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Covariation Of Song, Morphological, And Allozyme Frequency Characters In The Rufous-collared Sparrow, Zonotrichia Capensis

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COVARIATION OF SONG, MORPHOLOGICAL, AND ALLOZYME FREQUENCY CHARACTERS IN THE RUFOUS-COLLARED SPARROW, *ZONOTRICHIA CAPENSIS*.

by

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ABSTRACT

In the Rufous-collared Sparrow (*Zonotrichia capensis*) song dialects, defined by rate of delivery of the ter inal trill, are clearly associated with variation in vegetation. The local adaptation hypothesis suggests that these dialects may act as markers for different populations adapted to different local environmental conditions predicting that there will be a correlation between the patterns of vocal and genetic variation. Thus, covariation of allozyme frequencies, and morphological (external and skeletal) measures and song characters was investigated in northwestern Argentine populations of Rufous-collared Sparrows with particular reference to possible correlations between vocal dialects and population structure. Approximately 20 males were collected from each of four sites within each of six different vegetations (and thus, six vocal dialects): lowland chaco thornscrub, transition forest, montane woodland, montane grassland, Monte desert scrub, and puna high altitude scrub.

There was significant variability in both external and skeletal morphology among all 24 sites and among vegetation/dialect populations. Overall Wright's corrected inbreeding coefficient (F_{ST}) was 0.119 indicating significant genetic differentiation among sites within the study area. Hierarchical Wright's F statistics indicated that only 50 % of among site variability was due to a vegetation/dialect effect.

Puna scrub sites were differentiated from all other sites with respect to both morphology and allozyme frequencies. Heterogeneity at the PGM-1 locus among puna scrub sites was the major cause of the high F_{ST} value overall and within puna scrub vegetation (F_{ST}= 0.156). Puna scrub populations have traditionally been treated as a subspecies (*pulacayensis*) separate from other populations within the study area (*hypoleuca*) and my data support this contention.

Genetic differentiation overall among all non-puna sites (corrected F_{ST} = 0.018) was similar to differentiation among sites within each of the five non-puna vegetations (average corrected F_{ST} = 0.0132 ± 0.0069). Hierarchical Wright's F statistics indicated that none of the among site differentiation in this subset of samples was due to a vegetation/dialect effect. These observations are not consistent with the local adaptation hypothesis.

Overall covariation between morphology and allozyme frequencies was evident in that puna scrub populations were distinct from all other sampled populations. Mantel's non-parametric tests based on non-puna sites indicated that there was no covariation between morphological Mahalanobis and Rogers' genetic distance matrices. Degree of morphological differentiation was associated with both geographic distance and differences between habitats. There was no significant covariation between genetic distance and geographic distance suggesting no simple isolation-by-distance effect. Finally, there was no relationship between song Mahalanobis distances (based on frequency and temporal characters of song) and either morphology or habitat structure.

All significant genetic heterogeneity occurred among sites in mountainous habitats and I conclude that topography and patchiness of habitat were probably major factors involved in population differentiation, rather than vocal dialects.

"Did we but compare the miserable scantiness of our capabilities with the vast profundity of things, both truth and modesty would teach us a *dialect*, more becoming short-sighted mortality."

Joseph Glanville, The Vanity of Dogmatizing 1661.

I dedicate this thesis to my mother and father.

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1.0 INTRODUCTION

1.1 The Study of Geographic Variation

The study of geographic variation of various types of characters (e.g. morphological, physiological, genetic, behavioural etc.) is central to an understanding of evolution. Variation is the raw material for natural selection and drift; therefore, mapping variation over a given species range is an important first step in elucidating the processes involved in population differentiation. Thus, intraspecific patterns of variation in space may reveal much about mechanisms involved in subdivision of populations, in formation of clines and even in speciation (Endler, 1977; Zink and Remsen, 1987). Various authors regard the process of geographic differentiation within a species as being a suitable and accessible model of speciation (e.g. Zink, 1986).

A common objective of studies of geographic variation is to determine the degree of genetic differentiation among populations of a species (i.e. ranging from panmixia to complete subdivision; Zink, 1986). The degree of genetic divergence among, and the level of genetic variability within populations will be affected by various factors including bottlenecks, founder effects, differences in selective regimes in different environments and genetic drift (Wright, 1940; 1978b; Kilpatrick, 1981). Covariation between a trait of the studied organism and some environmental variable(s) may be used to assess adaptation (i.e. a positive correlation might imply adaptation to a given set of environmental conditions).

There have been numerous studies of geographic variation in a wide variety of avian taxa yet, surprisingly, there are still areas of investigation where data are lacking. In particular, empirical estimates of population structure and gene flow are necessary (Zink and Remsen, 1987). Studies of geographic variation of terrestrial

organisms have dealt primarily with insular populations (Endler, 1977) since the classical view of speciation requires divergence of populations in allopatry (Mayr, 1942; 1963) although it has been suggested that speciation may also occur in continental populations which are not necessarily geographically isolated (Endler, 1977). Thus, there is a need for studies of variability in continentally distributed populations.

Traditionally, inferences about levels of genetic differentiation between compared populations were made from differences in morphology. This approach has limitations, not the least of which is that morphological characters often involve interactions of many genes (Evans, 1987). Protein electrophoresis has been available since the mid-60's for analysis of genetic variation in natural populations (Hubby and Lewontin, 1966; Lewontin and Hubby, 1966). Electrophoresis allows for the scoring of stained bands on a gel which represent different proteins or different forms of the same protein. There is a direct relationship between the protein and the gene coding for it; thus, this method results in data that are relatively unambiguous and unbiased (Evans, 1987). Few studies of intraspecific geographic variation in birds have utilized electrophoretic data, even though such data can be used to directly assess genetic population structure, levels of gene flow and effective population size (Zink, 1986).

In many studies of geographic variation, more than one type of character is studied (e.g. Berlocher and Bush, 1982; Gorman and Kim, 1976; Lagercrantz and Ryman, 1990; Schnell et al. 1978; Schnell and Selander, 1981; Sene and Carson, 1977; Thompson, 1990; Turner et al. 1979; Zink, 1986; 1988). The various character suites may be subject to different selection pressures, and may show different levels or patterns of variation. For example, numerous studies have shown lack of concordance between morphological and genetic patterns of variation, an observation which may be due either to differences in selective pressures acting on the

two character suites (e.g. Schnell and Selander, 1981) or to differences in ability to discern statistical differences (Lewontin, 1984). Studies of geographic variation should involve many characters because patterns of variation in space are probably not the result of adaptation of one or a few characters to a single environmental variable; rather, it is more probable that the patterns of variation that are evident are due to adaptation of many characters to many different environmental factors (Sokal and Rinkel, 1963). To gain a complete understanding of potential factors influencing population structure within a species, variation in a variety of character types should be documented, recognizing the relative "strengths and weaknesses" (Zink, 1986) of each.

1.2 Variation in Vocalizations in Birds

Geographic variation in vocalizations has been documented for a wide variety of avian species (Mundinger, 1982). Various authors have suggested that a learned trait, like song in many oscine passerine bird species, may be biologically important in that it may influence population structure (Nottebohm, 1969; Baker and Cunningham, 1985; Balaban, 1988). Some bird species are characterized by a mosaic of different groups of individuals that produce different variants of a given vocalization. These different groups of individuals constitute "dialects populations" which may be defined as separate, adjacent aggregations of birds with well defined boundaries and with different vocalizations (Rothstein and Fleischer, 1987).

The genetic or local adaptation hypothesis articulated by Nottebohm (1969) and later elaborated by other workers (Payne, 1981; Rothstein and Fleischer, 1987) suggested that different song variants, in different dialect populations, may act as markers which evolved to restrict gene flow between populations adapted to different

environmental conditions. If this were the case, then correlations between patterns of genetic variation and song variation should be detected (at least with respect to the dialect distinguishing portion of the song). Possible proximate mechanisms which could result in restricted dispersal or gene flow from one dialect to another include positive assortative mating (females choosing males which sing the appropriate natal dialect vocalization) and/or higher levels of male aggression against males which possess a foreign song (Baker and Medwalt, 1978; Tomback et al. 1983; Tomback and Baker, 1984).

1.3 Ecology of the Rufous-collared Sparrow

The Rufous-collared Sparrow (*Zonotrichia capensis*), a small emberizine songbird, ranges from southern Mexico to Tierra del Fuego and from sea level to over 4000 m in altitude (Chapman, 1940; Nottebohm and Selander, 1972; Nottebohm, 1975; Handford and Nottebohm, 1976; Handford, 1988). It occurs in most types of habitats being absent only from areas of closed forest (Handford, 1988). Twenty-five subspecies have been described throughout the entire range (Chapman, 1940; Paytner, 1970).

The song of *Z. capensis* throughout its known range is relatively simple and is composed of two parts: an introductory theme consisting of between one to five whistled notes, and a terminal trill (Miller and Miller, 1968; Nottebohm, 1969; 1975; Handford and Nottebohm, 1976). The vocal behaviour and patterns of variation in song of the Rufous-collared Sparrow have been well studied especially in northwestern Argentina (Nottebohm, 1969; 1975; King, 1972; Handford and Nottebohm, 1976; Handford, 1981; 1988; Lougheed and Handford, 1989; Lougheed et al. 1989; Handford and Lougheed, 1991). This species possesses a geographically widespread

system of vocal dialects (defined by the inter-note interval of the terminal trill). The "trill rate" dialects of *Z. capensis* in northwestern Argentina are unique among birds because of the clear and consistent association between original vegetation and a certain range of trill intervals, and because of the remarkable temporal stability of form and pattern of the dialects (Handford, 1981, 1988). This terminal trill rate can remain relatively unchanged over large areas of homogeneous habitat, but where there are shifts in vegetation which occur over a short geographic distance (e.g. an altitudinal gradient) there is often a corresponding shift in trill interval of *capensis* songs (Nottebohm, 1975; Handford and Nottebohm, 1976; Handford, 1981; 1988). The boundary between dialects may occur over a very short distance (e.g. less than 1 km) and can be very well defined (Nottebohm, 1975; Handford, 1981; 1988; Lougheed et al. 1989). Two lines of evidence indicate a remarkable temporal stability of the pattern and form of these dialect areas. First, since Nottebohm's (1969) initial report, there have been ongoing studies of some dialect areas (in particular in the Argentine province of Tucuman); the boundaries between dialects and the defining trill rates have remained unchanged over this approximately 20 year period (Handford, 1988). Second, although much of the original vegetation has been destroyed in northwestern Argentina, the pattern of Rufous-collared Sparrow dialects quite accurately reflects the pattern of original vegetation, even though in some instances the original vegetation has been absent for up to 200 years (Handford, 1988).

As is the case with the extensively studied White-crowned Sparrow (*Z. leucophrys* ; e.g. Cunningham and Baker, 1983), the Rufous-collared Sparrow appears to have a closed learning period which ends at approximately 50 days of age after hatching (Egli, 1971; Kroodsma and Baylis, 1982; Tubaro, 1990); thus, juvenile *Z. capensis* probably learn the song of their natal area before dispersal. Migration

patterns of the various subspecies are relatively complex and not well studied; montane populations do migrate altitudinally (e.g. in populations of *Z. capensis pulacayensis* ; King, 1972; Handford, 1980; pers. obs.) and austral populations (e.g. *Z. capensis australis*) migrate latitudinally (Chapman, 1940; Olrog, 1979; pers. obs.). Lowland populations in northwestern Argentina, are probably sedentary (King, 1972). Rufous-collared Sparrows appear to be highly philopatric (males, females and possibly juveniles) at least where the phenomenon has been investigated (Handford and Nottebohm, 1976; Handford, 1980; pers. obs.) and often males can be seen in successive years singing from the same shrub or rock.

Two studies have examined possible correlations between the pattern of trill rate variation in song and genetic variation of Rufous-collared Sparrow populations, both in Argentina. Nottebohm and Selander's (1972) pilot study indicated that there was clinal variation in some allozyme frequencies but the collecting locales were too geographically widespread and the sample sizes were too small to properly assess relationships between vocal and genetic variation. Handford and Nottebohm (1976) examined the correlation between trill interval and variation at six polymorphic loci using data from five collecting sites along a mountain transect crossing one border between two dialect populations. Some clinal variation in allozyme frequencies at some loci was found, but there was no apparent relationship between variation in trill interval and pattern of genetic variation (i.e. there was no abrupt shift of allele frequencies at or near the dialect border). The results of the latter study were inconclusive because the study was too narrow in scope geographically (Baker, 1982; Balaban, 1988) and too few loci were examined, and also because the difference in trill interval between the two compared dialect populations was small considering the range of values described for the entire northwest (Handford, 1988). Therefore, the question still

remains - is there correlation between pattern of trill rate variation and pattern of genetic variation in the Rufous-collared Sparrow?

1.4 Research Questions

The Rufous-collared Sparrow is ideally suited for studies of geographic variation in behavioural, morphological and genetic characters because 1) it is geographically widespread, 2) it occurs in a diverse array of habitats, and 3) it displays a unique system of vocal dialects. Thus, I wished to investigate geographic variation in northwestern Argentine populations of this species. The study area is coincident with portions of the ranges of two putative subspecies: *Z. capensis hypoleuca* and *Z. capensis pulacayensis* (Chapman, 1940). This particular area was chosen because vocal variation in general, and the pattern of trill-rate dialects in particular, have been thoroughly documented (Nottebohm, 1975; Handford, 1981; 1988; Handford and Lougheed, 1991). I wished to address two questions:

1) What is the magnitude and pattern of variation in both genetic and morphological characters at two hierarchical levels: among collecting sites regardless of dialect affiliation and among vegetation/dialects?

It would be expected, in species like the Rufous-collared Sparrow, which occur in an array of environments, that marked morphological differentiation would be present. This trend is evident in a variety of North American avian taxa which inhabit the Rocky Mountains (e.g. among putative species of the sapsuckers *Sphyrapicus* spp. - Johnson and Zink, 1983; Song Sparrows, *Melospiza melodia* - Aldrich, 1984; the schistacea group of the Fox Sparrow, *Passerella iliaca* - Zink, 1986). It is not as readily apparent

how much genetic variation may be revealed by electrophoresis. For example, Zink (1986) found little genetic differentiation among mountain populations of the Fox Sparrow, even though seven putative subspecies occurred within the study area. The Rufous-collared Sparrow is a vagile species, occurring in almost all known habitats throughout its range, and breeds at altitudes up to 4000 meters; thus it is not obvious what might constitute a physical barrier to migration (and thus to gene flow) to this species.

However, vocal dialects, as was stated above, may act as "cultural" barriers to migration and gene flow. Thus, if dialect populations of Rufous-collared Sparrows are found to be differentiated with respect to allozyme frequencies, then this would lend support to the local adaptation hypothesis as an explanation for the existence of song differences (Payne, 1981; Rothstein and Fleischer, 1987). If this were the case, then there should be fewer genetic differences among sites within a dialect population compared to differences among sites in different dialects.

2) How do morphological, genetic and song characters covary with each other, and with geographic distance and environmental characteristics?

In bird species which have been studied, morphological differentiation is often evident without detectable differences in allozyme frequencies (Barrowclough, 1983). Therefore, based on other avian studies, it might be predicted that there will be no covariation between genetic and morphological traits. Wright (1943; 1978a) has suggested that geographic distance may play an important role in population structuring. Populations may be more similar genetically by virtue of their geographic proximity, compared to populations which are distant; thus, if isolation-by-distance is

important in populations of Rufous-collared Sparrows, then levels of differentiation of genetic and morphological characters (assuming that morphological differences reflect underlying genetic differences) between compared populations might be positively related to geographic distance. If Rufous-collared Sparrows are adapted to local environmental conditions, then it might be expected that either genetic and/or morphological distances would be positively related to degree of differentiation among habitats. Finally, frequency and temporal characters of song may be influenced by habitat characteristics (Morton, 1975; Bowman, 1979; 1983; Wiley and Richards, 1982) and body size (Nottebohm, 1975); a relationship between at least some attributes of song, and both morphological characteristics of the birds and some aspects of their habitat, would be predicted.

2.0 MATERIALS AND METHODS

2.1 Specimen Collection and Preparation

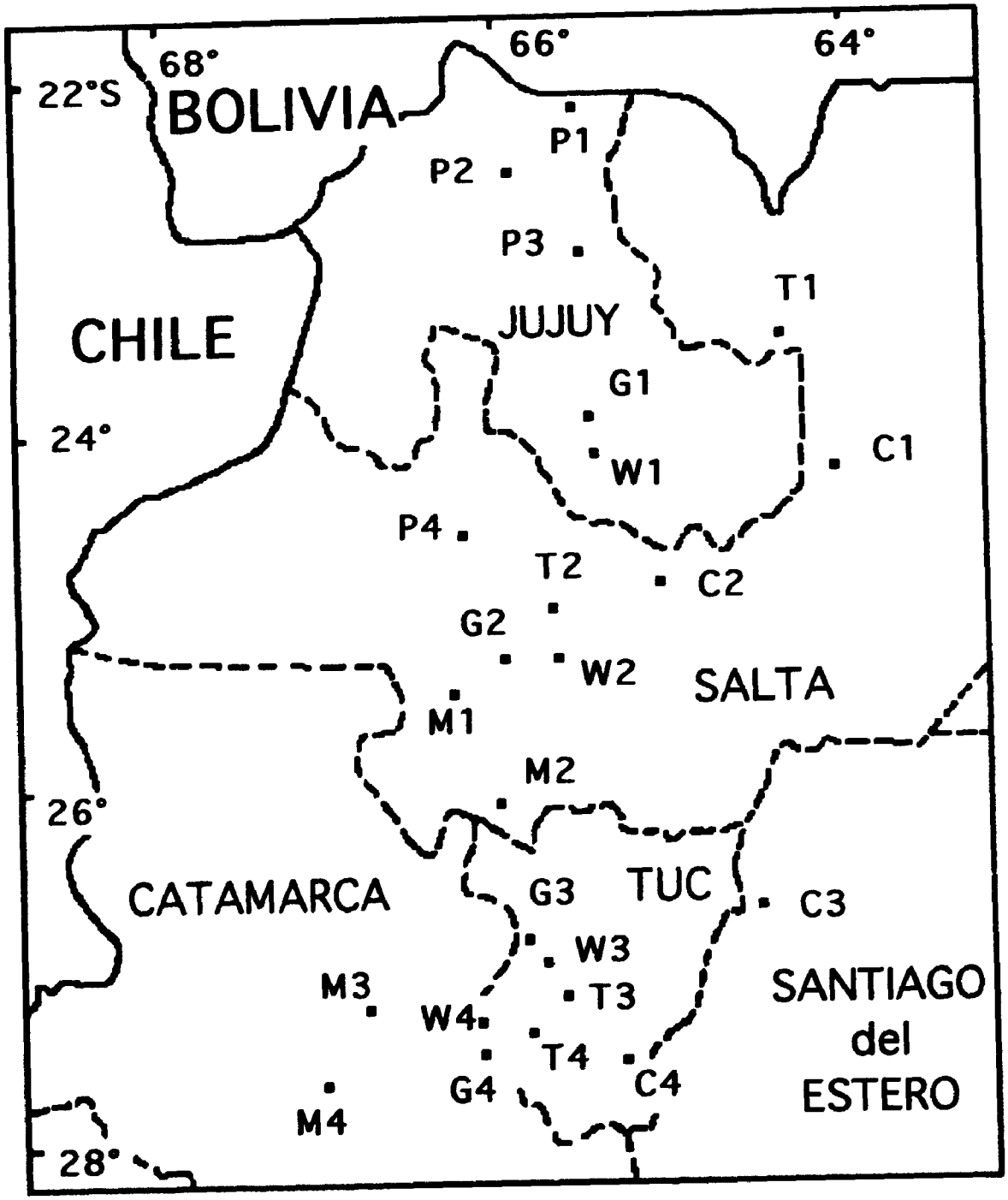
A total of 474 male *Z. capensis* was collected using mist nets and Potter traps during two field seasons in northwestern Argentina: September 1987 to March 1988, and September 1988 to March 1989. All specimens were collected during the breeding season to ensure that they were breeding resident birds. Only males were collected because male and female *Z. capensis* are morphologically different and because only males sing (Chapman, 1940; Handford, 1983; 1985). Males were identified by the presence of a cloacal protuberance. Approximately 20 specimens were collected at each of four sites (arranged in a latitudinal series), in each of six vegetation types: lowland chaco thornscrub, transition forest, montane woodland (= alder woodland in Handford, 1988), montane grassland, Monte desert scrub and puna high altitude scrub. These six vegetations were chosen because they are associated with five statistically distinct groups based on trill interval (Handford, 1988). Each vegetation has a particular range of trill intervals associated with it, but trill interval is not necessarily unique; however, the trills of all adjacent vegetations considered are statistically distinct. Table 1 gives sample sizes for all localities (Handford, 1988, provides a description of the various habitats). Figure 1 shows the collecting sites and Appendix 1 gives detailed locality information. Geographic coordinates were taken from a gazetteer (Paytner, 1985) or inferred from 1:500,000 maps published by the Instituto Geografico Militar, Buenos Aires. Altitude was estimated from these maps or read from an altimeter. Thus, there was a hierarchical structure with respect to sampled sites. Within the study area (for the purposes of discussion, the total population), there were six vegetation/dialect populations; within each of the latter

Table 1: Number of male Rufous-collared Sparrows sampled from each of six vegetation types (letter code in parentheses).

VEGETATION	SITE[1]	NUMBER SAMPLED
lowland chaco (C)	1	19
	2	20
	3	20
	4	21
transition forest (T)	1	19
	2	20
	3	17
	4	21
montane woodland (W)	1	20
	2	20
	3	19
	4	19
montane grassland (G)	1	17
	2	21
	3	20
	4	21
Monte desert scrub (M)	1	20
	2	18
	3	21
	4	21
puna high altitude scrub (P)	1	20
	2	20
	3	20
	4	20

1 - Sites were arranged in a latitudinal series within each vegetation (see Appendix 1).

Figure 1: Map of northwestern Argentina showing the 24 collecting localities used in the present study. Vegetation types are indicated by the first letter in each site code. C = chaco, T = transition forest, W = montane woodland, G = montane grassland, M = Monte desert scrub and P = puna high altitude scrub.. Latitudes and longitudes are shown on the upper and left figure borders respectively. TUC = Tucuman.


68°
66°
64°
22°S
BOLIVIA
P1
P2
P3
T1
CHILE
JUJUY
G1
24°
W1
C1
P4
T2
C2
G2
W2
SALTA
M1
M2
26°
CATAMARCA
G3
TUC
C3
W3
M3
T3
W4
SANTIAGO
del
ESTERO
T4
C4
G4
M4
28°

groups there were four sites sampled.

