that species have been evolving independently (relative to populations). Hence, at present we are limited to the conclusion that on average the evolution of avian species occurs in a time not exceeding that required for 5–10% of enzyme loci to diverge. Given the genetic similarity of Fox Sparrow samples, it is possible that the phenotypic differences that have arisen among population samples of Fox Sparrows studied here are not related to speciation (and possibly not even to local adaptation). Fixed differences between populations could be used as traits for the recognition of phylogenetic species. If there were marked differences evident at enzyme loci, one might conclude that associated phenotypic differences were of species level (but not without exception).

I suspect that the process of phenotypic change is one that varies from group to group in terms of rate and mechanism, whereas the process of enzyme divergence is more likely to be a uniform process. The nature of morphological differences within and among species can be examined in a similar manner to the protein data. Species of sparrows in genera such as *Zonotrichia* and *Melospiza,* closely related to *Passerella,* can be individuated by their discrete plumage traits as well as morphometric traits (Zink 1982). In contrast, the populations of Fox Sparrows differ mostly in size and phenotypic extremes grade into one another. If the morphologically most extreme samples of Fox Sparrows in the Schistacea group were considered as distinct species, they would not approach the level of qualitative plumage differences that separate species of many sparrows. In contrast, geographic variation in bill size and shape already exceeds that found between many species. Nonetheless, the quality of the interpopulation differences

in Fox Sparrows does not seem, to me, equivalent to that found among species in related genera. I recognize the subjective nature of this argument. It does, however, highlight the problem in determining how one infers aspects of speciation from a given pattern of geographic variation. I do not know if populations of Fox Sparrows are reproductively isolated. Also, I do not know if further independent evolution of populations would lead to the fixation of species-specific traits, which would then delimit phylogenetic, but not necessarily biological species. Thus, whereas geographic variation is, as Mayr noted, surely a stage in the speciation process (however defined), it is also possible that geographic differences can be evolutionary "noise" or temporally unstable. There are few, if any, consistent cues that permit recognition that a particular situation is actually speciation in progress and not "noise."

To recognize that speciation has occurred, a new species-specific phenotype must originate and become stabilized throughout a given range. Although geographic variation sometimes exists in species-specific characters (Mayr 1970), the origin of species-specific morphological differences is probably coupled with speciation, no matter how one envisions the origin of species. However, it is equivocal as to whether the kinds of qualitative differences that typify species are produced by geographic differentiation. It is hard to falsify Goldschmidt's (1940) claim that subspecies are more-or-less "diversified blind alleys within the species."

Hypotheses for the evolution of species-specific morphologies exist that do not use microevolutionary divergence as a model. Recent work in molecular genetics suggests that the genetic changes associated with reproductive isolation and speciation might not be inherited in a Mendelian fashion (Dover 1982; Rose and Doolittle 1982; Campbell 1983; Kidwell 1983). If these genetic changes alter morphological expression and spread rapidly throughout a geographic range via horizontal transmission (non-germline), a new qualitatively different species-specific morphology could result. Such mechanisms of genetic change would not require pre-existing geographic variation as a prerequisite for speciation—geographically uniform species could also undergo rapid speciation.

West-Eberhard (1983) suggested a model in which sexual selection causes rapid character divergence and speciation between populations with and without ecological differences, and without extensive genetic change. This model (see also Lande 1981) deserves consideration, especially in light of the observation of low genetic differences among avian populations and the potential importance of sexual selection in birds (Sibley 1957; Price et al. 1984b). Thus, study of the geography of variation in characters likely to be influenced by sexual selection (intra- or intersexual) might improve our understanding of the avian speciation process. Geographic variation in the kinds of morphological traits used in this study might contribute to the understanding of the process of local adaptation, but it probably is not the raw material from which new species are derived. The coming decade will, I suspect, witness a renaissance in the description of geographic variation using both morphological and biochemical methods, as well as concentration on discerning the evolutionary processes of differentiation. The application of quantitative genetic techniques (Atchley 1983; Price et al. 1984b) should prove invaluable in understanding the evolution of phenotypic differences among populations and species. Study of the geography of ontogenetic patterns in populations with differing adult morphologies will also be of considerable value.

I think that many phenotypic differences will probably prove to have a significant nongenetic component or a genetically simple developmental basis.

Conclusion

In my opinion, many studies of geographic variation might not have relevance to understanding speciation. I frankly cannot make definitive conclusions about avian speciation, even after a detailed, multidimensional study of genetic and morphological variation in the Fox Sparrow. I know of no way to tell if the probability of speciation is greater in the Fox Sparrow than in the Green-tailed Towhee. Competing hypotheses about the origin, maintenance, and evolutionary significance of geographic differences cannot be distinguished. Part of the problem stems from the way in which species have been defined—that is, there is no satisfying way to study speciation (reproductive isolation) when populations are allopatric. Perhaps the analysis of details of speciation will always be completely inferential and the components not amenable to testing. However, this conclusion requires further analysis. Distinguishing between the process of genotypic/phenotypic differentiation and the origin of reproductive isolation aids in showing that the role of geographic analysis rests with the former endeavor (Zink and Remsen, in press), which to some (Cracraft 1983) entails the essence of speciation. Possibly, problems inherent in current definitions of species inhibit study of speciation. At the least, reaching a consensus on species definitions and the role of geographic analysis should shed considerable light on the nature of the evolutionary process itself.

Taxonomy and the Search for Evolutionary Taxa

The limits of subspecies of the Fox Sparrow are based to an extent on characteristics not studied here, such as coloration and length of the central rectrices. However, because of the past prevalence of subspecific studies in ornithology (Fjeldsa 1985) I evaluate the variation documented in this study in light of current subspecific limits. In addition, I comment on the current status and value of subspecific taxonomies in avian systematics.

A series of articles on avian subspecies (*Auk,* 99:593–615, 1982) seemed to reach a consensus that subspecies were of value. The authors in this forum generally concluded that subspecies should be objectively and consistently definable. Several authors (O'Neill 1982; Barrowclough 1982; Monroe 1982) defined subspecies phenetically as groups of populations in which each population is more similar to those in its subspecies than to other populations in other subspecies. Subspecific names were considered to be useful "flags" for populations or groups of them that might be currently undergoing differentiation and, therefore, constitute potential natural laboratories in which to study evolution. Barrowclough (1982) pointed out that the subspecific name should be predictive, in the same sense that members of a genus all share diagnostic attributes. Fjeldsa (1985) lists a number of problems with past usage of the subspecies concept in ornithology. For example, many avian subspecies were described from inadequate series of individuals. Also, many subspecies fail the criterion of predictiveness—that is, the subspecies name does not allow significant prediction of patterns of character-state variation. Subspecies can be comprised of groups of populations that are not most similar to one another.

Most authors in the *Auk* forum implied that the future of subspecies would be in relation to investigations of evolutionary problems, rather than in the simple (but useful) task of pigeon-holing specimens in appropriate drawers in collections. Often noted was the historical contribution of studies of geographic variation toward the understanding of speciation. However, there was some disagreement whether subspecies could often be evolutionary units. Mayr (1982) suggested that only phenetically differentiated geographic isolates would be likely to undergo speciation, and that most examples of continental geographic variation were subject to the presumed homogenizing effect of gene flow, a view inconsistent with Endler's (1977) writings. Thus, the study of geographic variation has well-defined utility, because it contributes information on both taxonomy and evolution.