Songs of *Z. capensis* are highly stereotyped (Nottebohm, 1975) and about five song repetitions per bird are usually deemed sufficient to ascertain trill interval and frequency characteristics for a given bird (Handford, 1988). Additionally, trill rate of Rufous-collared Sparrows songs are sufficiently consistent within a locale so that only a small number of individuals need be recorded to decide dialect affiliation and to estimate temporal and frequency characteristics of song (Nottebohm, 1975; Handford, 1981). Accordingly, a series of songs from between four to six individuals were recorded at each site using a Sennheiser MKH 816 "shotgun" microphone and a UHER CT260 AV tape recorder. At each site notes were taken on vegetation characteristics (degree of openness, average height of vegetation, height of tallest trees etc.) and this information was supplemented with photographs.

Birds were killed using thoracic compression and immediately afterward eight external morphological measurements were taken ($\pm$ 0.1 mm) using dial callipers: wing chord, outer rectrix, tarsus length, hind toe plus claw, bill depth, bill width, culmen (measurements as described in Handford ,1985, and Zink,1986) and bill length from the gape (the distance from the gape to the tip of the upper mandible). Each specimen was subsequently placed in a plastic bag and maintained on dry ice (-87 ° C) until shipment to Canada.

Upon arrival in Canada, birds were partially thawed and kidney and liver tissues were removed for starch gel electrophoresis. Once tissues were removed, carcasses were shipped to the Royal Ontario Museum for preparation as skin/skeleton mounts. Dermestids were used to clean the skeletons of the bulk of remaining tissue. Any remaining adhering tissue was removed by hand and the bones were bleached. Thirteen skeletal characters ($\pm$ 0.1 mm) were measured using electronic digital callipers

(LESSOFT software; Marcus, 1986): partial skull length (from the foramen magnum to base of the bill), skull width across the bullae, width of the scapula at the proximate end, scapula length, coracoid length, humerus length, ulna length, keel depth, sternum length, femur length, width of proximal end of the femur, tibiotarsus length and synsacrum width across the acetabula (all measures described in Robins and Schnell, 1971 except for partial skull length).

2.2 Measurement of Song Characteristics

Sonograms were made from all of the song recordings using a UNISCAN II spectrum analyzer (Multigon Industries) set at 0 to 10 kHz and with either a 3.2 or a 1.6 second time base. For one sonogram per individual, at each site, five song characteristics were measured: maximum and minimum frequencies (KHz) of the song, song frequency range (maximum - minimum song frequency), song duration (msec), and trill interval (trill duration/number of trill notes - 1; units = msec). The first four variables were used in computing inter-site Mahalanobis distances (see section 2.7.1). Mean trill intervals were calculated (SYSTAT for the Macintosh, Version 3.2; Wilkinson, 1987) so that comparisons to other studies could be made to ensure that sites fell within the range of previously reported values.

2.3 Protein Electrophoresis

Allozyme variation was assayed using starch-gel electrophoresis. Sample preparations were as described by Bogart (1982). Electrophoretic methods were modified from Bogart (1982). All gel systems used (see Appendix 2) were from either Selander et al. (1971) or Clayton and Tretiak (1972). Sample supernatants were loaded onto each gel using wicks cut from extra-thick filter paper (Product No 470,

Schleicher and Schnell Inc. NH.) and prerun for approximately 15 minutes. Subsequently, the wicks were removed and the gels run until the red marker dye (food colouring) reached the anodal J-cloth electrode wick. Initially, a multi-pass electrophoretic survey using 24 enzyme and one general protein stains, for both source tissues, was performed on subsets of 32 samples (see Appendix 2). Electrophoretic runs varied not only in electrode/gel buffers used (e.g. see Aquadro and Avise, 1982) but also in running times (either the usual times reported in the literature or approximately 12 hours at 1/3 the usual current; see Murphy et al. 1990). Enzyme and protein staining protocols were modified from Shaw and Prasad (1970), Harris and Hopkinson (1976) and/or Murphy et al. (1990). Fifteen proteins (13 enzymes, haemoglobin and a general protein, possibly albumin - see Nottebohm and Selander, 1972) were resolvable for most samples, representing a total of 20 loci: AAT-1, AAT-2, ACPH-1, EST-5, GP-1, HB-2, G3PDH, IDH-1, IDH-2, LDH-1, LDH-2, MDH-1, MDH-2, MPI, PEP-A, PGD, PGM-1, PGM-2, PNP and SOD-1 (see Appendix 2 for acronym definitions). For enzymes encoded by more than one locus, the most anodal locus was labelled 1, next most anodal, 2, etc. Haemoglobin, although its constituent subunits are encoded by two loci, was treated as a single locus in statistical analyses (Richardson et al. 1986). For every individual the genotype was recorded at each of the 20 loci (i.e. heterozygous or homozygous for the various allozymes occurring). At each locus, the most common allozyme was designated either B or C (depending on how many allozymes existed); all other allozymes were given a letter coded to indicate mobility relative to the common one (e.g. if C was the common allele then A and B would designate allozymes which migrated further from the origin and D, E etc. would indicate allozymes which appeared closer to the origin).

2.4 Measurement Error of Morphological Characters

Measurement error was assessed for a subset of the specimens on selected characters (21 individuals from a single site : Belen, Catamarca see Appendix 1). Replicated measurements (three times for skeletals and two times for externals) and a nested analysis of variance [hereafter, nested ANOVA (using both PROC ANOVA and PROC NESTED; SAS Institute Inc., 1985)] were used according to the methods of Bailey and Byrnes (1990) for four external (outer rectrix, wing chord, tarsus length and hind toe) measurements and all thirteen skeletal measurements (from prepared specimens). Scapula width was found to have low repeatability (Lougheed et al. 1991) and was excluded from further analyses.

2.5 Variation of Morphological Characters

2.5.1 Among Sites

For all variables (externals and skeletal) means and standard deviations were calculated (PROC MEANS; SAS Institute Inc. 1985) for each site. To examine the relationships among morphological variables (external and skeletal separately), among site (i.e. analogous to using site means but correcting for within-site variation and covariation) and within site (i.e. among individuals at each site averaged over all 24 sites) correlation matrices were constructed (PROC NESTED; SAS Institute Inc., 1985). For each morphological variable, for each site, coefficient of variation (CV = character standard deviation/character mean X 100) was calculated and then averaged across all sites. A one-way analysis of variance (hereafter ANOVA; PROC ANOVA; SAS Institute Inc., 1985) was used to test for heterogeneity among site means for each external and skeletal variable. To test for differences among sites in multivariate space, I used a multivariate analysis of variance (hereafter MANOVA; PROC MANOVA;

SAS Institute inc., 1985) for externals and skeletals separately (all variables natural log transformed, see Bryant, 1986, for reasoning).

2.5.2 Among Vegetation/Dialects

Each external and skeletal character (natural log transformed) was subjected to nested ANOVA (using both PROC ANOVA and PROC NESTED; SAS Institute Inc., 1985); site (≈ latitude effect) was nested within vegetation/dialect; to test for heterogeneity among sites within a vegetation, and among vegetations. External and skeletal morphological data sets were subjected separately to MANOVA to test whether group (the six vegetation/dialect populations) centroids were significantly different (PROC MANOVA; SAS Institute Inc., 1985). To explore relationships among vegetation/dialect populations canonical variates analyses (CVA) using individual cases were performed for each morphological data set (all variables natural log transformed; MGLH module of Macintosh SYSTAT Version 3.2; Wilkinson, 1987). Finally, percentage of individuals correctly reclassified into their original vegetation/dialect population were calculated based on their CV scores for each morphological data set separately (MGLH module in SYSTAT for Macintosh Version 3.2; WILKINSON, 1987).

2.6 Variation in Allozyme Frequencies

2.6.1 Among Sites

All statistical analyses on allozyme data were performed using the PC version of BIOSYS-1 (Swofford and Selander, 1981). Two estimates of heterozygosity were calculated, one based on direct count of number of heterozygous loci at a given site,

and the other based on the Hardy-Weinberg expectations using Nei's (1978) unbiased estimate. Percentage polymorphic loci for each site was calculated using two criteria: 1) no criterion, that is, a locus was considered polymorphic if any variability occurred with the examined population and 2) a locus was considered polymorphic if the frequency of the most common allele was ≤ 0.95. Each polymorphic locus (no criterion), for each site, was tested for departure from Hardy-Weinberg equilibrium using the exact probability option of STEP HDYWBG, and using pooled genotype classes (three classes: 1-homozygotes for the most common allele, 2-heterozygotes of the common allele with one of the other alleles, and 3- all other genotypes); this statistical procedure is analogous to a Fisher's exact test for a 2 X 2 contingency table, and generates a significance probability of departure from expect Hardy-Weinberg equilibrium frequencies at a given locus (Elston and Forthofer, 1977; Swofford and Selander, 1981).

Degree of genetic population differentiation can be estimated using Wright's (1978b) F fixation coefficients: F_{IS}, F_{ST} and F_{IT}. Each of these inbreeding coefficients have two different points of reference indicated by the subscripts I = individual, S = subpopulation, and T = total population. These indices are mathematically related as follows:

$$F_{ST} = (F_{IT} - F_{IS})/(1 - F_{IS})$$

The "fixation index", F_{ST}, measures the reduction in heterozygosity of subpopulations due to random genetic drift (all F statistics as defined by Hartl, 1988). The "inbreeding coefficient", F_{IS}, is a measure of the increase in individual autozygosity brought about by nonrandom mating relative to the subpopulation. Finally, F_{IT} measures increase in individual autozygosity relative to the total population. The F_{ST} is the most often used

and cited of Wright's indices. F_{ST} ranges from zero to one, the higher the value of this coefficient, the greater the genetic subpopulation differentiation. F_{ST} can be thought of as the among subpopulation component of genetic variance; F_{ST} is a relative measure and partitioning at various levels will be affected by total variance.

For the purposes of the present analysis, I calculated F_{ST} to describe degree of differentiation among sites irrespective of dialect affiliation (i.e. subpopulation = site). F_{ST} values were calculated for each polymorphic locus separately and overall (arithmetic means of all values for each F index) using the STEP FSTAT. F_{ST} values corrected for sampling error were also calculated using the STEP WRIGHT78. Uncorrected F_{ST} were calculated to compare to published values for other organisms, while the corrected values were used in the discussion for interpretation of population structure. Significance probabilities cannot be generated directly for F coefficients. However, the following formula can be used to convert F_{ST} to a Chi^2 statistic testing for heterogeneity of allelic frequencies among subpopulations (Workman and Niswander, 1970; STEP HETXSQ):

$$Chi^2 = (k-1)(2N_T X F_{ST} - 1)$$

where k = number of alleles at a given locus, N_T = total number of individuals in the analysis, and degrees of freedom = (k - 1) X (number of subpopulations - 1). Both uncorrected and corrected F_{ST} values were converted to Chi^2 statistics using this formula.

2.6.2 Among Vegetation/Dialects

Hierarchical F coefficient analysis can be used to estimate components of

variance of allozyme frequencies at different levels (Wright, 1978b). In the present study, three hierarchy levels can be defined: 1) subpopulation or site (S), 2) vegetation/dialect (D), and 3) total population (T). Thus, components of variance were estimated for site-dialect (F_{SD}), dialect-total (F_{DT}), and site-total (F_{ST}) using STEP WRIGHT78. Although this hierarchical analysis shows which level(s) contributes the most to overall variance in allozyme frequencies, it does not identify levels of contribution of different site(s), vegetation/dialect(s), and/or loci. Therefore, Wright's F coefficients (uncorrected and corrected) were calculated for each vegetation/dialect population separately (i.e. four subpopulations within each of six populations) using STEP FSTAT and STEP WRIGHT78. As before, STEP HETXSQ was used to test for heterogeneity among sites, for each polymorphic locus, for each vegetation.

2.7 Covariation of Different Character Suites

2.7.1 Computation of Distance Matrices

Geographic distances between sites were calculated using the geographic coordinates for each site, and rounded to the nearest 10 km. A matrix of ecological distances reflecting differences in habitat was constructed as follows:

1) Each site was scored for four variables (see Table 2) based on photos, notes and field experience with each site, by two people independently (S.C.L. and P. Handford).
2) A Spearman rank correlation matrix (Seigel, 1958) was calculated based on all eight variables (four variables for two people).
3) A principal components analysis was performed on the Spearman correlation

Table 2: List of variables and variable scores used to describe the habitat structure at each site.

Variable Description	Range of Variable Values for each Score	Score
i) Maximum vegetation height	0 to 1 meter	1
	1 to 2 m	2
	2 to 5 m	3
	5 to 10 m	4
	> 10 m	5
ii) Average vegetation height	0 to 0.5 meters	1
	0.5 to 1 m	2
	1 to 5 m	3
	5 to 10 m	4
	> 10 m	5
iii) Percent vegetation cover	0 to 20	1
	20 to 40	2
	40 to 60	3
	60 to 80	4
	80 to 100	5
iv) Percentage cover by "trees" (nearest percentage)	0	1
	25	2
	50	3
	75	4
	100	5

matrix. Principal components analysis can be used to reduce the number of variables in a data set; these derived variables can then be used in subsequent statistical analyses (Pimentel, 1979). The first PC axis describes the greatest proportion of variation in the data set (e.g. see Campbell and Atchley, 1981); therefore, for each site, the PC-1 scores were calculated and the difference between scores for any two sites being compared was considered the ecological distance.

Mahalanobis distances were calculated, using each of the external and skeletal morphological data sets separately (natural log transformed data; PROC CANDISC; SAS Institute Inc., 1985), for each site pair. Mahalanobis distances are a measure of distance between group centroids in multivariate (canonical variate) space, corrected for correlation among variables (Campbell and Atchley, 1981). Mahalanobis distances were also calculated using three song frequency variables and one temporal variable (all natural log transformed): song maximum frequency, song minimum frequency and song frequency range (maximum - minimum frequency), and total song duration. Finally, Nei's (1978) genetic distance corrected for sample size, and Rogers (1972) genetic distance were calculated for each site pair using the SIMDIS procedure in BIOSYS-1. The former distance was computed for purposes of comparison to other published values only, and was not used in any subsequent analyses because of non-metricity (Evans, 1987).

The relationships among objects or sites as indicated by a distance matrix can be represented visually using non-metric multidimensional scaling (hereafter MDS; Kruskal and Wish, 1978; Pimentel, 1979). I performed MDS on the following matrices, scaling each to two dimensions: Rogers' genetic distance, ecological distance, and

external morphological, skeletal and song Mahalanobis distance matrices.

2.7.2 Test for Congruence of Pattern between Distance Matrices

To test for congruence of pattern among the various distance matrices, Mantel's (1967) non-parametric test was used, with 250 iterations per pair-wise test ("R"-package Legendre and Vaudor, 1985). A total of seven matrices were compared (acronyms used in discussion in brackets):

1) Geographic distance (GEO)
2) Inverse geographic distance (INV)
3) Ecological distance (ECO)
4) External morphological Mahalanobis distance (EXT)
5) Skeletal Mahalanobis distance (SKE)
6) Song Mahalanobis distance (SON)
7) Rogers' (1972) genetic distance (ROG)

Douglas and Endler (1982) suggested that a corrected α - level be used when more than one matrix comparison is being performed. Thus, I divided 0.05 by the number of pairwise comparisons {total of 20 matrix comparisons; therefore, the new, conservative α - value is 0.0025, and the corresponding critical t value (∞ d.f.) is 3.051}. Mantel's test assesses the independence of pattern between two distance matrices (Mantel, 1967; Sokal, 1979; Zink, 1986). The use of the inverse geographic distance matrix improves the probability of detecting local patterning in the data sets since it minimizes the effect of large distances (Jones et al. 1980).

3.0 RESULTS

3.1 Song

Representative sonograms from each site are shown in Figure 2. Average trill interval for each site is listed in Table 3. The range of trill intervals found at the four sites in each vegetation fall within the ranges described by Handford (1988) except for the northernmost lowland chaco site (C1); this site had a long trill interval for lowland chaco (290 msec), but Handford (1981) suggests that this vegetation is probably more complex phytographically than previously thought, and trill rate in Rufous-collared Sparrows possibly varies accordingly. Monte desert scrub songs have recently been re-evaluated in light of new analyses of song frequency and duration (Handford and Lougheed, 1991). In some cases, the nature of Monte sites' songs suggests that the theme part of the song has been modified so that it qualitatively appears similar to a normal song (i.e. theme + trill), while at other sites the songs appear to have a well-defined trill consisting of a very slow, languid series of morphologically similar whistled notes. Whatever the case, at the former sites, trill notes could not be unambiguously identified and therefore no trill interval could be calculated (sites M1 and M2). Trill intervals were calculated for sites M3 and M4 since these songs did possess clearly defined trills; the estimated trill intervals were typical of the Monte desert scrub populations described by Handford (1988).

3.2 Variation of Morphological Characters

3.2.1 Among Sites

Means and standard deviations for the eight external and twelve skeletal characters are presented in Appendices 3 and 4, respectively. The patterns of correlation between variables among individuals within sites and among sites were

Figure 2: Representative sonogram for songs recorded at each of the 24 collecting localities. All sonograms are shown with a time-base of 3.2 seconds (scale indicated by bar at lower left) and a frequency scale from 0 to 10 KHz. An "A" indicates the nothernmost site in each vegetation series through to "D" indicating the southernmost site.

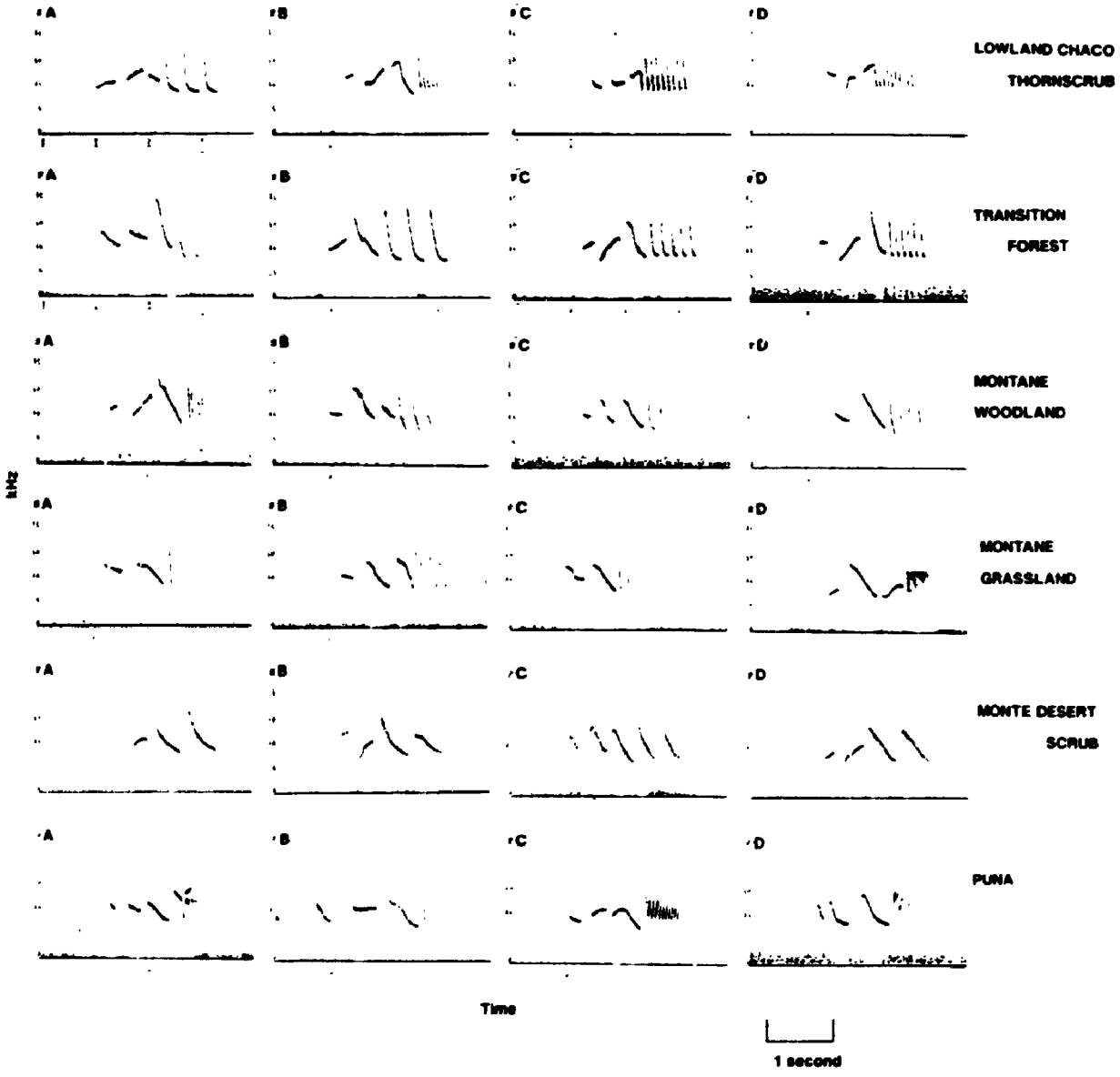

A
B
C
D
LOWLAND CHACO
THORNSCRUB
TRANSITION
FOREST
MONTANE
WOODLAND
MONTANE
GRASSLAND
MONTE DESERT
SCRUB
PUNA
kHz
Time
1 second

Table 3: Average trill intervals (in msec) with standard deviation (S.D.) for each of the 24 collecting sites. Number of recorded individuals is indicated by n. Site codes are as indicated in Table 1.

Site	n	Interval[1]	S.D.
C1	4	290	16.5
C2	4	74	9.6
C3	4	80	4.5
C4	5	65	2.8
T1	5	251	18.8
T2	6	344	21.2
T3	5	142	6.6
T4	5	93	3.4
W1	5	61	7.2
W2	5	188	33.7
W3	5	156	13.0
W4	5	138	2.8
G1	5	78	2.9
G2	5	72	5.1
G3	4	60	3.0
G4	5	36	8.0
M1	6	N.C.	N.C.
M2	5	N.C.	N.C.
M3	6	394	36.4
M4	5	474	26.4
P1	6	18	2.1
P2	5	31	3.1
P3	4	29	14.2
P4	6	36	13.1

1 - N.C. trill interval not calculated for reasons covered in the text.

similar for both external and skeletal variables (Tables 4,5,6 and 7). Virtually all correlations were positive and in general, among site correlations were greater in magnitude than corresponding within site correlations due to greater ranges of values among site means compared to individuals within sites. Coefficients of variation for external variables ranged from 3.15 (wing chord) to 4.02 (outer rectrix) with a mean of 3.64 ± 0.36 (Table 8). Coefficients of variation for skeletal variables ranged from 1.90 (skull width) to 3.97 (keel depth) with an average of 2.60 ± 0.64 (Table 8).

Results of one-way ANOVA's ("treatment" = site) for each morphological character are shown in Table 8. All morphological characters were significantly heterogeneous over the study area. Results of MANOVA on skeletal and external data sets also demonstrated significant morphological heterogeneity across sites (using Wilk's approximation of F: externals $F_{(184, 3262.71)} = 10.71$, $P << 0.001$; skeletals $F_{(276, 3824.72)} = 6.46$, $P << 0.001$).

3.2.2 Among Vegetation/Dialects

The results of nested ANOVA's performed on the eight external and on the twelve skeletal variables are presented in Tables 9 and 10, respectively. In all cases, there was significant heterogeneity among sites within vegetations (i.e. a significant variation in morphology across latitude). All but one (keel depth - Table 10) of the 20 nested ANOVA's indicated significant heterogeneity among vegetation populations for the morphological character in question. Given that there is a common latitude effect within each vegetation, it is possible that the use of nested ANOVA may be questioned; however, use of 2-way ANOVA's (i.e. site and vegetation as main effects) does not alter the interpretation of the results. MANOVA of each morphological data set indicated

Table 4: Matrix of within site (among individuals) correlation coefficients (r) of the eight external morphological characters. WC = wing chord length, OR = outer rectrix length, HT = length of hind toe + claw, TA = tarsus length, BD = bill depth, BL = bill length, CU = culmen length, and GA = bill length from gape.

	WC	HT	TA	BD	BW	GA	CU
OR	0.59	0.12	0.16	0.15	0.051	0.15	0.11
WC		0.081	0.13	0.20	0.14	0.16	0.24
HT			0.30	0.050	0.082	0.18	0.15
TA				0.032	0.097	0.12	0.095
BD					0.35	0.16	0.28
BW						0.15	0.15
GA							0.40

Table 5: Matrix of among site correlation coefficients (r) of the eight external morphological characters. Acronyms as defined in Table 4.

	WC	HT	TA	BD	BW	GA	CU
OR	0.97	0.60	0.80	-0.094	0.046	0.71	0.82
WC		0.45	0.77	-0.13	-0.034	0.65	0.77
HT			0.60	0.30	0.32	0.73	0.71
TA				0.29	0.37	0.87	0.85
BD					0.39	0.30	0.18
BW						0.091	0.31
GA							0.90

Table 6: Matrix of within site (among individual) correlation coefficients of the twelve skeletal characters. L =length, D = depth and W = width. Tibio. = tibiotarsus and Syn. = synsacrum.

	Skull W	Coracoid L	Scapula L	Sternum L	Keel D	Femur L	Femur W	Syn. W	Humerus L	Tibio. L	Ulna L
Skull L	0.45	0.38	0.34	0.26	0.30	0.32	0.18	0.24	0. 32	0.29	0.31
Skull W		0.32	0.36	0.34	0.28	0.33	0.14	0.34	0. 35	0.31	0.35
Coracoid L			0.57	0.43	0.33	0.58	0.26	0.34	0. 63	0.58	0.58
Scapula L				0.50	0.32	0.51	0.22	0.34	0. 52	0.44	0.47
Sternum L					0.38	0.34	0.17	0.27	0. 42	0.35	0.39
Keel D						0.21	0.067	0.26	0. 25	0.29	0.30
Femur L							0.28	0.29	0. 81	0.70	0.64
Femur W								0.15	0.25	0.16	0.21
Syn. W									0.27	0.28	0.29
Humerus L										0.66	0.74
Tibio. L											0.65

Table 7: Matrix of among site correlation coefficients of the twelve skeletal characters. L, D , W, Syn. and Tibio. as defined in Table 6.

	Skull W	Coracoid L	Scapula L	Sternum L	Keel D	Femur L	Femur W	Syn. W	Humerus L	Tibio. L	Ulna L
Skull L	0.75	0.77	0.81	0.75	0.39	0.85	0.85	0.87	0.85	0.84	0.83
Skull W		0.85	0.80	0.82	0.30	0.77	0.55	0.74	0.86	0.78	0.82
Coracoid L			1.00	0.98	0.16	0.97	0.70	0.94	0.98	0.98	0.95
Scapula L				0.99	0.23	0.96	0.70	0.95	0.98	0.96	0.97
Sternum L					0.24	0.94	0.68	0.91	0.96	0.94	0.90
Keel D						0.10	0.29	0.11	0.22	0.048	0.23
Femur L							0.79	0.97	0.97	1.00	0.91
Femur W								0.85	0.74	0.78	0.67
Syn. W									0.95	0.96	0.91
Humerus L										0.97	0.98
Tibio. L											0.91

Table 8: ANOVA results for all morphological characters (all values log-transformed). Degrees of freedom = d.f., SS = sum of squares, MS = mean square, and F is the test statistic. L, D and W as in Table 6.

Character	d.f.	SS	MS	F[1]	CV[2]
Outer Rectrix L					
Between groups	23	1.58	0.069	40.42***	4.02
Within groups	437	0.74	0.0017		
Wing Chord L					
Between groups	23	1.51	0.066	64.77***	3.15
Within groups	450	0.46	0.0010		
Tarsus L					
Between groups	23	0.56	0.024	22.36***	3.93
Within groups	447	0.49	0.0011		
Hind Toe L					
Between groups	23	1.035	0.045	27.63***	3.22
Within groups	450	0.73	0.0016		
Bill D					
Between groups	23	0.096	0.0042	3.56***	3.39
Within groups	450	0.53	0.0011		
Bill W					
Between groups	23	0.071	0.0031	2.44***	3.53
Within groups	450	0.57	0.0013		
Bill Gape L					
Between groups	23	0.56	0.024	14.53***	3.95
Within groups	450	0.75	0.0017		
Culmen					
Between groups	23	0.62	0.027	16.91***	3.90
Within groups	448	0.71	0.0016		
Skull W					
Between groups	23	0.081	0.0035	9.50***	1.90
Within groups	448	0.17	0.0004		
Skull L					
Between groups	23	0.10	0.0044	13.19***	1.76
Within groups	449	0.15	0.0003		

Table 8 continued.

Character	d.f.	SS	MS	F	CV
Coracoid L					
Between groups	23	0.30	0.013	17.27***	2.72
Within groups	448	0.34	0.0007		
Scapula L					
Between groups	23	0.30	0.013	13.81***	3.05
Within groups	435	0.42	0.001		
Sternum L					
Between groups	23	0.30	0.0085	10.31***	2.83
Within groups	448	0.37	0.0008		
Keel D					
Between groups	23	0.091	0.0040	2.38***	3.97
Within groups	445	0.74	0.0017		
Synsacrum W					
Between groups	23	0.69	0.030	24.87***	3.43
Within groups	444	0.54	0.0012		
Femur W					
Between groups	23	0.26	0.011	20.51***	2.19
Within groups	450	0.25	0.0006		
Femur L					
Between groups	23	0.73	0.032	54.42***	2.39
Within groups	447	0.26	0.0006		
Tibiotarsus L					
Between groups	23	0.51	0.022	36.67***	2.42
Within groups	409	0.25	0.0006		
Humerus L					
Between groups	23	0.69	0.030	24.87***	2.23
Within groups	444	0.54	0.001		
Ulna L					
Between groups	23	0.51	0.022	36.67***	2.33
Within groups	409	0.25	0.0006		

1 *** - $P < 0.001$

2 Coefficient of variation for each character was calculated as the mean of the 24 sample CV's.

Table 9: Nested ANOVA (site=latitude effect, nested within vegetation) of eight external characters. First line for each character gives percentage variation explained by each factor. Second line gives F values.[1] Individuals with damaged or missing characters were excluded from the analysis. Variable acronyms as defined in Table 4.

Character	Vegetation (d.f. = 5)	Site (d.f. = 18)	Error (d.f = 435)
OR	62.1 169.20***	8.7 6.69***	29.2
WC	75.8 278.74***	3.1 3.83***	21.1
HT	29.1 72.00***	31.2 16.00***	39.7
TA	42.0 78.69***	13.3 6.71***	44.7
BD	3.9 6.30***	8.8 2.92***	87.4
BW	0.9 3.16**	6.7 2.38**	92.4
CU	26.5 47.04***	20.8 8.54***	52.7
GA	29.4 45.83***	14.3 5.85***	56.3

1 - *** - $P < 0.001$, and ** - $P < 0.01$.

Table 10: Nested ANOVA (series=latitude effect, nested within vegetation) of twelve skeletal characters. First line for each character gives percentage variation explained by each factor. Second line gives F values.[1] L, D, and W as defined in Table 6. All individuals with broken bones were excluded from the analysis.

Character	Vegetation (d.f. = 5)	Site (d.f. = 18)	Error (d.f. = 366)
Skull W	21.4 25.03***	12.2 3.96***	66.4
Partial Skull L	26.5 33.02***	13.0 4.44***	60.5
Coracoid L	44.6 62.42***	6.4 3.10***	49.0
Scapula L	38.4 47.76***	6.0 2.74***	55.6
Sternum L	29.4 35.00***	9.6 3.54***	61.0
Keel D	0.0 1.20 n.s.	9.6 2.71***	90.4
Synsacrum W	49.3 80.26***	8.5 4.24***	42.2
Femur W	33.3 63.93***	25.5 10.95***	41.2
Femur L	65.2 177.08***	9.8 7.33***	25.0
Tibiotarsus L	64.1 144.70***	6.2 4.38***	29.7
Humerus L	68.8 177.74***	5.4 4.37***	25.8
Ulna L	72.1 186.90***	2.5 2.56***	25.4

1 - *** - $P < 0.001$, and n.s. - not significant.

that vegetation centroids are also significantly heterogeneous (externals - $F_{(40, 1951.22)} = 30.60$, $P << 0.001$; skeletals - $F_{(60,1750.39)} = 17.10$, $P << 0.001$).

Canonical variates analyses of external and skeletal variables separately reveal similar patterns. The first CV axis in both cases primarily describes variation in size (i.e. most variables are positively correlated with CV 1; see Tables 11 and 12) and accounts for a substantial proportion of the total variation (≈ 40 %) in each data set. Coefficients standardized to unit standard deviation within-groups are informative with respect to which variables contribute most to group separation (Campbell and Atchley, 1981). Wing chord is the most important variable for discriminating groups on the external CV 1 axis (Table 11) while ulna length, and to a lesser extent humerus length, coracoid length, keel depth and synsacrum width are the important variables on the skeletal CV axis 1. The second CV axis in both analyses is bipolar. The external CV2 axis describes 23.5 % of total variation with hind toe and culmen being important variables in group discrimination (Table 11). The trends for the CV2 axis from the CVA of skeletals are less clear. This axis explains 26.1 % of the total variation with ulna, tibiotarsus and femur being of particular importance in discriminating groups. In both analyses, puna populations are clearly defined on axis 1: they are, on average, much larger structurally than birds from any other population (Figure 3 and 4). From the external CVA, the arrangement of ellipses enclosing 50 % of cases suggests a clear relationship between altitude and structural size starting with puna populations through Monte scrub, grassland, woodland, transition forest ending finally with lowland chaco where birds are smallest (Figure 3). Monte desert scrub birds load more positively on CV2, transition forest, woodland, and grassland load centrally, while lowland chaco and puna load slightly negatively although the trends are not clear-cut.

Table 11: Results of a canonical variates analysis (*a priori* defined groups = vegetation) on eight external variables (log transformed). Shown are correlations between the original variables and the derived axes and the standardized coefficients for the first two CV axes. Variable acronyms defined in Table 4.

	Correlations		Standardized Coefficients	
Character	CV 1	CV 2	CV1	CV2
OR	0.680	-0.126	0.138	0.020
WC	0.917	-0.070	0.817	0.226
HT	0.219	-0.893	-0.075	-0.938
TA	0.408	-0.216	0.271	0.141
BD	-0.020	-0.194	-0.194	-0.202
BW	-0.008	0.005	-0.132	0.194
CU	0.260	-0.467	0.139	-0.310
GA	0.327	-0.302	0.066	0.016
% Variation Explained:	37.8	23.5		

Table 12: Results of a canonical variates analysis (*a priori* defined groups = vegetation) on twelve skeletal variables (log transformed). Shown are correlations between the original variables and the derived axes and and the standardized coefficients for the first two CV axes.. L, D and W as defined in Table 5.

	Correlations		Standardized Coefficients	
Character	CV 1	CV 2	CV1	CV2
Skull W	0.269	-0.119	-0.127	-0.189
Skull L	0.327	0.073	0.080	0.089
Coracoid L	0.473	0.101	-0.253	0.143
Scapula L	0.421	0.024	-0.039	-0.095
Sternum L	0.347	0.093	0.033	0.213
Keel D	0.010	-0.096	-0.344	-0.122
Synsacrum W	0.524	0.186	0.321	0.102
Femur W	0.385	0.346	0.177	0.293
Femur L	0.732	0.310	0.006	0.589
Tibiotarsus L	0.692	0.358	0.183	0.774
Humerus L	0.789	-0.062	0.357	-0.547
Ulna L	0.829	-0.333	0.589	-0.942
% Variation Explained:	37.3	26.1		

Figure 3: Plot of ellipses, enclosing 50 % of all individuals of each vegetation/dialect group, from a Canonical Variates analysis based on eight external morphological variables.

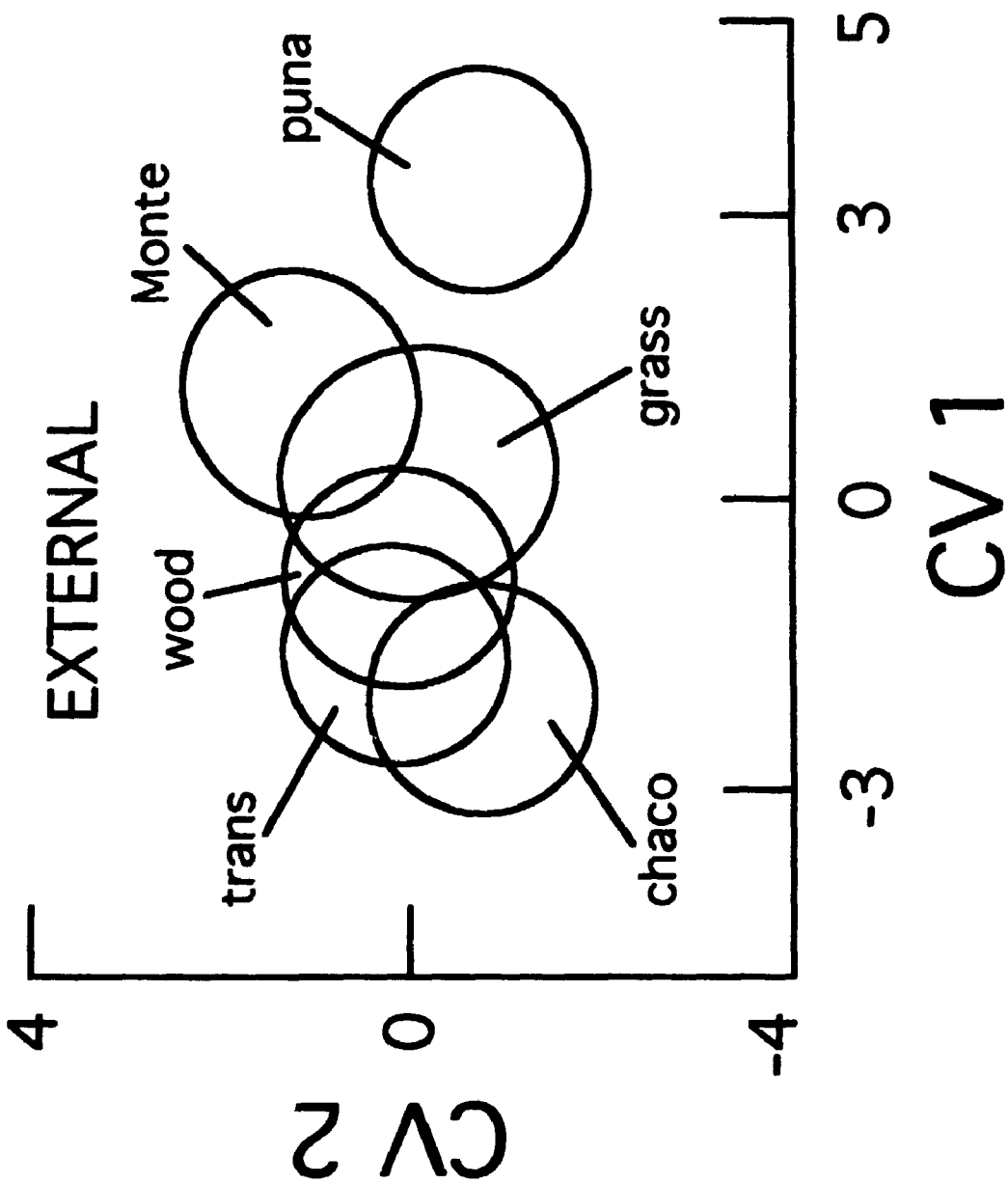
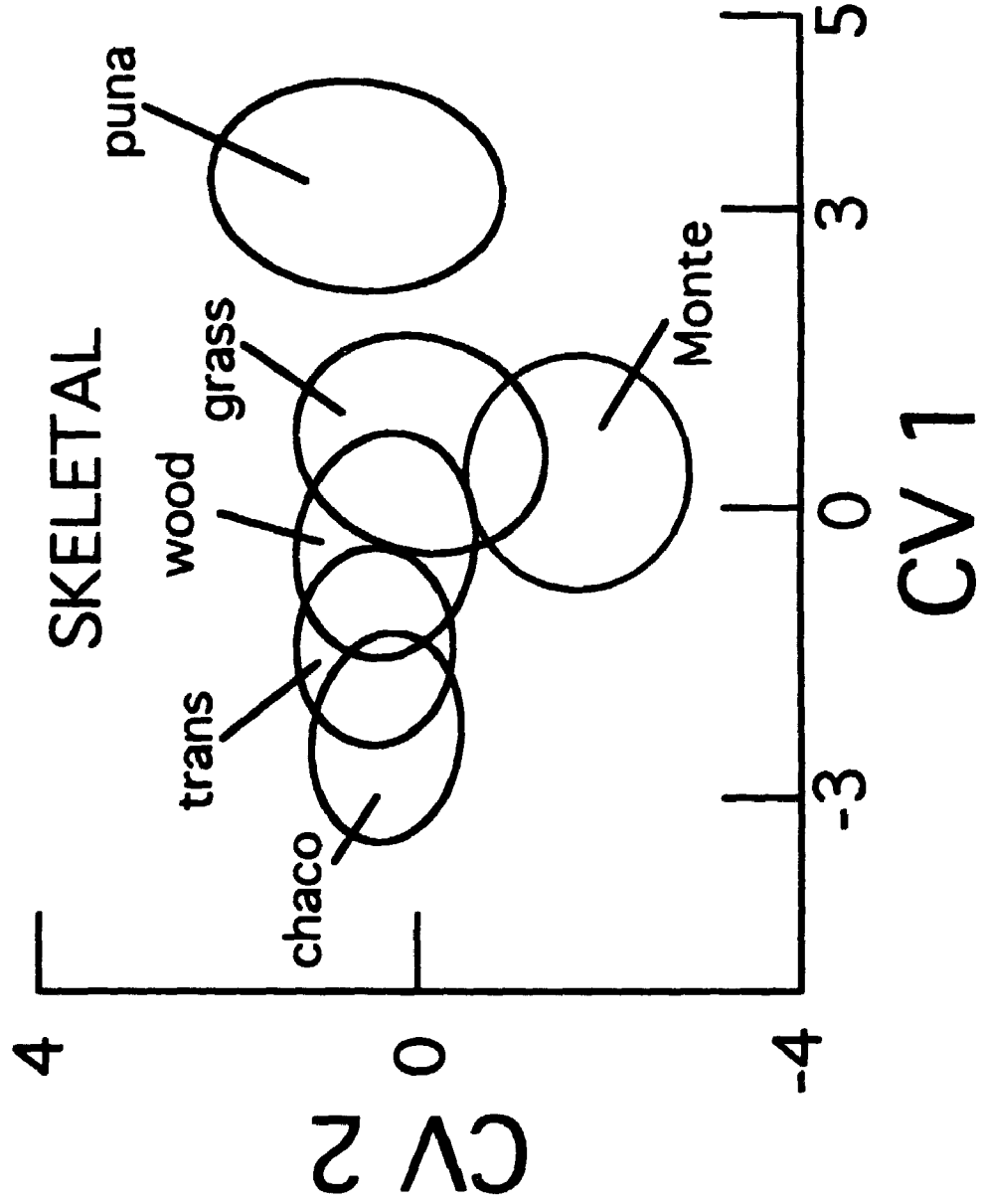

EXTERNAL
Monte
puna
wood
grass
trans
chaco
4
0
-4
-3
0
3
5
CV 2
CV 1

Figure 4: Plot of ellipses, enclosing 50 % of all individuals of each vegetation/dialect group, from a Canonical Variates analysis based on eight skeletal variables.


SKELETAL
puna
grass
wood
trans
chaco
Monte
4
0
-4
-3
0
3
5
CV 2
CV 1

For the skeletal CVA, there is also an altitudinal trend in structural size from puna through to lowland chaco populations (Figure 4); however, montane grassland and Monte desert scrub populations have similar loadings on CV1. The only clear separation on CV2 is that of Monte desert scrub from the other five vegetation types.

Tables 13 and 14 show percentages of individuals from each vegetation which were correctly classified based on the results of the CVA (i.e. distance to group centroid) of externals and skeletals, respectively. Based on the externals, 67.8 % were correctly classified; values for the six vegetations ranged from 50 % for alder woodland to 96.0 % for puna. Using the skeletals, a total of 70.8 % were correctly classified; values for the six vegetations ranged from 46.9 % for alder woodland to 89.7 % for puna. If the CVA for each morphological data set is done on only half the birds from each site (i.e. the first 10 birds captured) and the results used to classify the second half (i.e. the remaining individuals from each site), the results are very similar to those in Tables 13 and 14; this suggests that the derived axes are quite robust with respect to described trends.

3.3 Variation in Allozyme Frequencies

3.3.1 Among Sites

Of the 20 resolved isozymes, twelve were polymorphic (no criterion) for at least one of the 24 study sites; allozyme frequencies for these are presented in Appendix 5. Table 15 lists the descriptive statistics of allozyme frequency variation for each study site. Percent polymorphic loci at each site ranged from 5 to 25 using the 0.95 criterion or 10 to 40 using the "no criterion" method. Average number of alleles per locus ranged from 1.10 (± 0.07) to 1.60 (± 0.18). Direct count estimates of heterozygosity ranged from 0.016 (± 0.007) to 0.055 (± 0.021). Unbiased estimates

Table 13: Percentage correct classification based on canonical variates scores (from CVA on 8 external variables). Along left side are original vegetation designations and along the top are vegetations into which the specimens were actually classified. A total of 459 specimens were included in the analysis (the rest excluded because of missing measurements). Total correctly classified = 67.8 %.