The suggestion by Cracraft (1983) that ornithologists should adopt a phylogenetic species concept does not seem to leave much room for the recognition of subspecies. Unfortunately, the merits of Cracraft's view have not been given fair consideration by at least some (see Fjeldsa (1985) for a strongly biased review of the phylogenetic species concept). In Cracraft's view, species are evolutionary units, which are groups of individuals that share a diagnostic feature(s). These "least diagnosable units" are groups that potentially have had independent evolutionary histories, and Cracraft argues that such units should be what are called species. Many current avian species, defined using the biological species concept, probably consist of several evolutionary units, which might not even be monophyletic groupings. Fjeldsa (1985) suggested that what were species to Cracraft were in many cases simply well-marked subspecies; this characterization misses the point. Logically, evolutionary units should be species, not sometimes subspecies and sometimes species. I agree with Cracraft that basal taxonomic units should be called species, the basic unit of evolution. Nonetheless, populations linked by clinal variation, or those which are "nearly diagnosable" might be flagged as subspecies. It is my opinion that the utility of subspecies is in the marking of differentiation within phylogenetic species, and not for the marking of evolutionary units themselves. In short, I think that the biological species concept is in need of a major overhaul. Students of avian geographic variation are presented with several decisions: are subspecies to be retained, how should they be recognized, and are they of evolutionary or simply taxonomic utility? What is the role of geographic analysis of variation with respect to subspecific taxonomy if a phylogenetic species concept is adopted? It will take time for the merits of a phylogenetic species concept to be argued, agreed upon, and if accepted, implemented in theory and practice. I offer the following as an exercise in the application of a phylogenetic species concept.

To the modern student of geographic variation and subspecies, the goal is to discover least diagnosable groups of individuals no matter whether he or she later terms them species or subspecies. In most studies of geographic variation, one initially uses phenetic criteria, usually external morphology, to determine which specific individuals to sample from some geographic area of interest. One might not know at first if this taxon is one species or several. In my analysis I did not rely *a priori* on subspecies boundaries to guide my sampling (the past practice of pooling specimens from throughout the range of a subspecies into a single unit should be discouraged for most analyses). Instead, population samples of Fox Sparrows (the initial taxon) were taken to allow description of the nature of variation and to test whether particular groupings of individuals are genetically

or morphologically discrete. Detection of least diagnosable groups would lead to their formalization as phylogenetic species, followed by reconstruction of the history of these evolutionary units and analysis of geographic variation independently within each species.

Given these general considerations, the assessment of subspecies limits in Fox Sparrows of the Schistacea group is still problematic. Swarth (1920) recognized two groups (lineages ?) within Schistacea, a northern one showing color (browns) and bill (small to large) clines from east to west through the forms *schistacea, fulva,* and *brevicauda,* and a southern group, typified by grayer coloration and a striking east to west clinal increase in bill size (*canescens, monoensis,* "*mariposae*" (= *megarhyncha*), and *stephensi*). However, it was later shown (e.g., Grinnell and Miller 1944) that north to south clinal variation in the Sierra Nevada connected the two groups recognized by Swarth.

There are no distinct groupings of samples based on the analysis of protein variation. The phenetic analyses of skin and skeletal characters used in this study failed to confirm the existence of traditional subspecies. Therefore, the current subspecific framework fails the criterion of predictiveness for the characters examined herein. Groups defined by the morphological analyses, although not always clear-cut, are: (1) Great Basin samples, excluding WARN, (2) southern Sierra Nevada plus the two samples from *brevicauda* (North Coast Range), and some other samples (e.g., SHAV, SAWY) from *megarhyncha,* and (3) the remaining samples. Analyses of character variation, and composite measures of morphological variation (such as PCA and cluster analyses) disclosed that even these three groupings overlap, at least between groups (2) and (3). Further study is needed on the morphological similarity between *brevicauda* and *stephensi*—are they more closely related (historically) to one another than to adjacent populations, or are their environments very similar? Patterns of color variation, of importance to subspecies definitions in Fox Sparrows (Swarth 1920) and not discussed here, might alter my taxonomic conclusions. It is my feeling, however, that color varies congruently with the phenotypic features surveyed here. The primary exception is that the *brevicauda-stephensi* similarity might not be upheld; that is, they might be independent evolutionary taxa, and their resemblance a "primitive" state.