	Lowland Chaco	Transition Forest	Alder Woodland	Montane Grassland	Monte Scrub	Puna Scrub
Lowland Chaco	73.0	16.2	9.5	1.3	0	0
Transition Forest	11.9	57.9	18.4	10.5	1.3	0
Alder Woodland	9.0	23.0	50	10.3	7.7	0
Montane Grassland	5.1	10.3	9.0	59.0	6.3	10.3
Monte Scrub	0	2.6	3.8	10.3	71.8	11.5
Puna	0	0	0	1.3	2.7	96.0

Table 14: Percentage correct classification based on canonical variates scores (from CVA on 12 skeletal variables). Along left side are original vegetation designations and along the top are vegetations into which the specimens were actually classified. A total of 390 specimens were included in the analysis (the rest excluded because of missing measurements). Total correctly classified = 70.8%.

	Lowland Chaco	Transition Forest	Alder Woodland	Montane Grassland	Monte Scrub	Puna Scrub
Lowland Chaco	75.8	16.1	6.5	0	1.6	0
Transition Forest	16.4	55.7	19.7	3.3	4.9	0
Alder Woodland	10.9	10.9	46.9	18.8	12.5	0
Montane Grassland	1.7	7.5	16.4	50.7	16.4	7.3
Monte Scrub	2.9	1.5	4.4	14.7	75.0	1.5
Puna	0	0	1.5	8.8	0	89.7

Table 15: Descriptive statistics of genetic variability at each site. Two criteria were used to calculate percent polymorphic loci: 1) no criterion ($P_{n.c.}$) - locus is polymorphic if any variability occurred and 2) 0.95 ($P_{0.95}$) - a locus is polymorphic if the frequency of the common allele is ≤ 0.95. Two heterozygosity values are reported: 1) direct count ($H_{d.c.}$) = observed values and 2) unbiased estimate (H_{unb}) based on Hardy-Weinberg expectation corrected for sample size (Nei, 1978). Values in parentheses are standard errors.

Site	$P_{0.95}$	$P_{n.c.}$	Number of Alleles/Locus	$H_{d.c.}$	H_{unb}
C1	15	25	1.35 (0.15	0.016 (0.007)	0.029 (0.013)
C2	10	40	1.50 (0.15)	0.041 (0.020)	0.038 (0.017)
C3	25	40	1.60 (0.18)	0.055 (0.021)	0.055 (0.021)
C4	15	20	1.35 (0.17)	0.030 (0.015)	0.032 (0.017)
T1	10	15	1.20 (0.12)	0.025 (0.019)	0.027 (0.017)
T2	10	20	1.30 (0.15)	0.018 (0.009)	0.022 (0.012)
T3	15	30	1.35 (0.13)	0.029 (0.015)	0.033 (0.014)
T4	20	25	1.40 (0.18)	0.030 (0.019)	0.045 (0.020)
W1	10	20	1.20 (0.09)	0.33 (0.020)	0.037 (0.022)
W2	20	25	1.25 (0.10)	0.021 (0.012)	0.031 (0.014)
W3	25	25	1.35 (0.15)	0.039 (0.020)	0.050 (0.021)
W4	15	30	1.30 (0.11)	0.026 (0.014)	0.030 (0.013)
G1	15	25	1.30 (0.13)	0.030 (0.016)	0.039 (0.018)
G2	15	25	1.35 (0.15)	0.044 (0.025)	0.050 (0.027)
G3	5	10	1.10 (0.07)	0.018 (0.015)	0.016 (0.013)
G4	10	25	1.35 (0.15)	0.032 (0.018)	0.035 (0.018)
M1	15	25	1.30 (0.13)	0.035 (0.021)	0.044 (0.024)
M2	15	25	1.35 (0.15)	0.036 (0.020)	0.047 (0.025)
M3	5	25	1.25 (0.10)	0.021 (0.012)	0.020 (0.011)
M4	10	15	1.15 (0.08)	0.022 (0.014)	0.025 (0.015)
P1	15	30	1.35 (0.13)	0.045 (0.023)	0.044 (0.022)
P2	10	15	1.25 (0.14)	0.032 (0.023)	0.031 (0.022)
P3	20	20	1.25 (0.12)	0.043 (0.025)	0.046 (0.024)
P4	20	25	1.45 (0.20)	0.026 (0.014)	0.056 (0.030)

of heterozygosity (Nei, 1978) ranged from 0.016 (± 0.013) to 0.056(± 0.030).

A total of 114 exact probability tests for departure from Hardy-Weinberg equilibrium were performed (see Table 16). Ten (8.8 %) tests indicated significant departures: GP-1 at sites C1 and W2, IDH-2 at site T3, MPI at site P3, PEP-a at site T4, PGM-1 at sites W4, M2 and P4 and PGM-2 at sites T4 and W3.

Uncorrected F_{ST} values for the polymorphic loci varied from 0.020 (PGD) to 0.362 (PGM-1), while corrected F_{ST} values ranged from 0.000 (EST-6, MDH-1, MDH-2, and PGD) to 0.344 (PGM-1) (Table 17). Mean uncorrected and corrected F_{ST} values across all loci were 0.140 and 0.119, respectively. F_{IS} values ranged from -0.060 (PGD) to 0.516 (PGM-2). Mean F_{IS} across all loci was 0.129. Corrected Chi^2 tests revealed that allele frequencies for three loci were significantly heterogeneous among sites (Table 17): GP-1, MPI and PGM-1. When all loci were considered together (i.e. adding the Chi^2 statistics of all loci), there was significant heterogeneity across the study area.

3.3.2 Among Vegetation/Dialects

Table 18 lists the hierarchical F coefficients for all twelve polymorphic loci and overall. Only half of the overall among site variance in allozyme frequencies (F_{ST} = 0.118) was attributable to vegetation/dialect effect (F_{DT} = 0.060). Table 19 lists uncorrected and corrected F_{ST}, F_{IS}, and Chi^2 statistics assessing allozyme heterogeneity for each vegetation. Corrected overall F_{ST} values range from 0.006 (transition forest) to 0.156 (puna scrub). Corrected Chi^2 statistics testing for overall heterogeneity across sites within vegetations show that only puna scrub was

Table 16: Exact probability values testing for significant departure from Hardy-Weinberg equilibrium. Significant values are indicated in boldface.

	Site											
Locus	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4
AAT-1	0.08	1.00	1.00	-	-	1.00	-	-	1.00	-	-	1.00
EST-6	-	1.00	1.00	1.00	-	1.00	1.00	-	-	-	-	-
GP-1	**0.03**	-	-	-	-	-	1.00	-	1.00	**0.03**	0.17	-
IDH-1	-	1.00	1.00	1.00	1.00	-	1.00	1.00	-	1.00	-	1.00
IDH-2	-	-	-	-	-	-	**0.03**	-	-	-	-	1.00
MDH-1	-	-	1.00	-	-	-	1.00	-	-	-	-	-
MDH-2	-	1.00	-	-	-	-	-	-	-	-	-	-
MPI	-	1.00	-	-	-	-	-	-	-	1.00	1.00	1.00
PEP-A	1.00	1.00	1.00	-	-	-	-	**0.002**	-	-	-	-
PGD	0.16	0.55	1.00	0.34	1.00	0.24	1.00	1.00	0.47	1.00	1.00	1.00
PGM-1	1.00	1.00	0.35	-	0.09	1.00	-	0.16	1.00	0.08	1.00	**0.03**
PGM-2	-	-	1.00	1.00	-	-	-	**0.02**	-	-	**0.002**	-

Table 16 continued.

	Site											
Locus	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3	P4
AAT-1	1.00	-	-	-	-	1.00	-	-	1.00	-	-	1.00
EST-6	-	-	-	-	-	-	-	-	1.00	-	-	-
GP-1	1.00	0.08	-	1.00	-	1.00	1.00	-	1.00	1.00	1.00	-
IDH-1	-	1.00	-	1.00	0.08	-	1.00	1.00	-	-	-	1.00
IDH-2	-	-	-	-	-	-	1.00	-	-	-	-	-
MDH-1	-	-	-	-	-	-	-	-	-	-	-	-
MDH-2	-	-	-	-	-	-	-	-	-	-	-	-
MPI	-	0.13	-	-	1.00	-	-	-	1.00	-	**0.03**	1.00
PEP-A	0.09	1.00	1.00	-	1.00	1.00	1.00	-	-	-	-	-
PGD	1.00	0.63	1.00	1.00	0.59	1.00	1.00	1.00	0.55	1.00	1.00	0.14
PGM-1	0.19	-	-	0.17	0.24	**0.04**	-	0.25	0.47	1.00	1.00	**0.001**
PGM-2	-	-	-	1.00	-	-	-	-	-	-	-	-

Table 17: F_{ST}, F_{ST} corrected for sampling error and F_{IS} indices (Wright, 1978b) for the entire study area (sub-population = site, regardless of vegetation) for all polymorphic loci. Chi^2 statistics testing for heterogeneity of allelic frequencies are also indicated (Workman and Niswander, 1970).

Locus	F_{IS}	F_{ST} (uncorr.)	F_{ST} (corr.)	Chi^2 (uncorr.)[1]	Chi^2 (corr.)[1]	d.f.[2]
AAT-1	0.119	0.030	0.005	52.8	7.1	46
EST-6	-0.030	0.022	0.000	15.0	0.0	23
GP-1	0.202	0.070	0.045	128.5***	81.9***	46
IDH-1	0.010	0.040	0.014	106.7**	35.4	69
IDH-2	0.505	0.038	0.012	69.9*	20.7	46
MDH-1	-0.027	0.025	0.000	45.4	0.0	46
MDH-2	-0.026	0.024	0.000	21.8	0.0	23
MPI	0.186	0.085	0.061	156.4***	111.7***	46
PEP-A	0.360	0.045	0.020	82.6**	35.6	46
PGD	-0.060	0.020	0.000	70.7	0.0	92
PGM-1	0.349	0.362	0.344	963.5***	888.8***	69
PGM-2	0.516	0.055	0.031	97.7***	54.2	46
Overall	0.129	0.140	0.119	1811.0***	1235.4***	

1 - *** - $P < 0.001$, ** - $P < 0.01$, * - $P < 0.05$.
2 - d.f. = degree of freedom.

Table 18: F statistics (Wright, 1978b) for three hierarchical levels using all 24 sites: F_{SD} = site-dialect, F_{DT} = dialect-total and F_{ST} = site-total. Negative values can result from the method of computation and are interpreted as zero.

Locus	F_{SD}	F_{DT}	F_{ST}
AAT-1	0.004	0.001	0.005
EST-6	0.000	0.005	0.005
GP-1	0.040	0.004	0.045
IDH-1	0.014	0.000	0.014
IDH-2	0.016	-0.004	0.012
MDH-1	0.001	-0.002	-0.001
MDH-2	0.001	-0.001	0.000
MPI	0.065	-0.004	0.061
PEP-A	0.022	-0.002	0.020
6PGD	0.000	-0.003	-0.002
PGM-1	0.188	0.192	0.344
PGM-2	0.036	-0.005	0.032
TOTAL	0.062	0.060	0.118

Table 19: F_{ST}, corrected F_{ST}, F_{IS} and Chi^2 analysis of geographic heterogeneity of allozyme frequencies with each vegetation considered separately.[1] Dashes indicate that the locus in question was not variable within a given vegetation. Degrees of freedom = d.f. Trans. forest = transition forest. Montane grass. = montane grassland.

		AAT-1	EST-6	GP-1	IDH-1	IDH-2	MDH-1	MDH-2
Lowland	F_{IS}	0.299	-0.029	0.477	-0.092	-	-0.026	-0.026
Chaco	F_{ST}	0.028	0.007	0.033	0.040	-	0.019	0.019
	$F_{ST\ (corr.)}$	0.005	0.000	0.008	0.018	-	0.000	0.000
	Chi^2	7.0	0.0	8.3	16.2	-	2.0	2.0
	$Chi^2_{\ (corr.)}$	0.0	0.0	0.5	5.6	-	0.0	0.0
	d.f.	6	3	6	9	-	3	3
Trans.	F_{IS}	-0.026	-0.033	-0.029	-0.050	1.000	0.021	-
Forest	F_{ST}	0.019	0.016	0.021	0.020	0.042	0.021	-
	$F_{ST\ (corr.)}$	0.000	0.000	0.000	0.000	0.016	0.000	-
	Chi^2	1.6	0.9	2.3	5.8	5.6	2.3	-
	$Chi^2_{\ (corr.)}$	0	0	0	0	1.5	0	-
	d.f.	3	3	3	9	3	3	-
Montane	F_{IS}	-0.026	-	0.340	-0.044	-0.027	-	-
Woodland	F_{ST}	0.013	-	0.081	0.023	0.020	-	-
	$F_{ST\ (corr.)}$	0.000	-	0.056	0.000	0.000	-	-
	Chi^2	0.87	-	21.7**	2.1	2.0	-	-
	$Chi^2_{\ (corr.)}$	0	-	14.4*	0	0	-	-
	d.f.	3	-	6	3	-	-	-
Montane	F_{IS}	-0.030	-	0.159	-0.041	-	-	-
Grass.	F_{ST}	0.022	-	0.020	0.022	-	-	-
	$F_{ST\ (corr.)}$	0.000	-	0.000	0.000	-	-	-
	Chi^2	2.5	-	4.2	2.4	-	-	-
	$Chi^2_{\ (corr.)}$	0	-	0	0	-	-	-
	d.f.	3	-	6	3	-	-	-
Monte	F_{IS}	-0.029	-	-0.048	0.373	-0.024	-	-
Desert	F_{ST}	0.021	-	0.027	0.034	0.018	-	-
Scrub	$F_{ST\ (corr.)}$	0.000	-	0.001	0.011	0.000	-	-
	Chi^2	2.4	-	3.3	13.3	1.9	-	-
	$Chi^2_{\ (corr.)}$	0	-	0	2.3	0	-	-
	d.f.	3	-	3	9	3	-	-
Puna	F_{IS}	-0.026	-0.029	-0.047	-0.039	-	-	-
Scrub	F_{ST}	0.016	0.021	0.022	0.028	-	-	-
	$F_{ST\ (corr.)}$	0.000	0.000	0.003	0.007	-	-	-
	Chi^2	3.1	1.5	5.0	7.0	-	-	-
	$Chi^2_{\ (corr.)}$	0	0	0	0.2	-	-	-
	d.f.	6	3	6	6	-	-	-

Table 19 continued.

		MPI	PEP-A	PGD	PGM-1	PGM-2	Overall
Lowland	F_{IS}	-0.026	-0.027	0.025	0.129	-0.040	0.053
Chaco	F_{ST}	0.019	0.012	0.017	0.050	0.020	0.026
	$F_{ST\ (corr.)}$	0.000	0.000	0.001	0.027	0.001	0.008
	Chi^2	2.0	1.7	6.9	12.8*	4.2	63.1
	$Chi^2_{(corr.)}$	0	0	0	6.0	0	12.1
	d.f.	3	6	12	6	6	63
Trans.	F_{IS}	-	1.000	-0.067	0.398	1.000	0.181
Forest	F_{ST}	-	0.073	0.006	0.031	0.036	0.021
	$F_{ST\ (corr.)}$	-	0.051	0.000	0.005	0.013	0.006
	Chi^2	-	10.4*	0	7.1	4.1	39.9
	$Chi^2_{(corr.)}$	-	7.0	0	0	0.9	9.3
	d.f.	-	3	9	6	3	45
Montane	F_{IS}	-0.072	-	-0.077	0.411	1.000	0.167
Woodland	F_{ST}	0.027	-	0.005	0.013	0.081	0.033
	$F_{ST\ (corr.)}$	0.000	-	0.000	0.000	0.057	0.017
	Chi^2	3.1	-	0	2.0	11.6**	43.5*
	$Chi^2_{(corr.)}$	0	-	0	0	7.9*	22.2
	d.f.	3	-	3	6	3	30
Montane	F_{IS}	0.375	0.389	-0.158	0.449	-0.024	0.093
Grass.	F_{ST}	0.158	0.040	0.020	0.050	0.018	0.045
	$F_{ST\ (corr.)}$	0.137	0.016	0.000	0.022	0.000	0.023
	Chi^2	23.7***	10.6	6.1	12.8	1.4	63.7**
	$Chi^2_{(corr.)}$	20.4***	3.1	0	4.5	0	27.9
	d.f.	3	6	9	6	3	39
Monte	F_{IS}	-0.026	-0.026	-0.031	0.424	-	0.135
Desert	F_{ST}	0.019	0.007	0.028	0.055	-	0.035
Scrub	$F_{ST\ (corr.)}$	0.000	0.000	0.005	0.029	-	0.012
	Chi^2	1.9	0.1	10.4	14.7*	-	48.1
	$Chi^2_{(corr.)}$	0	0	0	6.8	-	9.1
	d.f.	3	3	9	6	-	39
Puna	F_{IS}	0.322	-	-0.043	0.310	-	0.147
Scrub	F_{ST}	0.014	-	0.021	0.311	-	0.176
	$F_{ST\ (corr.)}$	0.000	-	0.000	0.290	-	0.156
	Chi^2	1.2	-	7.0	86.3***	-	111.0***
	$Chi^2_{(corr.)}$	0	-	0	80.4***	-	80.6***
	d.f.	3	-	9	6	-	39

1 - *** - $P < 0.001$, ** - $P < 0.01$, * - $P < 0.05$.

statistically significant, although uncorrected Chi^2 statistics indicate both montane woodland and montane grassland as being significantly heterogeneous as well. Both GP-1 and PGM-2 were significantly heterogeneous across sites within montane woodland. Allozyme frequencies of MPI were significantly heterogeneous across sites within montane grassland and allozyme frequencies of PGM-1 were significantly heterogeneous across sites within puna scrub.

Corrected F_{ST} was much higher (an order of magnitude; $F_{ST\ (corr.)} = 0.156$) in puna scrub than in any of the other five vegetations (average $F_{ST\ (corr.)} = 0.0132 \pm 0.0069$). The major cause of the exceptional overall $F_{ST\ (corr.)}$ reported in Table 17, then, was differentiation at the PGM-1 locus within puna scrub ($F_{ST\ (corr.)} = 0.290$). Frequency of the common C allele at PGM-1 in all non-puna vegetations ranged from 0.824 to 1.000 (average 0.93 ± 0.056) whereas at puna scrub sites it ranged from 0.175 to 0.725 (average 0.451 ± 0.285). The southernmost puna site (P4) showed a high frequency of the C allele (0.667) while at the northernmost site (P1) the frequency was only 0.175 suggesting that a geographic cline may exist (but note that site P3 is anomalous - frequency of the C allele = 0.725). Finally, F_{IS} values for each of the six vegetations ranged from 0.053 (lowland chaco) to 0.181 (transition forest).

3.4 Covariation of Different Character Suites

Values resulting from scoring of the 24 sites by two individuals for four habitat variables are presented in Appendix 6. All distance matrices but INV are presented in Appendices 7 through 13. Results of MDS of ECO, SON, ROG, EXT and SKE are presented in Figures 5 through 9.

Of 20 pair-wise comparisons made using Mantel's (1967) test, 11 indicated

Figure 5: Non-metric multidimensional scaling of ecological distance matrix in two dimensions. Site codes are as indicated in Table 1. The ★ represents sites T3, T4, W3 and W4. The □ represents sites T1, T2, W1 and W2. The △ represents sites P1, P2 and P3. Stress for this configuration is 0.0083.

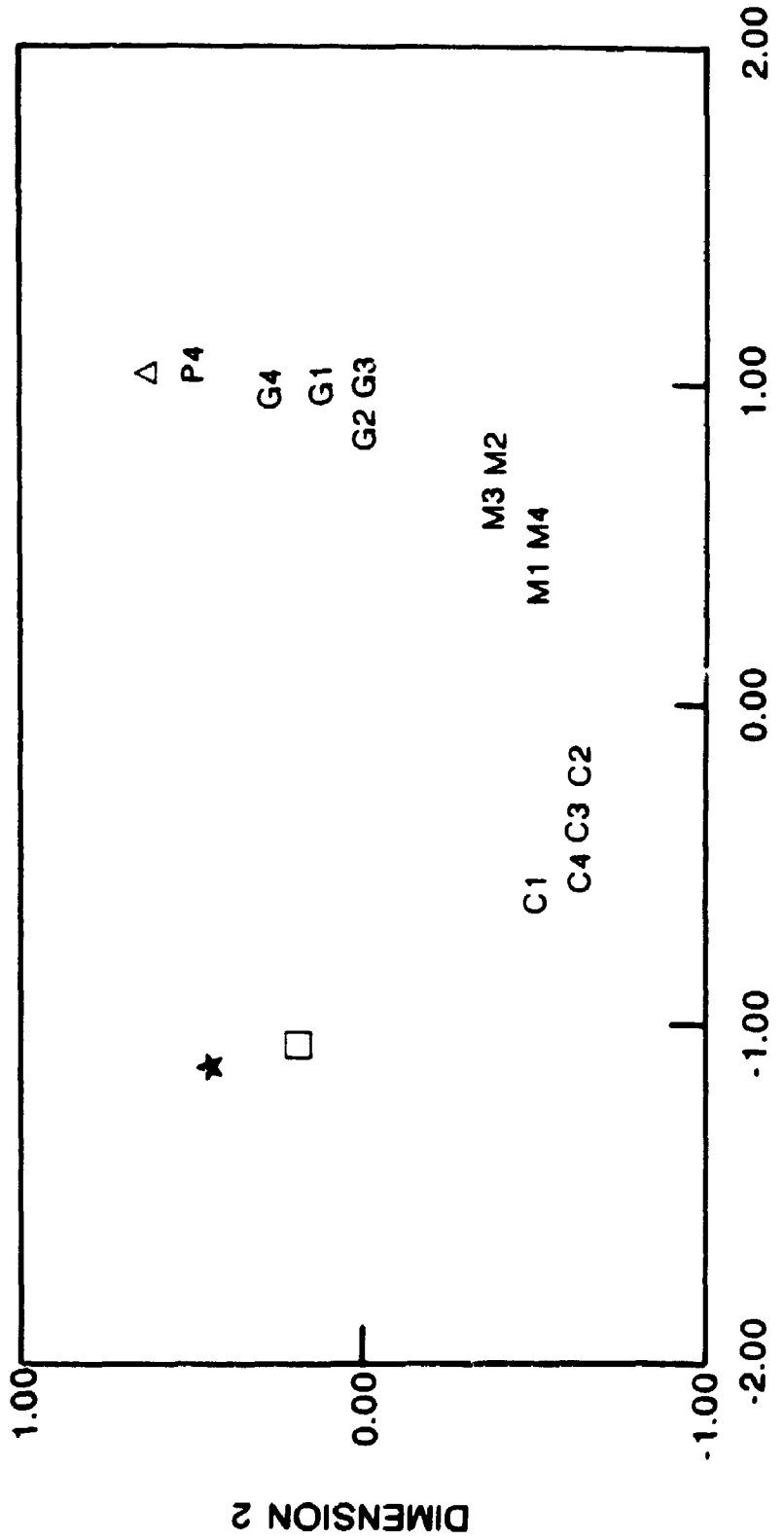

DIMENSION 2
1.00
0.00
-1.00
-2.00
-1.00
0.00
1.00
2.00
DIMENSION 1
△
P4
G4
G1
G2 G3
M3 M2
M1 M4
C1
C4 C3 C2
★
□

Figure 6: Non-metric multidimensional scaling of external Mahalanobis distance matrix in two dimensions. Site codes are as indicated in Table 1. Stress for this configuration is 0.090.

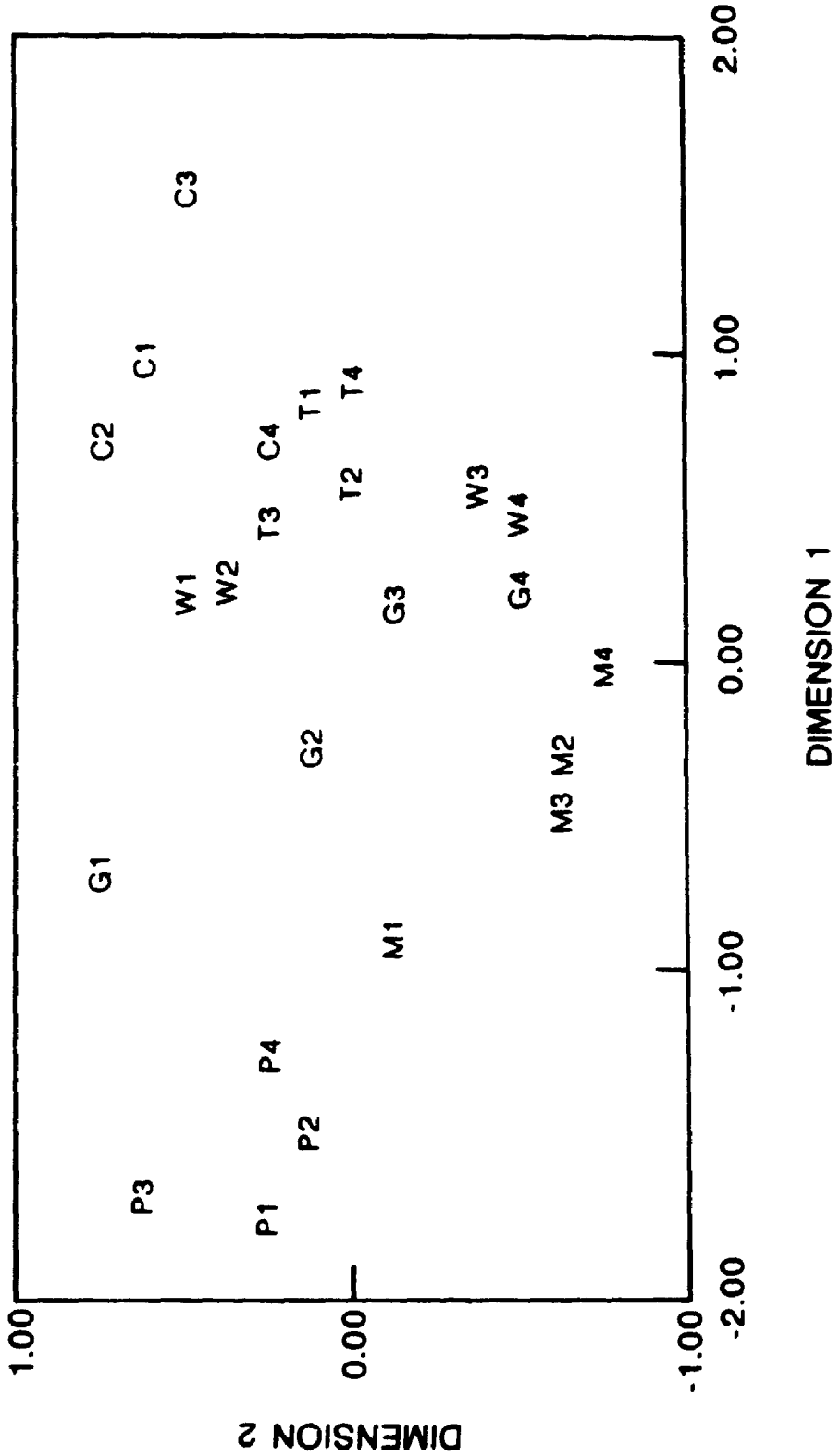

C3
C1
C2
T1
T4
C4
T2
W3
T3
W4
W1
W2
G4
G3
M4
G2
M3 M2
G1
M1
P4
P2
P3
P1
2.00
1.00
0.00
-1.00
-2.00
DIMENSION 1
1.00
0.00
-1.00
DIMENSION 2

Figure 7: Non-metric multidimensional scaling of skeletal Mahalanobis distance matrix in two dimensions. Site codes are as indicated in Table 1. Stress for this configuration is 0.086.

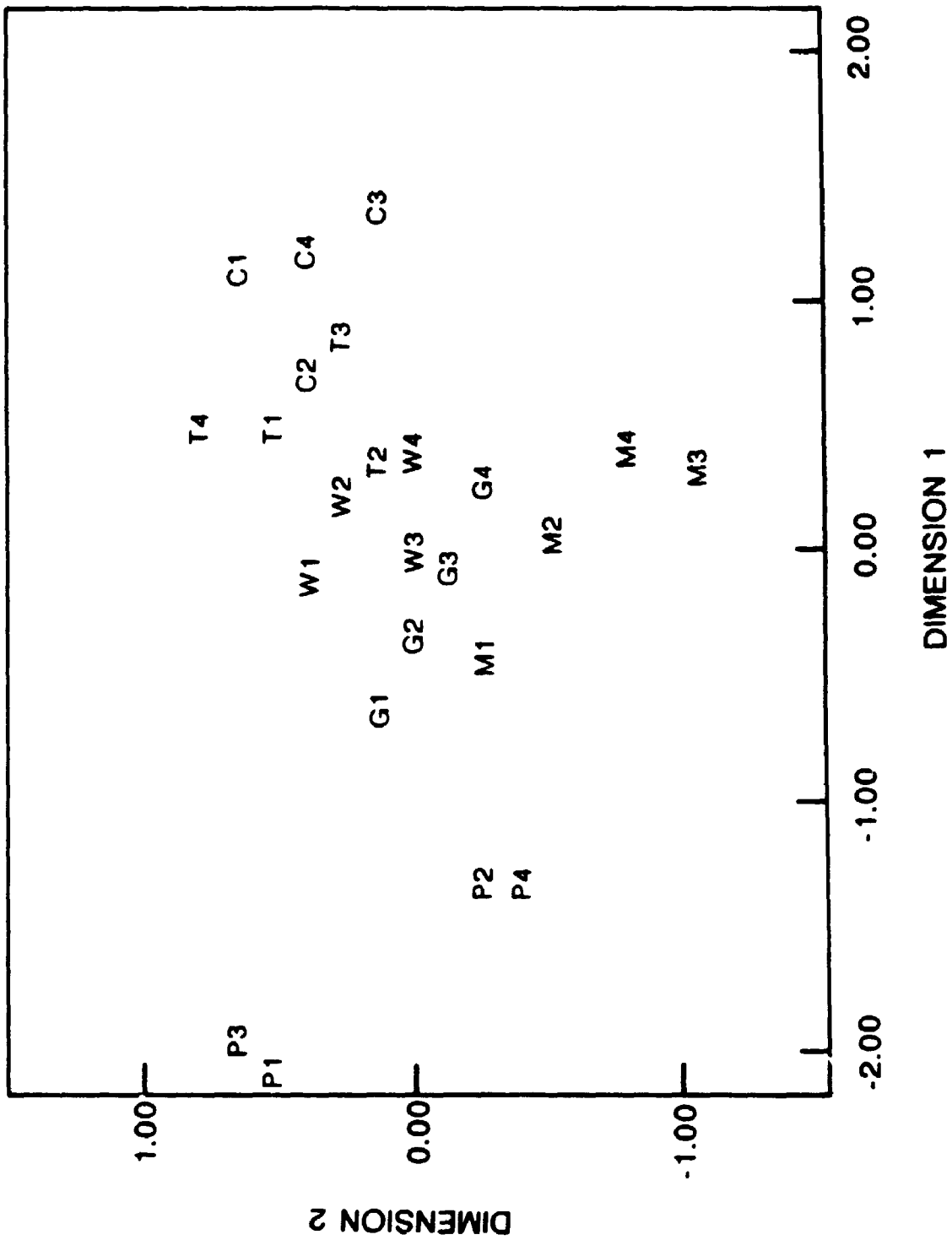

C3
C1
C4
T3
C2
T4
T1
T2
W4
W2
G4
M4
M3
W1
W3
M2
G3
G2
M1
G1
P2
P4
P3
P1
2.00
1.00
0.00
-1.00
-2.00
DIMENSION 1
1.00
0.00
-1.00
DIMENSION 2

Figure 8: Non-metric multidimensional scaling of Rogers' (1972) genetic distance matrix in two dimensions. Site codes are as indicated in Table 1. The □ represents sites T2, W4 and G3. The ★ represents sites T1, G4 and M4. Stress for this configuration is 0.115.

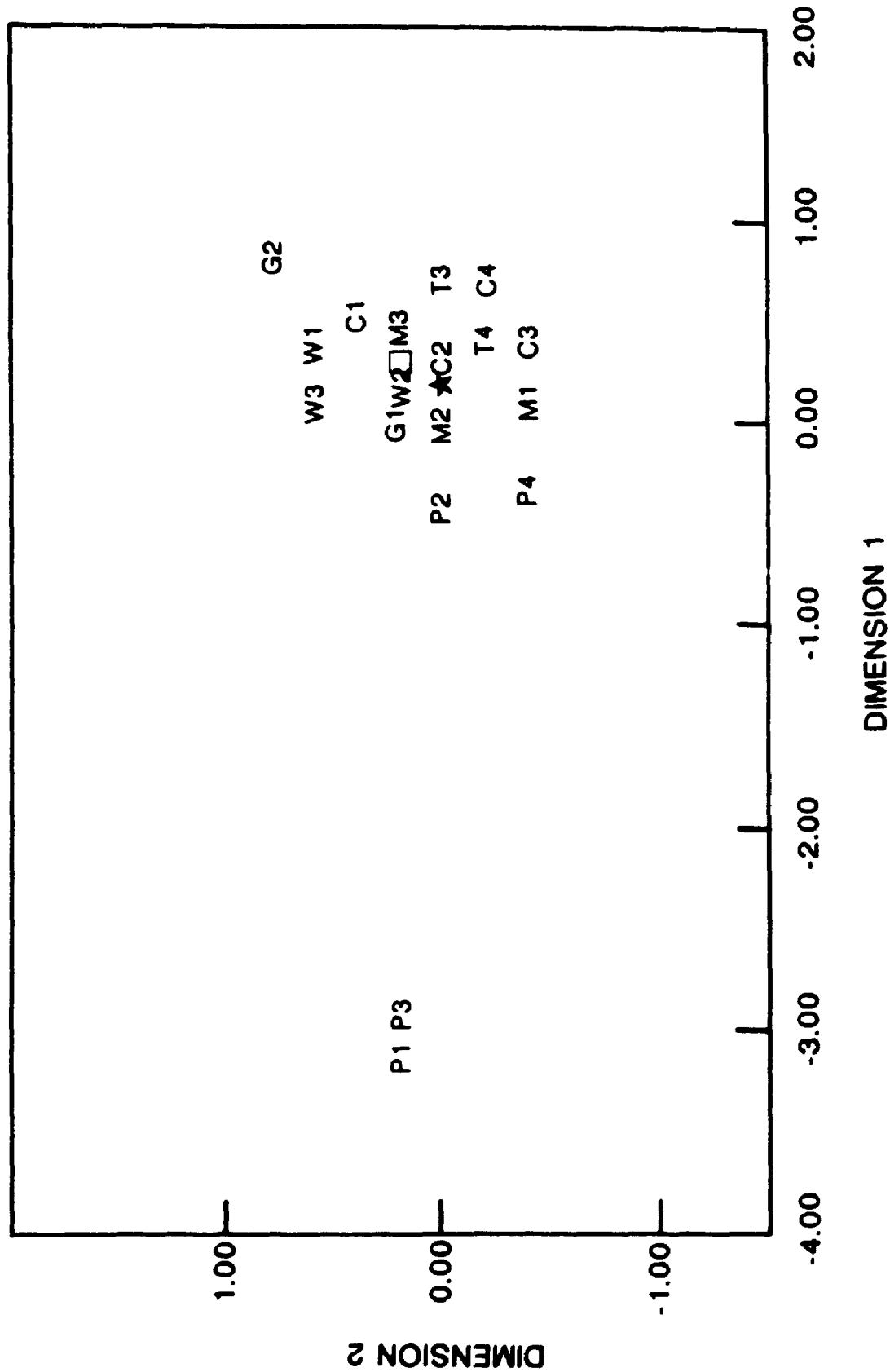
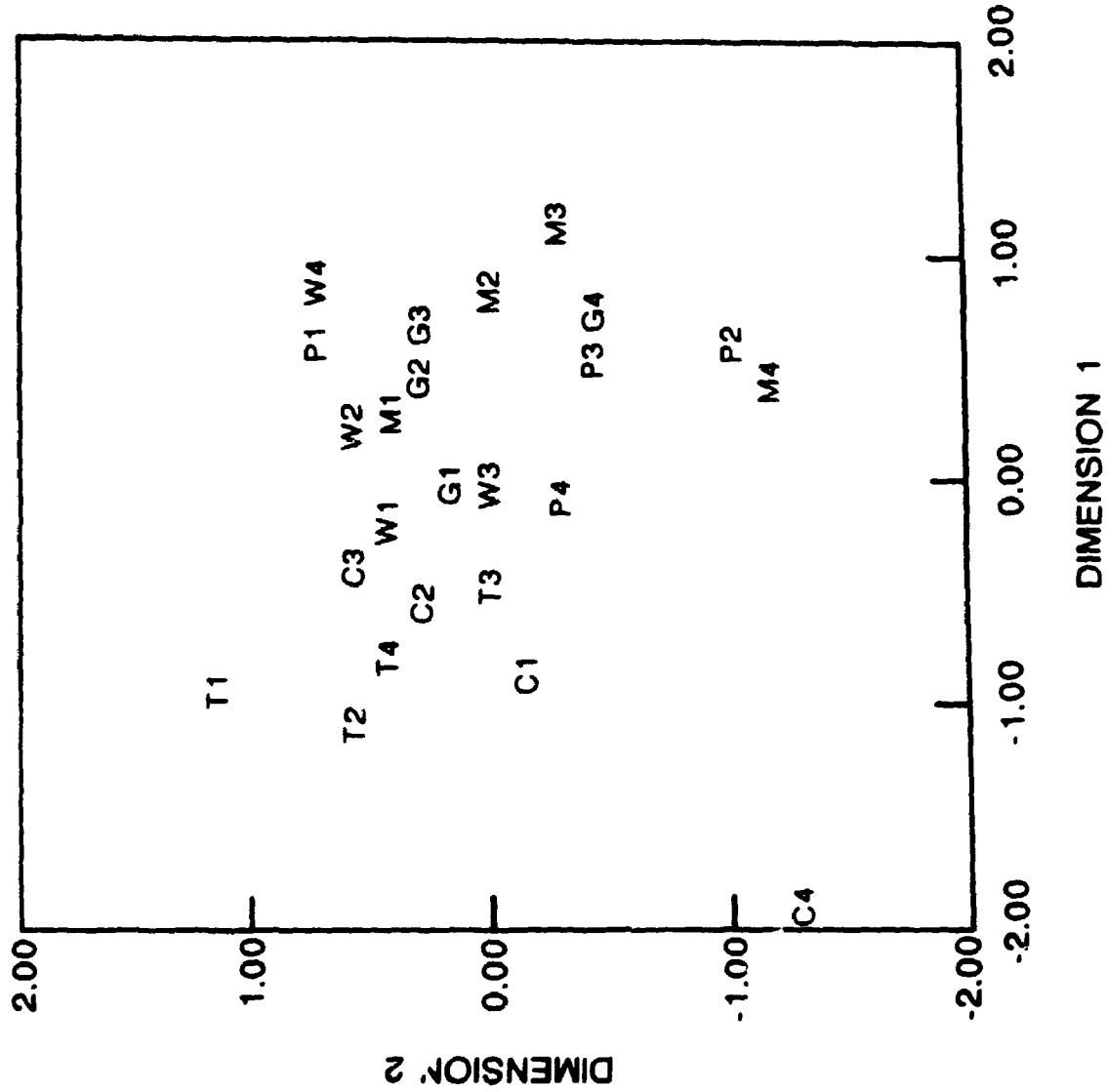

G2
W3 W1
C1
G1 W2 M3
M2 C2 T3
T4 C4
P2 M1 C3
P4
P1 P3
1.00
0.00
-1.00
-4.00
-3.00
-2.00
-1.00
0.00
1.00
2.00
DIMENSION 1
DIMENSION 2

Figure 9: Non-metric multidimensional scaling of song Mahalanobis distance matrix in two dimensions. Site codes are as indicated in Table 1. Stress for this configuration is 0.126.


2.00
1.00
0.00
-1.00
-2.00
DIMENSION 2
2.00
1.00
0.00
-1.00
-2.00
DIMENSION 1
T1
T2
T4
C3
C2
C1
W1
G1
T3
W3
P4
W2
M1
G2
G3
P1
W4
M2
P3
G4
M3
P2
M4
C4

significant congruence of pattern between the two test matrices (Table 20). Not surprisingly, the pattern of variation displayed by external morphological variables was very similar to that shown by skeletal variables. ROG was significantly congruent in pattern with EXT, SKE, GEO (i.e. the greater the geographic distance between any two compared sites, the greater the difference in allozyme frequencies) and ECO (i.e. the greater the difference in habitat characteristics of any two sites, the greater the difference in allozyme frequencies). Both EXT and SKE were similar in pattern to GEO (i.e. the greater the geographic distance between any two sites, the greater the divergence in morphology), to INV (i.e. some local patterns were evident) and to ECO (i.e. the greater the difference in habitat characteristics of any two sites, the greater the differences in morphology).

Table 20: Matrix of t-statistics resulting from pair-wise distance matrix comparisons (all 24 sites included) using Mantel's (1967) non-parametric test. Significant t-values are indicated in boldface. Conservative critical t value used in these comparisons is 3.051 (for $\alpha = 0.05$, t = 1.960; for $\alpha = 0.01$, t = 2.576).

	Skeletals	Rogers'	Song	Geographic	Inverse	Ecological
Externals	**8.38**	**4.75**	1.10	**6.30**	**-5.28**	**8.50**
Skeletals		**4.77**	1.56	**5.80**	**-4.82**	**6.43**
Rogers			-0.75	**3.58**	-2.11	**3.41**
Song				1.28	-1.80	1.29
Geographic						1.89
Inverse						-0.64

4.0 DISCUSSION

4.1 Variation of Morphological Characters

4.1.1 Among Sites

Positive correlations between morphological characters among individuals within sites (Tables 4 and 6) indicate that generally within sites birds vary primarily with respect to size. Positive correlations between morphological characters among sites (Tables 5 and 7) show that across the whole study area there is a similar trend towards variation in overall size. This will be discussed in more detail in the subsequent section dealing with variation in morphology of putative vegetation/dialect populations. Morphological characters show extreme inter-site variability as indicated by the significant F values resulting from ANOVA (Table 6). Different characters do, however, show different relative amounts of between-locality character variability as indicated by the between-group sum of squares from the ANOVA. In other words, different characters show different levels of among-site differentiation, a result which has been reported for other avian taxa (e.g. Fox Sparrows, *Passerella iliaca* - see Zink, 1986). Conclusions of significant morphological heterogeneity among sites based on the univariate cases are strengthened by the highly significant results from the MANOVA's.

It is useful to compare levels of morphological variability among sites in *Z. capensis* to levels of variability in another species occurring over a similarly large study area. Zink (1986) studied geographic variation of the schistacea group of the Fox Sparrow in the southwestern United States. The study area was phytogeographically heterogeneous, and was comparable in size to that of the present study. Zink (1986) sampled from a total of 31 localities from within the ranges of seven putative subspecies, measuring nine external and 15 skeletal characters on each specimen.

Coefficients of variation for external characters (male specimens only) ranged from 3.0 % (tarsus length) to 4.9 % (culmen) with an average of 4.0 ± 0.67 %. Coefficients of variation for skeletal characters ranged from 2.0 % (humerus length) to 5.6 % (posterior synsacrum length) with an average of 3.09 ± 1.04 %. Six external variables were used in common between Zink's and the present study (all but gape and outer rectrix length); for *P. iliaca* average CV for these variables was 3.89 ± 0.75 % while for *Z. capensis* the average CV was 3.5 ± 0.33 %. Ten skeletal variables were used in common between the *Z. capensis* and the *P. iliaca* studies (all but scapula length and keel depth from the present study); for *P. iliaca* average CV for these variables was 2.69 ± 0.66 % and for *Z. capensis* the average CV was 2.42 ± 0.48 %. The Fox Sparrow is one of the most morphologically differentiated emberizine species which has yet been studied, but it is clear that levels of variability in morphology are similar in *P. iliaca* and *Z. capensis* .

4.1.2 Among Vegetation/Dialects

Nested ANOVA's (Tables 9 and 10) and MANOVA's of both morphological data sets show that there is significant heterogeneity in morphology among putative vegetation/dialect populations. However, it is also apparent that for every morphological character there is a significant level of variability within each vegetation (i.e. an effect of latitude). For most variables (16 of 20) a greater percentage of the variation for each is explained by vegetation than by site (Tables 9 and 10). Overall correct percent classification based on both external (67.8 %) and skeletal (70.8 %) individual CVA scores was exceptional (Tables 13 and 14). Handford (1985) studied the morphological relationships (external only) among 22 described putative subspecies of *Z. capensis* . He found that overall percent correct classification of subspecies was

only 51.7 % for males and 47.8 % for females; therefore, percent correct classification was substantially greater for specimens of different dialect/vegetation populations than it was for specimens of different subspecies originating from over the entire South American continent.

It is clear that birds from different putative dialect/vegetation populations differ morphologically, primarily with respect to size, an observation consistent with Bergmann's ecogeographic rule (body size is inversely correlated with temperature and humidity - see Zink and Remsen, 1987). Average loading on the first CV axis for each site is positively and significantly correlated with altitude for both morphological data sets (externals - $r^2 = 0.77$, $\underline{P} = 0.0001$; skeletals - $r^2 = 0.89$, $\underline{P} = 0.0001$). Recall that the first CV axes for both analyses described variation in size (Tables 11 and 12).