I, therefore, propose a radical change in the subspecific taxonomy within the Schistacea group (see legend to Fig. 1). I recommend merging the subspecies *stephensi, megarhyncha, brevicauda, monoensis,* and *fulva* (including WARN but excluding STEN) under the name *megarhyncha,* which has nomenclatorial priority (Swarth 1920). There might be a basis for recognizing two groups, *stephensi* plus *brevicauda* vs the other three. However, the majority of morphological characteristics *grade* between these forms without step-clines. The subspecies *canescens* and *schistacea* could be combined with the population breeding at Steens Mountain under *schistacea.* Because only one sample of *canescens* was used, however, this decision awaits more detailed analysis of Great Basin populations. It is unlikely that these groups represent distinct evolutionary units. This proposal differs markedly from Parkes' opinion (in Arbib 1981), which favors retention of all currently recognized subspecies. Parkes' opinion, however, is influenced by the extremes of variation in a few characters, which do not define consistent, discrete groups.

I think that it is appropriate to recognize the subspecies groups schistacea, iliaca,

and unalaschcensis as species. I believe that this scheme would have predictiveness, and these three taxa probably represent evolutionary units. Although variation is extreme within these groups, they are discretely recognizable; a possible exception is *altivagans,* showing intermediate characteristics between iliaca and unalaschcensis. Thus, it is my opinion that one could argue effectively that at least three species, not one, of Fox Sparrows currently exist in North America.

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SUMMARY

A detailed, multidimensional microgeographic study of patterns of variation in the Schistacea group of the Fox Sparrow forms the basis for inferring the nature of evolutionary processes. Samples were collected from riparian and chaparral habitats at elevations between 1,340 m and 2,865 m, at 31 sites in Oregon, Nevada,

and California. Disjunct and continuous portions of the range were sampled, as were populations with varying morphologies. The objective was to document levels and patterns of genetic and morphologic variation and their covariation. Geographic and ecological correlates of variation were examined. From each specimen, data were recorded for skin (8) and skeletal (15) characters, and genotype at 38 allozyme loci, determined by horizontal starch-gel electrophoresis of whole-tissue extracts.

Levels of variation in morphological characters are typical for birds; coefficients of variation range from 2% to 5% within populations. All characters are significantly heterogeneous among sites (ANOVA), but not all characters exhibit the same pattern of variation. Many study skin and skeletal characters (1) are small in the Great Basin, and (2) increase clinally from north to south, reaching largest size in the North Coast Range and southern California (a bifurcation). Size, as measured by cube-root of mass, is a dominant component of morphological variation. Mantel's test revealed that morphological and geographic distances among samples are significantly non-random. Cluster and principal components analyses showed three general groupings of samples: (1) Great Basin, (2) North Coast Range and southern California, and (3) the remainder of samples spread throughout the Sierra Nevada-Cascade axis. Although variation in shape exists, it is not geographically ordered. A canonical correlation analysis did not consistently identify temperature or rainfall variables that might explain morphological patterns; morphology does not seem to vary in ways predicted by ecogeographic "rules."

Electrophoretic analysis revealed that the (1) average individual heterozygosity per population ranges from 2.3% to 5.2% (average = 3.85%), (2) average number of polymorphic loci per population is about 22% (range among populations is from 16% to 31%), and (3) average number of alleles per polymorphic locus is 2.3, with a range among populations of 2.1 to 2.6. Allelic frequencies and measures of within-population genetic variation have few if any ecological or geographic correlates. Although within-population levels of genetic variation are typical of vertebrates, genetic differentiation between populations is low, with an average genetic distance of 0.002 (range = 0.0–0.0039), and an F_{ST} of 1.35%. A phenogram summarizing genetic distances did not join samples from given areas, elevations, or habitat types; genetic and geographic (minimum pairwise) distances are random with respect to each other (Mantel's test). The allelic frequency data are consistent with a hypothesis of high gene flow. The nature of genetic polymorphism within populations is in agreement with neutral theory, specifically, the Infinite alleles-Constant mutation rate model.

Genetic variation in Fox Sparrows is compared to other birds and vertebrates. Four hypotheses were evaluated that could potentially explain the low level of genetic differentiation among samples: (1) recency of common ancestry, (2) high levels of gene flow, (3) slow rates of molecular evolution, and (4) natural selection. Habitat and climatic fluctuations during the Pliocene and Pleistocene possibly allowed a more continuous distribution without genetic differentiation. High gene flow probably accounts for current genetic homogeneity. Also, Fox Sparrows might have only recently occupied the current range, providing insufficient time for genetic differentiation.

In contrast to genetic variation, considerable morphological variation is distributed among sites, and it is geographically ordered. Thus, the two data sets are

not concordant; evolution at these two levels could be decoupled in the Fox Sparrow. A potential paradox is posed by the discordance of the data sets and the inference of high gene flow. I propose that local environmental conditions acting during the nestling period shape inherent phenotypic plasticity, effecting spatial patterns. Morphological differences could thus be maintained in spite of gene flow. A hypothesis of environmental modification of the developmental program is advanced, and the need for "common garden," or reciprocal transplant (James 1983) experiments is stressed.

The process of geographic differentiation is often viewed as a model for the evolution of species and their characteristics. I contrast morphological and genetic variation among populations of Fox Sparrows and some other species of related sparrows, to assess whether or not species differences seem to be an extension of geographic differences. The objective is to identify potential correlates of the speciation process. Average interspecific genetic distance in sparrows is 0.06, and among local populations it is 0.002, a difference of an order of magnitude. Level of morphometric differentiation in skeletal characters among subspecies can exceed interspecific levels, showing that absolute level of phenetic distance is not related to speciation. Species tend to be characterized by discrete plumage differences, whereas these types of characteristics grade between extremes in the Fox Sparrow. Thus, it is equivocal as to whether the origin and nature of differences among populations of Fox Sparrows represent processes associated with the evolution of sparrow species. The evolutionary significance of geographic variation is unclear, because critical tests of the adaptive importance of geographic variation and its relationship to speciation have not been performed.

The analysis of morphological variation does not support the continued recognition of several subspecies. There appears to be little evidence that evolutionary units, or phylogenetic species, exist within the Schistacea group.