Three explanations for the observation of morphological differentiation among sites and among vegetation/dialect populations seem possible. First, natural selection may act directly on the morphological character(s) in question, and the mode and direction of selection may differ among environments (Rising, 1988). The action of natural selection has been documented for a variety of morphological characters, including body size (e.g. Boag and Grant, 1981; Endler, 1976; Grant, 1985). Second, observed patterns of morphological differentiation may be due to environmentally induced variability which is non-adaptive. Finally, differentiation among vegetation/dialect populations may be due to adaptive plasticity; i.e. natural selection may have "chosen" that genotype or genotypes which vary among environments in an adaptive manner (e.g. Stearns et al. 1991). Unfortunately, my data cannot distinguish the three alternatives.

4.2 Variation in Allozyme Frequencies

4.2.1 Among Sites

The observed heterozygosities (H_{obs} = direct count heterozygosity, see Table 15) found in the present study were comparable to those found for other species of emberizines and for birds in general (e.g. Avise et al. 1980a; Avise et al. 1980b; Barrowclough and Corbin, 1978; Corbin et al. 1979; Zink, 1986). Average H_{obs} across all 24 study sites for *Z. capensis* was 0.031. Evans (1987) reported an average value of H_{obs} of 0.044 across 86 avian taxa. In the same study, from 32 studies of emberizine taxa, the average H_{obs} was 0.047. Avise et al. (1980b) calculated H_{obs} for 12 emberizine species; the overall average H_{obs} was 0.056. Zink (1982) examined allozymic differentiation among 11 species of emberizines (including *Z. capensis*); for *Z. capensis* H_{obs} was 0.045 ± 0.031 and across all 11 taxa the average H_{obs} was 0.039.

Average estimates of percent polymorphic loci (using 0.95 % criterion, average = 14.4; using no criterion, average = 24.2) are consistent with that reported for other bird species (e.g. Corbin, 1987; Evans, 1987; Zink, 1982). Evans (1987) reported that average percent polymorphic loci (frequency of the common allele ≤0.99) for 103 birds species was 24.0%. Restricting this to 35 emberizine taxa, the average percent polymorphic loci was 22.1 % (Evans, 1987). Average percent polymorphic loci (0.99 % criterion) reported by Zink (1982) for 11 emberizine species was 20.3.

Estimates of mean number of alleles per locus for Rufous-collared Sparrows in the present study also fall within the ranges listed in the avian literature (e.g. Zink, 1982; Zink, 1986). Values reported for the present study were calculated for all loci

(monomorphic + polymorphic); however, it is an easy matter to convert the values to number of alleles per polymorphic locus. If this is done the average across all 24 study sites is 2.30. Zink (1982) calculated mean number of alleles per polymorphic locus for various emberizine taxa; these values ranged from 2.17 (*Pipilo chlorurus*) to 2.67 (*Zonotrichia atricapilla*) with an average of 2.40. The value for *Zonotrichia capensis* (a Paraguay population) was 2.40 (Zink, 1982).

The amount of allozyme variability in the present study, as indicated by a variety of measures, is similar to numerous other studies of avian populations.

Chi^2 tests for each locus in each population sample showed significant departure from the Hardy-Weinberg expectation in ten of 114 (8.8 %) of the cases (Table 16). This is somewhat greater than the percentage which would be expected by chance (if $\alpha = 0.05$ then 5.7 of 114 could show significance by chance alone). F_{IS} values are also measures of deviation from the Hardy-Weinberg expectation within subpopulations. Five F_{IS} values (EST-6, IDH-1, MDH-1, MDH-2,and PGD; Table 17) were very close to zero indicating that allozyme frequencies were consistent with the Hardy-Weinberg expectation. The remaining F_{IS} values were positive suggesting a deficiency of heterozygotes (AAT-1 GP-1 IDH-2, MPI, PEP-A, PGM-1, PGM-2). These measures suggest that there may be some effect of departures from random mating, selection, drift, migration, or mutation (e.g. see Zink, 1986) on population structure in *Zonotrichia capensis.* This is an important point since for many natural populations, particularly for animals and outcrossing plants, F_{IS} is often assumed to be or usually is close to zero (Hartl, 1988). For example, in Zink's (1986) study of the schistacea group of Fox Sparrows, average F_{IS} across all 31 population samples for 14 polymorphic loci was 0.0072, while for the present study across 12 polymorphic loci

the average value was 0.129. However, F_{IS} values presented here were probably strongly influenced by sampling error. IDH-2 illustrates this point. This particular locus was virtually monomorphic across all sites (21 of 24); the rare IDH-2 C allozyme was present at sites T3 and M3 only (frequency of 0.056 and 0.024 respectively), while the rare IDH-2 A allozyme was found at site W4 (frequency of 0.026). The exact probability tests indicated that allozyme frequencies departed from the Hardy-Weinberg expectation at only a single site (T3) yet F_{IS} for this locus was the second highest found (0.505). The Wahlund effect is an unlikely explanation for obtained F_{IS} values because of precautions taken to ensure that collected birds were breeding residents (described in the MATERIALS AND METHODS).

Both the uncorrected and corrected F_{ST} values (0.140 and 0.119, respectively) and Chi^2 statistics, across all 12 polymorphic loci, indicated significant differentiation among sites with respect to allozyme frequencies (Table 17). For natural populations of birds, these values are exceptionally high (Barrowclough, 1983; Evans, 1987), although not the highest reported (e.g. *Empidonax difficilis* populations uncorrected F_{ST} = 0.153 - Johnson and Marten, 1988). For example, the average uncorrected F_{ST} for 23 studies of a wide variety of avian taxa was 0.048 (Evans, 1987); from the same study average uncorrected F_{ST} for 11 multilocus surveys of various emberizine taxa was 0.044. Barrowclough (1983) reported average F_{ST} values among populations within species for five vertebrate classes: fish (0.114; 9 species), amphibians (0.383; 15 species), reptiles (0.304; 3 species), mammals (0.230; 25 species) and birds (0.022; 5 species). The F_{ST} values reported for *Z. capensis*, then, are comparable to some intraspecific comparisons within other vertebrate

classes. Although corrected F_{ST} and Chi^2 statistics indicate three of twelve loci listed in Table 17 are significantly heterogeneous, it is clear that PGM-1 is the most highly differentiated across sites (corrected F_{ST} = 0.344) and contributes most to the overall F_{ST} (discussed in more detail later in the discussion).

Wright (1931) has shown that for neutral alleles, $F_{ST} \approx 1/(1 + 4Nm)$, where N is local population size and m represents the average rate of immigration assuming an "island" model of population structure (i.e. every population is equally accessible from every other; see Slatkin, 1987). Obviously the nature of the data presented herein precludes calculation of N and m; however, the value of Nm together can be estimated and this combination permits the evaluation of the relative contributions of gene flow versus genetic drift (Slatkin, 1987). Values of Nm calculated for each polymorphic locus (using uncorrected F_{ST} values) range from 0.44 (PGM-1) to 12.3 (PGD). If corrected F_{ST} values are used then estimates of Nm range from 0.48 (PGM-1) to approaching ∞ (EST-6, MDH-1, MDH-2 and PGD); the latter estimates of Nm result from corrected F_{ST} values which are essentially zero. If Nm < 1 then substantial population differentiation could result from genetic drift, but this is not the case if Nm > 1 (Slatkin, 1987). Thus, if all sites are included in the analysis, all loci but PGM-1 seem to indicate that gene flow is sufficiently strong to counteract any influence of drift (using uncorrected F_{ST} values, average Nm = 7.2, ranging 2.7 for MPI to 12.3 for PGD). Since PGM-1 differs noticeably from the other 11 loci (Nm < 1) it seems possible that it (or a closely linked locus) is subject to natural selection favouring different alleles in different populations (there is an alternative explanation which will be discussed later).

4.2.2 Among Vegetation/Dialects

Hierarchical F coefficient analysis indicated that only 50 % of total among site differentiation in allozyme frequencies was due to a vegetation/dialect effect (Table 18) contrary to what would be expected if song was influencing genetic population structure as predicted by the local adaptation hypothesis. The analysis of allozyme frequency heterogeneity of each vegetation separately indicated that the F_{ST} for puna sites was exceptionally high and that this high value was, to a large extent, caused by variability at the PGM-1 locus (discussed in detail in section 4.4). Johnson and Marten (1988, p. 183) have indicated the utility of calculating F_{ST}'s for subsets of the population so that " ... geographic unevenness in the amount of genetic differentiation" may be identified. Thus, I recalculated the hierarchical F coefficients excluding all four puna sites (Table 21). Overall F_{ST} for this subset of 20 sites was 0.017. F_{SD} was 0.019 and F_{DT} was essentially zero; thus, this analysis suggests that none of the allozyme frequency variation was due to a vegetation/dialect effect among the 20 non-puna sites. Level of genetic differentiation as indicated by F_{ST} across all 20 sites (minus puna) were similar to levels of differentiation among sites within each of five non-puna vegetations ($F_{ST(corr.)}$ ranging from 0.006 to 0.023, average 0.0132 ± 0.0069; see Table 19).

The critic will note that there is substantial variation within a putative trill-rate dialect population (see Table 3). Since one of the present studies' objectives (i.e. assessing the local adaptation hypothesis) is predicated on the idea of associations between trill rate and vegetation, this intra-vegetation variation would at first glance seem problematic. Handford (1988) established, with extensive sampling of songs over my study area, that almost 50 % of trill-rate variation is explained by original

Table 21: F statistics (Wright, 1978b) for three hierarchical levels with four puna sites removed. F_{SD}, F_{DT} and F_{ST} are defined in Table 18

Locus	F_{SD}	F_{DT}	F_{ST}
AAT-1	0.006	0.001	0.007
EST-6	0.000	0.008	0.008
GP-1	0.047	0.006	0.053
IDH-1	0.014	-0.001	0.013
IDH-2	0.016	-0.004	0.011
MDH-1	0.001	-0.002	-0.001
MDH-2	0.001	-0.001	-0.001
MPI	0.091	-0.007	0.085
PEP-A	0.022	-0.005	0.017
6PGD	0.000	-0.002	-0.002
PGM-1	0.029	-0.008	0.022
PGM-2	0.036	-0.007	0.030
TOTAL	0.019	-0.003	0.017

vegetation. Each vegetation type is associated with a particular range of trill intervals. Dispersal of birds from their natal area, if it does occur, is probably a leptokurtic function (i.e. the majority of birds will disperse only short distances; see Barrowclough and Rockwell, 1987); therefore, my test of the local adaptation hypothesis assumes only that birds at adjacent demes within a vegetation sing songs with similar trill intervals, and that songs at adjacent sites in different vegetations have markedly different trills. If trill rate is important in mate attraction and territorial defense, then successful dispersal (and thus, gene flow) is more likely to occur between adjacent sites within a vegetation.

Baker et al. (1982), in their study of genetic differentiation of dialect populations of Nuttall's White-crowned Sparrows, suggested that the relationship between genetic distance and geographic distance may be quite different between sites within a dialect and between sites between dialects. Sites which are geographically proximate but located in different dialects should show greater genetic differentiation than will sites within dialects (Zink and Barrowclough, 1984). Thus, I compared Rogers' genetic distances between sites within a vegetation type with those between sites in different vegetation types (again excluding puna sites), while controlling for the effects of geographic distance using an analysis of covariance (ANCOVA). The geographic scales (i.e. the covariate) for within-dialect and between-dialect groups were similar and thus, should not influence the results. There was no significant difference between slopes of these two groups ($F = 0.00$, $P = 0.99$); thus, I excluded the interaction term from the model. There was no difference between elevation of the two regression lines ($F = 0.06$, $P = 0.81$) nor was the slope significantly different from zero ($F = 0.55$, $P = 0.46$). These results should be interpreted with caution since observations are not statistically independent (i.e. for three hypothetical

sites A, B, and C, the distance from A to C is not independent of the distances between sites A and B, and B and C); however, they do support the contention that song is not structuring the population.

It would appear that genetic structuring corresponding to putative vocal dialect populations among the five non-puna populations in Rufous-collared Sparrows is not present, even though the range of trill intervals (36 to 474 msec) within this area covers almost the entire range of values described (Handford, 1988).

Three bird species have previously been examined with respect to possible relationship between patterns of variation in allozyme frequencies and song: Rufous-collared Sparrows (Nottebohm and Selander, 1972; Handford and Nottebohm, 1976), White-crowned Sparrows (*Z. leucophrys*; Baker, 1974; 1975; Baker et al. 1982; Baker et al. 1984a; 1984b) and Swamp Sparrows (*Melospiza georgiana*; Balaban, 1988). The results from both Nottebohm and Selander's (1972) and Handford and Nottebohm's (1976) studies of vocal dialects and genetic population structure were equivocal for reasons discussed in the introduction. M.C. Baker and coworkers (Baker, 1974; 1975; Baker et al. 1982) have extensively studied correlations between song dialect variation and genetic population structure in the sedentary subspecies of White-crowned Sparrow (*Z. leucophrys nuttalli*) and have claimed that their results indicate reduced gene flow between dialect populations. For example, Baker et al. (1982) examined allozyme frequencies of seven polymorphic enzymes for sparrows collected from nine sites sampled from four dialect populations of Nuttall's White-crowned Sparrow from the Point Reyes Peninsula, California and calculated an F_{ST} of 0.042 among dialects, a value which they suggested indicated substantial differentiation. Separate regressions of Nei's (1972) genetic distance on geographic distance for inter-site comparisons within dialects and for inter-site comparisons between dialects yielded

nonsignificance in the former and significance in the latter case; the difference between these two regression lines Baker et al. (1982) suggested was due to greater differentiation between sites in different dialects due to reduced gene flow.

Baker's interpretation of his data has been the subject of intense debate (Balaban, 1988; Baker and Cunningham, 1985 and following commentaries; Hafner and Petersen, 1985; Zink and Barrowclough, 1984). For example, Zink and Barrowclough (1984) questioned the validity of some of their statistical analysis; a hierarchical F_{ST} analysis revealed substantial within dialect component of allozyme variability indicating that pooling sites within dialects obscures interpretation. Zink and Barrowclough (1984) also compared the slopes of regression of Nei's (1978) genetic distance on geographic distance among three sets of points (rather than Baker et al.'s two) using ANCOVA: inter-site comparisons within dialects, inter-site comparisons between adjacent dialects, and inter-site comparisons between non-adjacent dialects. None of the slopes was significantly different indicating that the relationship between genetic and geographic distance was similar in each of the three groups. Balaban (1988) has rightly suggested that population differentiation among dialect populations in Baker et al. (1982) may be severely confounded by a boundary between subspecies (*nuttalli* and *pugetensis*) to the north of Baker's study area (described by Corbin, 1981).

Balaban (1988) examined covariation between song and genetic variation over a large portion of the Swamp Sparrow's range. Allozyme frequency data from nine polymorphic loci indicated three subdivisions among the study locations roughly concordant with subspecies ranges. Within the two most geographically extensive subdivisions, there was a correlation between pattern of song syllable variation and genetic variation which was not related to geographic distance. An important distinction to make between the crowned sparrow studies and Balaban's study is that

in the former dialect populations were described *a priori* (and also are readily detectable by human ear), while in the latter case song groups were discerned statistically.

4.3 Covariation of Distance Matrices

4.3.1 Comparison of Genetic Distances to Studies of Other Avian Taxa

Nei's (1978) and Rogers' (1972) genetic distances between sites P1 and P3 and all other study sites are high for intraspecific comparisons of populations in birds: between site P1 and all other sites excluding P3 (average Nei's distance = 0.031 ± 0.0050; average Rogers' distance = 0.051 ± 0.0052) and between site P3 and all other sites excluding P1 (average Nei's distance = 0.026 ± 0.0046; average Rogers' distance = 0.048 ± 0.0050) (see Appendices 9 and 10 and Figure 8). Barrowclough (1980) has summarized degree of genetic differentiation, as indicated by Nei's (1978) genetic distance, for various taxonomic levels in birds: among local populations, mean distance = 0.0024 ± 0.0028 (n = 113 comparisons), among subspecies, mean distance = 0.0048 ± 0.0049 (n = 86 comparisons) and among species, mean distance = 0.044 ± 0.0221 (n = 71 comparisons). It is evident that genetic distances between these two puna sites (P1 and P3), and all other sites, are similar in magnitude to among species comparisons in other avian taxa suggesting significant genetic differentiation between high altitude puna scrub populations and all other sampled populations from within the present study area..

For all other inter-site comparisons in the present study, genetic distance values are within the ranges reported for other intraspecific local population comparisons for birds: range of Nei's distances from 0.000 to 0.007; range of Rogers' distances from 0.005 to 0.039. For example, Baker et al. (1990) examined genetic

differentiation among 19 sites (both island and continental) of Common Chaffinches (*Fringilla coelebs*). For the five continental sites (2 sites in Morocco and 3 sites on the Iberian peninsula), the average Rogers (1972) genetic distance was 0.034 ± 0.0038 and average Nei's (1978) was 0.014 ± 0.009. Zink (1986), in his study of geographic variation of Fox Sparrows, found that the average Nei's (1978) genetic distance between pairs of localities in the same subspecies was 0.00032 ± 0.00041 (104 comparisons).

4.3.2 Mantel's Tests

Mantel's tests (Table 20) indicated concordance between both EXT, SKE and ROG, and GEO suggesting that isolation-by-distance may be an important factor in among site differentiation (Wright, 1943; 1978a). There was also significant similarity between EXT and SKE, and ECO indicating that there may be regional morphological patterning due to ecological factors. Interestingly, at least at this scale of analysis, there was significant concordance between patterns of EXT and SKE, and ROG. Lack of concordance between patterns of variation in morphological and genetic character suites has been suggested as being possible evidence for differences in evolutionary rates and processes of different types of traits (e.g. Berlocher and Bush, 1982; Gorman and Kim, 1976; Schnell et al. 1978; Schnell and Selander, 1981; Sene and Carson, 1977; Turner et al. 1979; Zink, 1986). This trend has been observed in various avian taxa also. For example, Zink (1988) found that there was no relationship between genetic and morphological distances in populations of Brown Towhees (*Pipilo fuscus* complex). Other studies have shown that, at least in some naturally occurring populations, there is concordance between these two types of characters. For example, Lagercrantz and Ryman (1990) found similar patterns between morphology

and allozyme frequencies in Norway Spruce (*Picea abies*) populations in Europe. Baker and Hough (1983) has noted that, generally in birds, morphological differentiation among populations is often evident without a similar level of differentiation of allozyme frequencies, although Lewontin (1984) has cautioned that the statistical power for discriminating population differences is different for these two classes of characters.

The fact that there is not concordance between SON and EXT or SKE, or between SON and ECO is at first puzzling. One would certainly predict that song frequency might be correlated to body size (e.g. see Nottebohm, 1975, but also see Handford and Lougheed, 1991) or habitat structure (Morton, 1975; Bowman, 1979; 1983). The theme and trill portions of Rufous-collared Sparrows song possibly serve different functions (Handford and Lougheed, 1991); therefore, treating song as a whole might obscure the fact that theme and trill might be subject to very different selection pressures. For example, if only characteristics of the theme are measured and used to construct a distance matrix to be used in Mantel's test the following is found: comparing the theme distance matrix and EXT, $t = 2.67$; comparing the theme distance matrix and ECO, $t = 2.18$. These t values are still not significant (that is if a conservative test statistic is still used) but have increased two-fold over the values reported in Table 20. Another factor to be considered is that the analysis of habitat was quite crude and involved a subjective scoring system. It is possible, then, that some variables included in the analysis of vegetation structure here are not directly related to song characteristics in *Z. capensis*.

4.4 Comparison between Puna Scrub and Other Five Vegetation Populations

4.4.1 Subspecific Status

It is evident from the CVA of morphological characters (Figures 3 and 4), from

analyses of allozyme frequency heterogeneity (Table 19) and from the results of MDS (Figures 6,7 and 8) that puna populations are markedly divergent from the other five vegetation/dialect populations considered herein. Chapman (1940) considered these high altitude, puna scrub populations to be a different subspecies (*pulacayensis*) from the other lower altitude populations which occur within the present study area (*hypoleuca*). He based this distinction on morphology (primarily wing chord length) and plumage characters (e.g. degree of rufescence of the collar and nape). Nei's (1978) and Rogers' (1972) genetic distances indicate substantial divergence in structural genes, at least for two of the four sites. Levels of genetic divergence between sites P1 and P3 and all other sites are at least as great as has been reported between avian subspecies and even between species within a genus (e.g. Barrowclough, 1980). The data presented herein strongly suggest that there were indeed two subspecies within the study area. However, to adequately assess degree of variation within *pulacayensis* requires a larger number of samples throughout this putative subspecies' range. The four puna scrub sites from the present study were distributed at the southern terminus of described *pulacayensis* range, only.

4.4.2 Variation of PGM-1 Allozyme Frequencies.

Puna sites were distinct with respect to allozyme frequencies at the PGM-1 locus. Allozyme C was the most common allozyme at all non-puna sites. Allozyme B was increasingly common in puna sites at lower latitudes (Appendix 5). These data are suggestive of the existence of a cline although more sites need to be sampled in the extreme northwest to establish this conclusively. If a cline does exist at PGM-1 then site P2 was anomalous with respect to the relative frequency of allozymes at this locus. It would be predicted that the frequency of PGM-1 B should be intermediate

between its frequency at sites P3 (0.763) and P1 (0.825) whereas it was in fact 0.250. This may, however, have been a result of the relative isolation of site P2 from other puna sites. Site P2 was located in a narrow river valley where Rufous-collared Sparrows were locally abundant separated from other areas of apparently suitable habitat by at least 20 km. In fact, seven male specimens were collected from a site in the town of Abra Pampa (site aborted because of low bird density) in an area of puna vegetation which was essentially contiguous with sites P1 and P3. The frequency of PGM-1 B at this site was 0.64.

Chapman (1940) among others (e.g. Zink, 1982) proposed that the crowned sparrows (genus: *Zonotrichia*) originated in North America where four extant Rufous-collared Sparrow congeners are found: White-crowned Sparrow (*Z. leucophrys*), White-throated Sparrow (*Z. albicollis*), Harris's Sparrow (*Z. querula*) and the Golden-crowned Sparrow (*Z. atricapilla*). Chapman argued that there were two primary corridors of invasion of the South American continent by *capensis* , one along the Andes mountain chain, and the other along the eastern margin of Brazil (evidence from present day distributions). Chapman further suggested that these two routes met first in Bolivia within what is now the range of *Z. c. hypoleuca* . Thus, with this possible scenario, two previously allopatric populations could have met near the present day border between the subspecies *Z.c. pulacayensis* and *Z. c. hypoleuca* , where there is now the putative cline in PGM-1 allozyme frequencies (i.e. secondary intergradation *sensu* Endler, 1977).