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APPENDIX I

Locations of Sample Sites

Precise descriptions of collecting sites; some "sites" have more than one description, which indicates more than one locality within a very small area. Localities defined in Table 1. All sites are in California unless otherwise noted. T. = Township, R. = Range. A. (BERN) 1.6 km N, 3.2 km E Butler Peak, 2,210 m, San Bernardino Co. [T. 2N, R. 1W, SW ¼ sec. 10]; 1.2 km N, 2.4 km E Butler Peak, 2,230 m, San Bernardino Co. [T. 2N, R. 1W, SW 1/16 sec. 10]; 0.8 km NE Clark's Summit, 2,330 m, San Bernardino Co. [T. 2N, R. 1W, NE ¼ sec. 36]; Clark's Summit, 2,350 m, San Bernardino Co. [T. 2N, R. 1W, SE ¼ sec. 36]. B. (PINO) 2.0 km E Mt. Pinos, 2,550 m, Kern Co. [T. 9N, R. 21W, SW ¼ sec. 33]. C. (REDM) vicinity of Red Mountain, 1,905 m, Kern Co., [T. 25S, R. 32E]. D. (DOME) 11.2 km N Dome Rock, 2,400 m, Tulare Co. [T. 20S, R. 32E, E ½ sec. 20]; 5.6 km N Dome Rock, 2,225 m, Tulare Co. [T. 21S, R. 32E, W ½ sec. 9]. E. (LOOK) 1.6 km W Lookout Peak, 2,350 m, Fresno Co. [T. 13S, R. 30E, SW ¼ sec. 21]; 6.4 km N, 1.6 km E Shell Mountain, 2,120 m, Fresno Co. [T. 13S, R. 29E, NE ¼ sec. 36]; 0.8 km S, 2.0 km W Lookout Peak, 2,200 m, Fresno Co. [T. 13S, R. 30E, NE ¼ sec. 29]; 3.2 km N Shell Mountain, 2,250 m, Tulare Co. [T. 14S, R. 29E, N ½ sec. 11]. F. (SHAV) 0.8 km S, 4.0 km W Bald Mountain, 1,650 m, Fresno Co. [T. 10S, R. 25E, N ¼ sec. 4]. G. (MTOM) 3.2 km S, 1.6 km E Mt. Tom, 2,225 m, Fresno Co. [T. 7S, R. 26E, sec. 5]; 1.6 km E Mt. Tom, 2,255 m, Fresno Co. [T. 6S, R. 26E, SW ¼ sec. 29]. H. (JACK) 1.6 km E Jackass Rock, 2,010 m, Madera Co. [T. 6S, R. 25E, sec. 6]. I. (CHER) 3.2 km N Woods Ridge Lookout, 1,555 m, Tuolumne Co. [T. 2N, R. 18E, sec. 35]. J. (EBET) 1.6 km N, 3.2 km W Sapps Hill, 1,890 m, Tuolumne Co. [T. 7N, R. 17E, W ½ sec. 25]; 1.6 km N, 4.8 km W Sapps Hill, 1,980 m, Tuolumne Co. [T. 7N, R. 17E, SW ¼ sec. 26]. K. (MONO) 3.2 km S, 0.8 km W Lee Vining Peak, 2,300 m, Mono Co. [T. 7N, R. 25E, NE ¼ sec. 15]. L. (WALK) 4.8 km E Mineral Mountain, 2,410 m, Alpine Co. [T. 8N, R. 22E, E ½ sec. 21]; 5.6 km E Mineral Mountain, 2,400 m, Mono Co. [T. 8N, R. 22E, W ½ sec. 21]. M. (WOOD) 0.8 km S, 1.6 km W Woodfords, 1,860 m, Alpine Co. [T. 11N, R. 19E, SE ¼ sec. 33]; 2.0 km W Hawkins Peak, 2,360 m, Alpine Co. [T. 10N, R. 19E, SW ¼ sec. 5]; 0.8 km W Pickett Peak, 2,400 m, Alpine Co. [T. 10N, R. 19E, NE ¼ sec. 5]. N. (TAHW) 5.6 km E Ward Peak, 2,010 m, Placer Co. [T. 15N, R. 16E, NE ¼ sec. 14]. O. (TAHE) 3.2 km N, 1.6 km W Duane Bliss Peak, 2,130 m, Douglas Co., Nevada [T. 14N, R. 19E, NW ¼ sec. 6]; 4.0 km N, 1.6 km W Duane Bliss Peak, 2,050 m, Carson City Corp. Bdy., Nevada [T. 15N, R. 19E, SW ¼ sec. 31]. P. (SAGE) 2.4 km N, 3.2 km W Billy Hill, 1,920 m, Nevada Co. [T. 19N, R. 16E, SE ¼ sec. 32]; 2.4 km N, 2.4 km W Billy Hill, 1,920 m, Nevada Co. [T. 19N, R. 16E, SE ¼ sec. 32]. Q. (BUCK) 3.2 km S, 0.8 km E Spanish Peak, 1,645 m, Plumas Co. [T. 24N, R. 8E, NW ¼ sec. 32]. R. (LASS) 10.4 km N, 11.2 km E Lassen Peak, 2,375 m, Shasta Co. [T. 32N, R. 5E, SW ¼ sec. 35]; 11.2 km N, 8.8 km E Lassen Peak, 1,735 m, Shasta Co. [T. 32N, R. 5E, NW ¼ sec. 34]. S. (SHAS) 14.4 km N, 8.0 km E Mt. Shasta, 1,800 m, Siskiyou Co. [T. 43N, R. 2W, SE ¼ sec. 20]; 13.6 km N, 3.2 km E Mt. Shasta, 2,050 m, Siskiyou Co. [T. 43N, R. 3W, SW ¼ sec. 26]. T. (SPEN) 3.2 km N, 4.8 km E Buck Mountain, 1,230 m, Klamath Co., Oregon [T. 39S, R. 6E, SW ¼ sec. 2]. U. (LAUG) 17.6 km S, 3.2 km W Mt McLaughlin, 1,430 m, Jackson Co., Oregon [T. 38S, R. 4E, SW ¼ sec. 4]; 3.2 km S, 3.2 km W Mt. McLaughlin, 1,500 m, Jackson Co., Oregon [T. 36S, R. 4E, NE ¼ sec. 28]. V. (WARN) 2.4 km S Sugar Hill, 1,850 m, Modoc Co. [T. 46N, R. 14E, SW ¼ sec. 35]; 2.4 km S, 1.0 km E Sugar Hill, 1,850 m, Modoc Co. [T. 46N, R. 14E, SW ¼ sec. 35]; 3.2 km S, 1.6 km W Cedar Mountain, 1,730 m, Modoc Co. [T. 43N, R. 15E, SW ¼ sec. 29]. W. (ODEL) 1.6 km S, 0.4 km E Odell Butte, 1,580 m, Klamath Co., Oregon [T. 24S, R. 7E, SW ¼ sec. 26]. X. (BLAC) 2.4 km N, 0.4 km W Black Butte, 2,010 m, Glenn Co. [T. 22N, R. 9W, NW ¼ sec. 21]; 0.4 km N Black Butte, 2,080 m, Glenn Co. [T. 22N, R. 9W, NW ¼ sec. 27]; 0.4 km E Anthony Peak, 1,950 m, Mendocino Co. [T. 23N, R. 10W, SW ¼ sec. 15]. Y. (YOLL) 12.8 km N, 9.6 km W North Yolla Bolly Mountain, 1,480 m, Trinity Co. [T. 2S, R. 11W, NW ¼ sec. 3]. Z. (SAWY) 2.4 km N, 4.8 km E Eaton Peak, 1,650 m, Siskiyou Co. [T. 40N, R. 10W, SW ¼ sec. 14]; 2.4 km N, 4.0 km W Eaton Peak, 1,830 m, Siskiyou Co. [T. 40N, R. 10W, SE ¼ sec. 14]. 1. (PYRA) 1.6 km S, 4.8 km W Pyramid Peak, 1,580 m, Siskiyou Co. [T. 18N, R. 6W, NW ¼ sec. 10]; 5.6 km W Pyramid Peak, 1,660 m, Siskiyou Co. [T. 18N, R. 6W, NE ¼ sec. 4]. 2. (WHIT) 5.4 km S Bucks Peak, 2,635 m, Inyo Co. [T. 6S, R.