There is an obvious ecological gradient associated with decreasing latitude and increasing altitude There are numerous environmental factors like annual precipitation and temperature, day length, etc. which vary along this gradient so that the putative cline could have developed parapatrically (i.e. primary intergradation *sensu* Endler,

1977). Ult ately, the two possibilities cannot be distinguished. Endler (1977, p. 155) has indicated that "... unless we observe a zone of intergradation within a few hundred generations of secondary contact, it will be impossible to distinguish secondary intergradation from primary intergradation."

4.4.3 Covariation of Distance Matrices minus Puna Sites.

Since puna sites are so markedly different from other sites, it seems probable that the Mantel's comparisons made previously may have been confounded. For example, conclusions of simple isolation-by-distance may be confounded by the fact that all puna scrub sites were in the northwest of the study area. Thus, I compared distance matrices (omitting skeletal distances since patterns of external and skeletal variation are similar) using only the 20 non-puna sites (Table 22). External Mahalanobis distances showed similar patterns to both geographic and inverse geographic distances (as before, the greater the distance between any two compared sites then the greater was be morphological differences between resident birds). The external distance matrix also showed concordance with the ecological distance matrix. There was similarity in pattern between the ecological and geographic distance matrices; therefore at this scale of analysis there was a confounding of the effects of geographic distance and degree of habitat differentiation. Concordance of pattern between morphological and genetic distances is no longer evident, the previous significant Mantel's t statistic being an artifact of inclusion of morphologically and genetically distinct puna sites. Moreover, there is no longer a significant comparison between Rogers' genetic distance and the geographic distance matrices; it would appear, then, that there is no simple isolation-by-distance among the 20 non-puna sites.

Table 22: Matrix of t-statistics resulting from pair-wise distance matrix comparisons (20 X 20 matrices with all puna sites removed) using Mantel's (1967) non-parametric test.

	Rogers'	Song	Geographic	Inverse	Ecological
Externals	1.22	0.67	**3.14**	**-3.78**	**4.23**
Rogers		-1.12	-0.47	0.87	0.08
Song			0.96	-1.90	1.27
Geographic					**13.26**
Inverse					0.86

4.5 Other Possible Ecological Correlates of Population Structure

The degree of genetic differentiation among subpopulations of a species will be affected by a number of factors including population size, selection and levels of gene flow (Wright, 1940; 1978b). The relative importance of each of these factors will be influenced by a species' distribution which is in turn influenced by the distribution of suitable habitat. Many species have distributions which are either uniform or clumped as dictated by dispersion of suitable habitat, rather than having a continuous distribution throughout their range (Rockwell and Barrowclough, 1987). In insular populations, for example, relative magnitude of gene flow will be affected by distance to the mainland ancestral population (e.g. Baker et al. 1990). The further an island is from the mainland population, then the smaller will be the potential magnitude of gene flow, and the greater will be the probability of population differentiation. A similar situation can occur in continental populations of a species if they are not distributed continuously. Between such continental populations, then, the magnitude of gene flow will also be affected by inter-population geographic distance or degree of isolation due to some other barrier, the greater the distance or degree of isolation, the smaller will be potential gene flow. In species where suitable habitat is patchily distributed, greater levels of genetic differentiation are expected, compared to species where suitable habitat is continuously distributed. Increased population differentiation possibly due to patchiness of habitat distribution has been observed in natural populations, primarily in small mammals (e.g. the pika *Ochotona princeps* - Glover et al. 1977; pocket gophers of the genera *Geomys* and *Thomomys* - Penny and Zimmerman, 1976; Patton and Yang, 1977).

Rufous-collared Sparrows are not distributed continuously either within or among different vegetations. Within xeric habitats (puna and Monte), Rufous-collared

Sparrows are only locally abundant in riparian zones usually along permanent water courses. In grassland, although generally densities are high it is again evident that there are areas where *capensis* is abundant separated by areas where densities were quite low. In fact, at higher altitudes generally it seems quite clear that there are patches of apparently suitable habitat separated by, in some cases, substantial areas of apparently unsuitable habitat (assuming that sparrow occupancy is an indicator of suitability). Finally, the Rufous-collared Sparrow is essentially an open country bird. In forest or woodland habitats, *capensis* only occupies clearings or forest edges so again there is a fair degree of patchiness with respect to suitable habitat. Topography may also play an important part in determining density and distribution of Rufous-collared Sparrows. In lowland chaco, which is relatively uniform and flat, *capensis* appears to be more or less continuously distributed throughout while in topographically varied regions distribution is more discontinuous (pers. obs.). There is some evidence that habitat patchiness and/or topography has had some influence on population structure in Rufous-collared Sparrow. All statistically significant heterogeneity in allozyme frequencies is found in mountainous habitats where it seems likely that suitable habitat is more disjunct than in lowland habitats (Table 19). If the two classes of sites are separated (lowland and mountainous) and Wright's F coefficients recalculated the following is found: $F_{ST(corr.)}$ calculated for the eight lowland sites is 0.007, while for twelve mountainous sites excluding puna scrub the value is 0.021.

Populations which are isolated are often associated with reduced genetic variability possibly resulting from founder effect, bottlenecking, genetic drift, changes in selection pressures or combinations of these four factors (Wright, 1940; Kilpatrick, 1981). Thus, it seems reasonable to test for differences in measures of genetic variability between sites which represent samples from continuous distributions of

sparrows and those that represent populations which are patchily distributed. I compared the lowland habitat (lowland chaco and transition forest; n = 8 sites) with the high altitude habitats (n = 16 sites) with respect to three measures of genetic diversity. Mean number of polymorphic loci was not statistically different between the two groups ($t_{(d.f.\ 22)} = 1.36$, $P = 0.19$; lowland site mean = 3.00, high altitude site mean = 2.82), nor was mean observed heterozygosity ($t_{(d.f.\ 22)} = -0.22$, $P = 0.83$; lowland site mean = 0.0305, high altitude site mean = 0.0314). However, mean number of alleles per locus was significantly different between the two groups ($t_{(d.f.\ 22)} = 2.25$, $P = 0.035$; lowland site mean = 1.38, high altitude site mean = 1.28). Therefore, one of the three measures (mean number of alleles per locus) does differ in the predicted manner; that is, high altitude sites showed reduced genetic variability with respect to this single measure. Obviously the pattern is not clear-cut because the other two measures were not significant.

Various aspects of population demography of a species can affect amount of population differentiation which occurs (Bowen, 1982; Rockwell and Barrowclough, 1987). One might expect that density of local populations may be one parameter which could influence genetic structure (e.g. it might be related to effective population size). As was alluded to above, there were large differences in the densities of birds at different sites. I did not measure density formally at any site. However, at all sites I set approximately the same number of mist nets (between 15 and 20); the number of days it took to capture a sample of approximately 20 males is probably a good albeit rough indicator of local Rufous-collared Sparrow densities. I calculated Spearman Rank correlations (Seigel, 1956) between days to capture sample and each of three indicators of genetic diversity but found no significant relationships: number of

polymorphic loci (r^2 = 0.049, P = 0.297), number of alleles per locus (r^2 = 0.00, P = 0.999) and observed heterozygosity (r^2 = 0.023, P = 0.479). Thus, there appears to be no simple relationship between these three measures of genetic variability and local density of male Rufous-collared Sparrows.

One might expect that the pattern of allozyme variability would reflect the relative migratoriness of different Rufous-collared Sparrow populations. Migratory populations appear to have a possibility of greater dispersal distance than sedentary populations and thus, might show greater levels of gene flow or lower levels of differentiation. Within the genus *Zonotrichia*, for example, at the specific level there appears to be a positive relationships between morphological differentiation (number of recognized races) and degree of sedentariness (Baker, 1982). Lowland populations in Rufous-collared Sparrows within the study area are probably sedentary (probably even these undertake local movements) while highland, Andean populations show altitudinal migration patterns (Handford, 1980; King, 1972; Olrog; 1979). The pattern of allozyme variability is opposite to the expectation of greater differentiation with greater sedentariness. Sites in lowland chaco and transition forest are not significantly heterogeneous yet populations are probably sedentary, while all other vegetations show significant heterogeneity and resident birds are probably migratory (Table 19). There is no published information on average dispersal distance of any population of Rufous-collared Sparrow. However, it is known that for at least for one altitudinally migratory population (grassland, Tucuman province), adult males and females, and possibly juveniles are highly philopatric (Handford and Nottebohm, 1976).This implies that dispersal distance may be quite low in at least this single migratory population although year-to-year philopatry may not be that important when considering long-term impact on genetic structure of populations.

5.0 CONCLUSIONS

Although there was marked genetic heterogeneity among sites within the present study area, there was no discernable relationship between the pattern of trill rate variation and genetic population structure in Rufous-collared Sparrows in northwestern Argentina. Putative dialect/ vegetation populations were morphologically differentiated although at present it cannot be stated unequivocally that this reflects underlying genetic differences. There was little evidence to suggest that song was influencing population structure in this bird species (i.e. the genetic or local adaptation hypothesis is not supported in this species within the present study area).

On a gross scale, there was covariation between morphology and allozyme frequencies; puna scrub populations were differentiated from all other sites morphologically with respect to structural size, and genetically, primarily with respect to PGM-1. Moreover, at this same scale there appeared to be simple isolation-by-distance as indicated by a significant Mantel's test statistics between compared genetic and geographic distance matrices. However, removal of puna scrub sites from the analyses showed that these results were artifacts of inclusion of these highly differentiated high altitude sites. Among non-puna sites there was in fact no covariation between genetic and morphological distances nor was there concordance between genetic and geographic distance matrices. Finally, Mantel's tests between the song Mahalanobis distance matrix and the external morphological Mahalanobis and combined ecological distance matrices indicated that there was no simple relationship between frequency and temporal characteristics of the song, and either body size or habitat.

There did appear to be structure in the allozyme data. I would suggest that

genetic population structure was probably influenced by topography (e.g. mountainous versus flat) and distribution of suitable habitat since all statistically significant allozyme heterogeneity was found in highland populations where suitable habitat appears to be patchily distributed. Marked heterogeneity at the PGM-1 locus, primarily among puna scrub sites was suggestive of the existence of a cline. If there is indeed a cline present then it could be due either to primary intergradation (cline along an environmental gradient in puna scrub) or secondary intergradation (secondary contact of two previously isolated populations).

If local adaptation does not explain the unique pattern of song variation that is evident in Rufous-collared Sparrows, then how can it be explained? Nottebohm (1985) and Handford (1988) have argued that the most probable explanation is one of acoustic adaptation. In other words, there is direct adaptive significance in the type of learned vocalizations that are evident in different type of environments (Rothstein and Fleischer, 1987). Songs, within a population, which carry greater distances may be preferentially copied by juvenile birds during their critical learning periods (Morton, 1986; Morton et al. 1986). This has been documented in at least one bird species, the Carolina Wren, *Thyrothorus ludovicianus* (Morton et al. 1986). There are problems with this interpretation, as discussed in detail by Handford (1988). For example, it is not clear why song characteristics do not always appear to reflect sound transmission properties of present day habitats but rather those of sometimes long absent vegetations. Predictions can be made as to the types of sound which will transmit best in different types of habitats; for example, it is predicted songs with fast trills will be evident in open habitats and songs with frequency modulated whistled elements evident in more closed habitats (Wiley and Richards, 1982). In general, fast trilled songs are found in open habitats (eg. montane grassland and puna scrub) and slower trilled songs

in more closed habitats (eg. transition forest and lowland chaco). However, there is a marked exception to this prediction. Monte desert scrub birds, throughout most of the extent of this vegetation, sing songs which possess songs either with extremely slow trills or songs where trill is entirely absent, even though we would expect, based on openness of this habitat, that songs should have fast trilled elements (Handford, 1988; discussed at length in Handford and Lougheed, 1991).

Handford (1988) has elaborated on ideas presented by Nottebohm (1975) with regard to a modified version of the acoustic adaptation hypothesis. It was suggested that both the physical attributes of the habitat where a bird exists and the auditory environment should be considered. Songs of other species of birds (some of which do not learn their vocalizations; e.g. Furnariids) in various habitats often have similar qualities to resident Rufous-collared Sparrow songs, in some cases with trilled elements that are virtually indistinguishable from that of *Z. capensis* (Handford and Nottebohm, 1976; Handford, 1988). Song of Rufous-collared Sparrows in different habitats may diverge over time to reflect the dominant sounds in their auditory environment (e.g. of other sympatric bird species), as well as those conspecific songs which transmit best. In some areas where *Z. capensis* densities are high (e.g. grasslands and some agricultural areas), then conspecifics may provide the common and dominant sounds of the auditory environment; in habitats where densities of *Z. capensis* are low then other avian species' vocalizations may be predominate in the auditory background (Handford, 1988).

APPENDIX 1: Locality information for the 24 Rufous-collared Sparrow collection sites: site code (letter indicates vegetation type, number indicates series[1]), locality name (nearest settlement or route number), geographic coordinates and altitude (± 50 m).

SITE CODE	LOCALITY NAME	PROVINCE	LATITUDE	LONGITUDE	ALTITUDE
C1	Chaguaral	Salta	24° 3'	64° 0'	400
C2	Cabeza de Buey	Salta	24° 45'	65° 1'	700
C3	San Felix	San. del Estero	26° 38'	64° 22'	300
C4	Monteagudo	Tucuman	27° 31'	65° 10'	300
T1	Calilegua	Jujuy	23° 44'	64° 42'	500
T2	Campo Quijano	Salta	24° 55'	65° 39'	1500
T3	Soldado Moldonado	Tucuman	27° 8'	65° 33'	350
T4	Alpachiri	Tucuman	27° 20'	65° 45'	400
W1	Leon	Jujuy	24° 2'	65° 25'	1600
W2	El Nogal	Salta	25° 8'	65° 40'	1550
W3	Km 43 Route 307	Tucuman	26° 57'	65° 39'	1700
W4	La Banderita	Catamarca	27° 19'	65° 57'	1600
G1	Volcan	Jujuy	23° 54'	65° 27'	2100
G2	Cuesta El Obispo	Salta	25° 9'	65° 50'	2800
G3	Km 78 Route 307	Tucuman	26° 47'	65° 43'	2750
G4	Agua de las Palomas	Catamarca	27° 37'	66° 8'	1850
M1	El Churcal	Salta	25° 22'	66° 14'	2000
M2	El Barrial	Salta	25° 54'	65° 56'	1650
M3	Los Nacimientos	Catamarca	27° 10'	66° 44'	1850
M4	Belen	Catamarca	27° 39'	67° 2'	1000
P1	La Quiaca	Jujuy	22° 7'	65° 34'	3400
P2	Abra Pampa	Jujuy	22° 35'	65° 50'	3500
P3	Tres Cruces	Jujuy	22° 56'	65° 30'	3600
P4	La Poma	Salta	24° 43'	66° 13'	3000

[1] Vegetation codes: C=lowland chaco thornscrub, T=transition forest, W=montane/alder woodland, G=montane grassland, M=Monte desert scrub, and P=puna high altitude semi-desert scrub (for habitat descriptions see Handford, 1988 and Verfoorst, 1982).

APPENDIX 2: List of enzymes used. Acronyms for each enzyme are given in parentheses. Enzyme commision (E.C.) numbers follow the International Union of Biochemistry (1984). The number of loci indicates the number resolved and scored for a given protein. Source tissues that were used for each enzyme were: L=liver and K=kidney. Electrophoretic conditions used for each protein were: 1) morpholine citrate pH 6.7 (Clayton and Tretiak 1972), 2) tris citrate pH 6.7 (Selander et al. 1971), borate pH 8.2 (Selander et al. 1971), and 4) lithium hydroxide pH 8.2 (Selander et al. 1971). Ten enzymes were not sufficiently resolved to score.[1]

ENZYME/PROTEIN	E. C. NUMBER	NUMBER OF LOCI	TISSUE	CONDITION
ACID PHOSPHATASE (ACPH)	E.C. 3.1.3.2	1	L	1
ASPARTATE AMINOTRANSFERASE (AAT)	E.C .2.6.1.1	2	L	1 AND 3
ESTERASES (EST)	E.C. 3.1.1.1	1	K OR L	1
GLUCOSE-3-PHOSPHATE DEHYDROGENASE (G3PDH)	E.C. 1.1.1.8	1	L	1
ISOCITRATE DEHYDROGENASE (IDH)	E.C. 1.1.1.42	2	K	1
LACTATE DEHYDROGENASE (LDH)	E.C. 1.1.1.27	2	K	1
MALATE DEHYDROGENASE (MDH)	E.C.1.1.1.37	2	K	2
MANOSE PHOSPHATE ISOMERASE (MPI)	E.C.5.3.1.8	1	L	1
PEPTIDASE - A (PEP-A)	E.C. 3.4.-.-	1	K OR L	3
PHOSPHOGLUCONATE DEHYDROGENASE (PGD)	E.C. 1.1.1.44	1	K OR L	1
PHOSPHOGLUCO-MUTASE (PGM)	E.C. 5.4.2.2	2	K OR L	1
PURINE NUCLEOSIDE PHOSPHORYLASE (PNP)	E.C. 2.4.2.1	1	L	3

APPENDIX 2 continued.

ENZYME/PROTEIN	E. C. NUMBER [2]	NUMBER OF LOCI	TISSUE	CONDITION
SUPEROXIDE DISMUTASE (SOD)	E.C. 1.15.1.1	1	K OR L	1
HAEMOGLOBIN (HB)	N. A.	1	K OR L	1
GENERAL PROTEIN (GP-1)	N. A.	1	K OR L	1

1 - Non-resolvable enzymes with source tissue and electrophoretic conditions used were: aconitase hydratase (E.C. 4.2.1.3; K-1; L,K - 2), alcohol dehdrogenase (E.C. 1.1.1.1; K - 1; L,K - 3), creatine kinase (E.C. 2.7.3.2; K - 1), dihydrolipoamide dehdrogenase (E.C. 1.8.1.4; L,K - 1; K - 2,3), glucose-6-phosphate dehdrogenase (E.C. 1.1.1.49; L,K - 1), glucose-6-phosphate isomerase (E.C. 5.3.1.9; K - 1), hexokinase (E.C. 2.7.1.1; L,K - 1), NADP-dependent malate dehydrogenase (E.C. 1.1.1.40; L,K - 1; K - 2), peptidase - B (E.C. 3.4.-.-; K - 3,4), and sorbitol-6-phosphate dehdrogenase (E.C. 1.1.1.140; K -1).

2 - not applicable.

APPENDIX 3: Means and standard deviations (mm), by site, for eight external characters used in this study. Site codes the same as in Appendix 1. L = length, D = depth, and W = width.

Site	Outer Rectrix L	Wing Chord L	Tarsus L	Hind Toe L	Bill D	Bill W
C1	60.3 ± 2.45	65.1 ± 1.88	13.8 ± 0.66	22.6 ± 0.74	6.4 ± 0.21	5.6 ± 0.16
C2	61.2 ± 2.50	66.8 ± 2.04	13.9 ± 0.34	22.4 ± 0.99	6.3 ± 0.22	5.6 ± 0.16
C3	59.7 ± 2.43	66.8 ± 2.03	13.3 ± 0.76	21.2 ± 0.84	6.4 ± 0.20	5.5 ± 0.19
C4	60.9 ± 3.14	67.2 ± 1.97	13.2 ± 0.56	22.5 ± 0.61	6.4 ± 0.18	5.6 ± 0.17
T1	61.4 ± 1.98	66.4 ± 2.36	13.3 ± 0.50	23.1 ± 0.94	6.4 ± 0.25	5.6 ± 0.13
T2	62.2 ± 2.40	68.0 ± 2.10	12.9 ± 0.61	22.9 ± 0.74	6.5 ± 0.21	5.7 ± 0.14
T3	62.0 ± 2.85	68.2 ± 2.70	13.3 ± 0.83	23.8 ± 1.23	6.4 ± 0.21	5.8 ± 0.28
T4	59.3 ± 1.46	66.0 ± 2.14	12.9 ± 0.58	22.9 ± 0.56	6.4 ± 0.25	5.6 ± 0.21
W1	63.0 ± 2.32	68.8 ± 1.56	13.9 ± 0.37	23.6 ± 0.56	6.5 ± 0.21	5.7 ± 0.20
W2	63.5 ± 2.93	68.4 ± 2.52	13.3 ± 0.70	23.1 ± 0.51	6.3 ± 0.23	5.6 ± 0.24
W3	60.2 ± 2.68	68.2 ± 2.33	12.7 ± 0.45	23.2 ± 0.75	6.3 ± 0.24	5.5 ± 0.16
W4	61.2 ± 2.18	68.6 ± 2.02	12.5 ± 0.52	23.0 ± 0.67	6.3 ± 0.19	5.5 ± 0.19
G1	66.3 ± 1.57	72.5 ± 2.46	14.3 ± 0.58	24.2 ± 0.68	6.5 ± 0.26	5.6 ± 0.23
G2	66.0 ± 2.69	72.0 ± 1.72	13.6 ± 0.39	23.4 ± 0.53	6.5 ± 0.21	5.5 ± 0.22
G3	63.2 ± 2.44	70.2 ± 2.34	13.2 ± 0.41	23.6 ± 0.64	6.4 ± 0.21	5.5 ± 0.20
G4	63.7 ± 3.51	70.9 ± 2.51	12.5 ± 0.46	22.7 ± 0.98	6.3 ± 0.30	5.5 ± 0.18
M1	68.4 ± 2.56	75.4 ± 2.62	13.6 ± 0.57	23.8 ± 0.96	6.3 ± 0.24	5.6 ± 0.23
M2	66.7 ± 2.43	74.3 ± 2.58	12.7 ± 0.49	23.0 ± 0.93	6.3 ± 0.25	5.6 ± 0.20
M3	66.5 ± 2.99	73.3 ± 2.48	12.9 ± 0.47	23.0 ± 0.59	6.2 ± 0.17	5.6 ± 0.21
M4	63.4 ± 2.45	71.9 ± 2.03	12.4 ± 0.43	22.8 ± 0.64	6.3 ± 0.21	5.6 ± 0.20
P1	72.4 ± 3.00	78.9 ± 2.53	14.4 ± 0.49	24.8 ± 0.63	6.3 ± 0.21	5.6 ± 0.20
P2	70.4 ± 3.62	77.5 ± 2.08	14.1 ± 0.50	24.6 ± 0.84	6.4 ± 0.15	5.6 ± 0.20
P3	72.7 ± 2.69	77.6 ± 2.43	14.8 ± 0.51	24.4 ± 0.70	6.3 ± 0.19	5.6 ± 0.22
P4	69.0 ± 2.82	76.7 ± 2.01	14.1 ± 0.45	24.7 ± 0.73	6.6 ± 0.19	5.7 ± 0.15

APPENDIX 3 continued.