35E, S ¼ sec. 9]; 5.4 km S, 3.2 km E Bucks Peak, Inyo Co. [T. 6S, R. 35E, NE ¼ sec. 14]; 6.4 km S Iron Mountain, 2,260 m, Inyo Co. [T. 6S, R. 36E, center sec. 18]; 2.4 km S Kennedy Point, 2,745–2,865 m, Esmeralda Co., Nevada [T. 1S, R. 33E, S ½ sec. 9]; 1.6 km S, 0.8 km E Kennedy Point, 2,590 m, Esmeralda Co., Nevada [T. 1S, R. 33E, NW ¼ sec. 10]; 1.6 km S, 1.6 km E Kennedy Point, Esmeralda Co., Nevada [T. 1S, R. 33E, NE ¼ sec. 10]. 3. (RUBY) Harrison Pass Ranger Station, 1,850 m, Elko Co., Nevada; 0.4 km S, 1.6 km E Snow Flake Peak, 2,610 m, Elko Co., Nevada [T. 31N, R. 58E, NE ¼ sec. 1]; 4. (MART) Martin Creek Ranger Station, 2,060 m, Humboldt Co., Nevada [T. 44N, R. 39E, NW ¼ sec. 24]. 5. (STEN) 0.8 km N, 1.6 km E Lost Lake, 2,230 m, Harney Co., Oregon [T. 32N, R. 33E]; 1.6 km E Lost Lake, 2,260 m, Harney Co., Oregon [T. 32N, R. 33E].

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