Site	Bill Gape L	Culmen
C1	13.9 ± 0.46	11.6 ± 0.39
C2	13.7 ± 0.52	11.8 ± 0.69
C3	13.2 ± 0.66	11.7 ± 0.49
C4	13.6 ± 0.45	11.7 ± 0.49
T1	13.9 ± 0.38	11.3 ± 0.46
T2	13.8 ± 0.56	11.8 ± 0.49
T3	13.3 ± 0.88	11.7 ± 0.65
T4	13.6 ± 0.58	11.6 ± 0.27
W1	14.0 ± 0.65	11.9 ± 0.50
W2	14.1 ± 0.35	12.2 ± 0.38
W3	13.9 ± 0.61	11.7 ± 0.41
W4	13.9 ± 0.66	11.6 ± 0.48
G1	14.8 ± 0.38	12.7 ± 0.44
G2	13.9 ± 0.56	12.0 ± 0.50
G3	13.8 ± 0.51	11.6 ± 0.33
G4	13.8 ± 0.62	11.5 ± 0.44
M1	14.2 ± 0.70	12.2 ± 0.53
M2	13.6 ± 0.48	11.7 ± 0.49
M3	13.4 ± 0.52	11.8 ± 0.53
M4	13.4 ± 0.40	11.8 ± 0.47
P1	14.8 ± 0.63	12.6 ± 0.37
P2	14.9 ± 0.60	12.9 ± 0.41
P3	14.4 ± 0.68	12.3 ± 0.39
P4	14.8 ± 0.36	12.6 ± 0.44

APPENDIX 4: Mean and standard deviation (mm) for twelve skeletal characters used in this study, by site. Site codes as in Appendix 1. All measurements in mm. L, D and W as in Appendix 3.

Site	Skull W	Skull L	Coracoid L	Scapula L	Sternum L	Keel D
C1	15.4 ± 0.34	18.2 ± 0.39	16.4 ± 0.45	18.7 ± 0.64	19.3 ± 0.55	6.7 ± 0.39
C2	15.7 ± 0.27	18.7 ± 0.26	16.7 ± 0.46	19.0 ± 0.61	19.6 ± 0.60	6.9 ± 0.23
C3	15.3 ± 0.31	18.3 ± 0.27	16.3 ± 0.73	18.5 ± 0.82	19.0 ± 0.45	6.8 ± 0.28
C4	15.5 ± 0.28	18.3 ± 0.33	16.4 ± 0.41	18.6 ± 0.50	19.1 ± 0.56	6.7 ± 0.28
T1	15.3 ± 0.34	18.2 ± 0.35	16.8 ± 0.52	19.0 ± 0.57	19.5 ± 0.64	6.8 ± 0.30
T2	15.7 ± 0.29	18.6 ± 0.23	16.9 ± 0.44	19.3 ± 0.70	19.80 ± 0.67	7.0 ± 0.28
T3	15.3 ± 0.23	18.4 ± 0.17	16.5 ± 0.44	18.9 ± 0.61	19.3 ± 0.53	6.8 ± 0.22
T4	15.2 ± 0.37	18.5 ± 0.31	16.5 ± 0.30	18.9 ± 0.48	19.2 ± 0.41	6.8 ± 0.21
W1	15.1 ± 0.23	18.4 ± 0.30	17.2 ± 0.37	19.5 ± 0.48	19.8 ± 0.47	6.8 ± 0.26
W2	15.7 ± 0.31	18.4 ± 0.35	17.0 ± 0.55	19.2 ± 0.56	19.7 ± 0.67	6.8 ± 0.26
W3	15.8 ± 0.28	18.8 ± 0.27	17.1 ± 0.42	19.3 ± 0.55	19.7 ± 0.38	6.9 ± 0.22
W4	15.5 ± 0.34	18.4 ± 0.33	16.8 ± 0.39	19.0 ± 0.63	19.5 ± 0.63	6.8 ± 0.25
G1	15.9 ± 0.32	18.9 ± 0.36	17.5 ± 0.52	19.9 ± 0.55	20.2 ± 0.49	6.8 ± 0.23
G2	15.6 ± 0.30	18.5 ± 0.36	17.1 ± 0.50	19.4 ± 0.74	19.9 ± 0.54	6.7 ± 0.31
G3	15.6 ± 0.28	18.3 ± 0.33	17.2 ± 0.42	19.5 ± 0.48	20.1 ± 0.48	6.9 ± 0.21
G4	15.5 ± 0.32	18.5 ± 0.35	16.8 ± 0.55	19.4 ± 0.58	19.6 ± 0.69	6.8 ± 0.22
M1	15.7 ± 0.23	18.5 ± 0.29	17.2 ± 0.50	19.8 ± 0.71	19.9 ± 0.56	6.8 ± 0.33
M2	15.7 ± 0.43	18.8 ± 0.74	16.7 ± 0.49	19.2 ± 0.45	19.8 ± 0.54	7.0 ± 0.26
M3	15.8 ± 0.29	18.5 ± 0.38	17.2 ± 0.52	19.5 ± 0.73	19.8 ± 0.61	6.9 ± 0.34
M4	15.8 ± 0.27	18.5 ± 0.27	16.8 ± 0.39	19.2 ± 0.53	19.3 ± 0.45	6.8 ± 0.26
P1	15.9 ± 0.27	19.2 ± 0.19	17.7 ± 0.40	20.0 ± 0.62	20.3 ± 0.51	7.0 ± 0.27
P2	15.9 ± 0.31	18.9 ± 0.37	17.5 ± 0.53	19.9 ± 0.66	20.1 ± 0.51	6.6 ± 0.22
P3	15.8 ± 0.31	19.2 ± 0.28	17.6 ± 0.46	20.1 ± 0.50	20.0 ± 0.80	6.8 ± 0.46
P4	15.9 ± 0.22	18.9 ± 0.36	17.9 ± 0.35	20.5 ± 0.49	20.7 ± 0.51	6.9 ± 0.21

APPENDIX 4 continued.

Site	Synsacrum W	Femur W	Femur L	Tibiotarsus L	Humerus L	Ulna L
C1	8.9 ± 0.27	3.0 ± 0.057	17.3 ± 0.46	28.8 ± 0.75	18.2 ± 0.35	20.3 ± 0.43
C2	8.9 ± 0.37	3.0 ± 0.036	17.7 ± 0.52	29.4 ± 0.89	18.6 ± 0.56	20.5 ± 0.66
C3	8.6 ± 0.33	3.0 ± 0.060	17.0 ± 0.48	28.5 ± 0.95	18.0 ± 0.51	20.1 ± 0.54
C4	8.5 ± 0.27	2.9 ± 0.056	17.2 ± 0.29	28.8 ± 0.56	18.3 ± 0.38	20.3 ± 0.41
T1	8.8 ± 0.35	3.0 ± 0.056	17.8 ± 0.59	29.6 ± 0.82	18.6 ± 0.53	20.7 ± 0.57
T2	8.9 ± 0.26	3.0 ± 0.074	18.0 ± 0.41	29.7 ± 0.67	18.9 ± 0.41	2C1 ± 0.49
T3	8.8 ± 0.34	3.0 ± 0.098	17.4 ± 0.40	29.1 ± 0.59	18.3 ± 0.43	20.5 ± 0.43
T4	8.9 ± 0.31	3.0 ± 0.091	17.7 ± 0.34	29.5 ± 0.67	18.3 ± 0.33	20.7 ± 0.36
W1	9.1 ± 0.37	3.0 ± 0.040	18.5 ± 0.35	30.5 ± 0.56	19.3 ± 0.28	21.4 ± 0.42
W2	8.9 ± 0.35	3.0 ± 0.061	18.1 ± 0.47	30.2 ± 0.76	19.0 ± 0.50	21.0 ± 0.51
W3	9.1 ± 0.40	3.0 ± 0.048	18.2 ± 0.41	30.5 ± 0.69	19.2 ± 0.41	21.5 ± 0.38
W4	8.9 ± 0.24	3.0 ± 0.062	17.8 ± 0.49	29.7 ± 0.75	18.9 ± 0.46	21.2 ± 0.62
G1	9.3 ± 0.31	3.1 ± 0.057	18.9 ± 0.48	31.5 ± 0.80	19.7 ± 0.46	22.0 ± 0.48
G2	9.2 ± 0.33	3.0 ± 0.041	18.5 ± 0.41	30.5 ± 0.63	19.4 ± 0.46	21.7 ± 0.42
G3	9.1 ± 0.35	3.0 ± 0.062	18.1 ± 0.48	30.3 ± 0.72	19.3 ± 0.40	21.6 ± 0.41
G4	8.8 ± 0.26	3.0 ± 0.045	17.8 ± 0.40	29.7 ± 0.89	19.0 ± 0.39	21.4 ± 0.47
M1	9.3 ± 0.31	3.0 ± 0.052	18.4 ± 0.51	30.4 ± 0.80	19.5 ± 0.53	21.9 ± 0.54
M2	8.9 ± 0.30	3.0 ± 0.067	18.0 ± 0.38	29.7 ± 0.81	19.3 ± 0.42	21.7 ± 0.61
M3	8.9 ± 0.23	2.9 ± 0.094	17.9 ± 0.46	29.8 ± 0.72	19.4 ± 0.42	22.0 ± 0.55
M4	9.0 ± 0.21	3.0 ± 0.089	17.7 ± 0.25	29.5 ± 0.70	19.0 ± 0.36	21.6 ± 0.39
P1	9.8 ± 0.41	3.3 ± 0.10	19.6 ± 0.41	32.2 ± 0.66	20.4 ± 0.27	22.8 ± 0.42
P2	9.5 ± 0.37	3.1 ± 0.049	19.4 ± 0.42	32.0 ± 0.84	20.2 ± 0.50	22.5 ± 0.61
P3	9.9 ± 0.30	3.2 ± 0.16	19.5 ± 0.55	31.9 ± 0.75	20.1 ± 0.47	22.6 ± 0.81
P4	9.8 ± 0.24	3.1 ± 0.034	19.4 ± 0.44	31.9 ± 0.57	20.4 ± 0.40	22.8 ± 0.43

APPENDIX 5: Allozyme frequencies, by site, for polymorphic loci.

		C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4
AAT-1	A	0.079	0.000	0.050	0.000	0.000	0.025	0.000	0.000	0.025	0.000	0.000	0.026
	B	0.921	0.975	0.950	1.000	1.000	0.975	1.000	1.000	0.975	1.000	1.000	0.974
	C	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EST-6	B	1.000	0.972	0.975	0.969	1.000	0.974	0.964	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.028	0.025	0.031	0.000	0.026	0.036	0.000	0.000	0.000	0.000	0.000
GP-1	A	0.029	0.000	0.000	0.000	0.000	0.000	0.028	0.211	0.000	0.056	0.000	0.029
	B	0.941	1.000	1.000	1.000	1.000	1.000	0.972	0.789	0.941	0.889	1.000	0.971
	C	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.056	0.000	0.000
IDH-1	A	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.024	0.000	0.050	0.000	0.026
	B	0.000	0.000	0.075	0.095	0.000	0.000	0.056	0.024	0.000	0.000	0.000	0.000
	C	1.000	0.975	0.900	0.881	0.964	1.000	0.944	0.929	1.000	0.950	1.000	0.974
	D	0.000	0.000	0.025	0.024	0.036	0.000	0.000	0.024	0.000	0.000	0.000	0.000
IDH-2	A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026
	B	1.000	1.000	1.000	1.000	1.000	1.000	0.944	1.000	1.000	1.000	1.000	0.974
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.056	0.000	0.000	0.000	0.000	0.000
MDH-1	A	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	B	1.000	1.000	0.975	1.000	1.000	1.000	0.972	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000
MDH-2	B	1.000	0.975	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MPI	A	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.088	0.053
	B	1.000	0.975	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975	0.912	0.947
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEP-A	A	0.000	0.025	0.025	0.000	0.000	0.000	0.000	0.095	0.000	0.000	0.000	0.000
	B	0.971	0.975	0.975	1.000	1.000	1.000	1.000	0.905	1.000	1.000	1.000	1.000
	C	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGD	A	0.053	0.000	0.025	0.000	0.026	0.025	0.000	0.000	0.000	0.000	0.000	0.000
	B	0.053	0.175	0.150	0.095	0.158	0.100	0.111	0.150	0.175	0.111	0.167	0.132
	C	0.895	0.800	0.825	0.857	0.816	0.875	0.861	0.825	0.825	0.889	0.833	0.868
	D	0.000	0.000	0.000	0.048	0.000	0.000	0.028	0.025	0.000	0.000	0.000	0.000
	E	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGM-1	B	0.000	0.029	0.025	0.000	0.000	0.026	0.000	0.000	0.025	0.000	0.026	0.000
	C	0.974	0.941	0.850	1.000	0.917	0.947	1.000	0.895	0.975	0.921	0.921	0.947
	D	0.026	0.029	0.125	0.000	0.083	0.026	0.000	0.105	0.000	0.079	0.053	0.053
PGM-2	A	0.000	0.000	0.025	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	B	1.000	1.000	0.950	0.947	1.000	1.000	1.000	0.952	1.000	1.000	0.895	1.000
	C	0.000	0.000	0.025	0.026	0.000	0.000	0.000	0.048	0.000	0.000	0.105	0.000

APPENDIX 5 continued.

		G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3	P4
AAT-1	A	0.029	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.025
	B	0.971	1.000	1.000	1.000	1.000	0.972	1.000	1.000	0.975	1.000	1.000	0.975
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000
EST-6	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.972	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000
GP-1	A	0.029	0.053	0.000	0.024	0.000	0.056	0.024	0.000	0.025	0.025	0.025	0.000
	B	0.971	0.921	1.000	0.976	1.000	0.944	0.976	1.000	0.975	0.975	0.925	1.000
	C	0.000	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000
IDH-1	A	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.025
	B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000
	C	1.000	0.976	1.000	0.952	0.925	1.000	0.976	0.976	1.000	1.000	1.000	0.950
	D	0.000	0.024	0.000	0.048	0.075	0.000	0.000	0.000	0.000	0.000	0.000	0.025
IDH-2	A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	B	1.000	1.000	1.000	1.000	1.000	1.000	0.976	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.000
MDH-1	A	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.0000	0.000	0.000
MDH-2	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MPI	A	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.056	0.050
	B	1.000	0.800	1.000	1.000	0.975	1.000	1.000	1.000	0.950	1.000	0.944	0.950
	C	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEP-A	A	0.000	0.024	0.025	0.000	0.025	0.028	0.024	0.000	0.000	0.000	0.000	0.000
	B	0.912	0.976	0.975	1.000	0.975	0.972	0.976	1.000	1.000	1.000	1.000	1.000
	C	0.088	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGD	A	0.000	0.000	0.000	0.028	0.025	0.000	0.000	0.000	0.000	0.025	0.000	0.053
	B	0.147	0.262	0.150	0.139	0.250	0.194	0.119	0.119	0.175	0.050	0.175	0.132
	C	0.853	0.714	0.850	0.833	0.725	0.750	0.881	0.881	0.800	0.925	0.825	0.789
	D	0.000	0.024	0.000	0.000	0.000	0.056	0.000	0.000	0.025	0.000	0.000	0.026
	E	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGM-1	B	0.094	0.000	0.000	0.056	0.125	0.059	0.000	0.000	0.825	0.250	0.763	0.083
	C	0.875	1.000	1.000	0.889	0.875	0.824	1.000	0.868	0.175	0.725	0.237	0.667
	D	0.031	0.000	0.000	0.056	0.000	0.118	0.000	0.132	0.000	0.025	0.000	0.250
PGM-2	A	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	B	1.000	1.000	1.000	0.976	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

APPENDIX 6: Habitat scores, by site, for each of the four variables listed in Table 2 scored by two people independently (as indicated by numbers 1 and 2). Site codes as in Appendix 1.

	Maximum Vegetation Height		Average Vegetation Height		Percent Vegetation Cover		Percent Cover by Trees	
Site	1	2	1	2	1	2	1	2
C1	4	4	3	3	5	5	2	2
C2	4	3	3	3	5	5	1	2
C3	3	3	3	3	5	5	2	2
C4	4	4	3	3	5	5	1	2
T1	5	5	3	4	5	5	2	3
T2	5	4	3	4	5	5	2	3
T3	5	5	4	4	5	5	2	3
T4	5	5	4	4	5	5	3	3
W1	3	5	3	3	5	5	3	4
W2	4	5	4	3	5	4	3	4
W3	4	5	3	4	5	5	3	4
W4	4	5	3	4	5	5	3	4
G1	1	2	1	2	5	3	1	1
G2	1	1	1	1	5	5	1	1
G3	1	1	1	1	5	5	1	1
G4	1	1	1	1	5	4	1	1
M1	3	5	2	3	4	3	1	1
M2	3	3	2	3	4	3	1	1
M3	3	4	2	3	4	3	1	1
M4	3	5	2	3	4	3	1	1
P1	1	2	1	1	4	3	1	1
P2	1	2	1	1	4	3	1	1
P3	1	1	1	1	4	3	1	1
P4	2	2	1	1	3	3	1	1

APPENDIX 7: Matrix of inter-site distances (km) calculated from geographic coordinates. All distances are straight-line and are rounded to the nearest km. Site codes are as indicated in Appendix 1.

C2	129											
C3	289	219										
C4	402	307	126									
T1	79	117	324	423								
T2	192	66	230	293	163							
T3	376	270	130	57	387	246						
T4	404	296	157	61	413	268	30					
W1	144	89	307	387	80	101	344	368				
W2	207	78	211	269	184	24	222	244	125			
W3	362	252	132	79	370	226	23	44	325	202		
W4	412	300	174	80	417	268	44	20	368	244	50	
G1	148	104	322	402	78	115	359	382	15	139	339	383
G2	223	93	220	271	195	32	222	242	131	17	201	241
G3	349	236	135	98	354	207	42	61	307	183	20	64
G4	450	337	206	96	454	304	79	49	404	280	88	38
M1	268	140	233	261	238	77	208	223	169	63	185	218
M2	283	157	176	195	271	113	142	160	214	89	120	157
M3	441	318	242	159	432	272	117	99	372	249	110	79
M4	501	379	287	184	493	333	157	131	433	310	157	113
P1	268	298	516	601	200	311	557	579	213	335	557	579
P2	248	254	473	552	172	260	506	527	166	284	485	526
P3	197	208	426	510	121	221	466	489	122	245	446	489
P4	236	121	282	328	188	61	276	294	111	72	254	290
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

APPENDIX 7 continued.

G2	144										
G3	321	182									
G4	418	275	101								
M1	181	47	165	250							
M2	227	84	100	192	66						
M3	385	241	109	77	206	161					
M4	445	302	162	89	266	223	61				
P1	198	338	518	613	367	422	573	632			
P2	151	285	466	560	312	368	517	575	59		
P3	107	284	428	524	280	332	486	546	91	52	
P4	119	62	235	322	72	134	277	336	296	240	211
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

APPENDIX 8: Matrix of between-site ecological distances based on difference in site PC-1 score from a PCA of Spearman rank correlation matrix of eight variables (four variables for each of two people) listed in Appendix 6. Site codes are as indicated in Appendix 1.

C2	0.60											
C3	0.50	0.10										
C4	0.50	0.20	0.10									
T1	1.60	2.30	2.10	2.10								
T2	1.40	2.00	1.90	1.80	0.20							
T3	1.90	2.50	2.40	2.30	0.30	0.50						
T4	2.00	2.60	2.50	2.40	0.40	0.60	0.10					
W1	1.30	1.90	1.80	1.70	0.30	0.10	0.60	0.70				
W2	1.50	2.20	2.00	2.00	0.10	0.10	0.30	0.50	0.30			
W3	1.90	2.50	2.40	2.40	0.30	0.50	0.00	0.10	0.60	0.40		
W4	1.90	2.50	2.40	2.40	0.30	0.50	0.00	0.10	0.60	0.40	0.00	
G1	3.70	3.00	3.10	3.20	5.30	5.10	5.50	5.70	4.90	5.20	5.60	5.60
G2	3.30	2.70	2.80	2.80	4.90	4.70	5.20	5.30	4.60	4.80	5.20	5.20
G3	3.30	2.70	2.80	2.80	4.90	4.70	5.20	5.30	4.60	4.80	5.20	5.20
G4	3.80	3.20	3.30	3.40	5.40	5.20	5.70	5.80	5.10	5.30	5.70	5.70
M1	2.10	1.50	1.60	1.60	3.70	3.50	4.00	4.10	3.40	3.60	4.00	4.00
M2	2.60	1.90	2.00	2.10	4.20	4.00	4.40	4.60	3.80	4.10	4.50	4.50
M3	2.40	1.80	1.90	1.90	4.00	3.80	4.30	4.40	3.70	3.90	4.30	4.30
M4	2.10	1.40	1.60	1.60	3.70	3.50	4.00	4.10	3.40	3.60	4.00	4.00
P1	4.40	3.70	3.80	3.90	6.00	5.80	6.20	6.40	5.60	5.90	6.30	6.30
P2	4.50	3.90	4.00	4.10	6.10	5.90	6.40	6.50	5.80	6.10	6.40	6.40
P3	4.50	3.90	4.00	4.10	6.20	5.90	6.40	6.50	5.80	6.10	6.50	6.50
P4	4.30	3.70	3.80	3.80	5.90	5.70	6.20	6.30	5.60	5.80	6.20	6.20
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

APPENDIX 8 continued.

G2	0.40										
G3	0.40	0.00									
G4	0.10	0.50	0.50								
M1	1.60	1.20	1.20	1.70							
M2	1.10	0.70	0.70	1.30	0.50						
M3	1.30	0.90	0.90	1.40	0.30	0.20					
M4	1.60	1.20	1.20	1.70	0.00	0.50	0.30				
P1	0.70	1.10	1.10	0.60	2.30	1.80	2.00	2.30			
P2	0.90	1.20	1.20	0.70	2.40	2.00	2.10	2.50	0.20		
P3	0.90	1.20	1.20	0.70	2.40	2.00	2.10	2.50	0.20	0.00	
P4	0.60	1.00	1.00	0.50	2.20	1.70	1.90	2.20	0.10	0.20	0.20
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

Appendix 9: Matrix of Nei's (1978) genetic distances (X 10^3), corrected for sample size, for all 24 sites.

C2	0.0											
C3	1.0	0.0										
C4	1.0	0.0	0.0									
T1	0.0	0.0	0.0	0.0								
T2	0.0	0.0	0.0	0.0	0.0							
T3	0.0	0.0	0.0	0.0	0.0	0.0						
T4	1.0	0.0	0.0	0.0	0.0	0.0	1.0					
W1	1.0	2.0	3.0	2.0	2.0	2.0	1.0	3.0				
W2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0			
W3	1.0	0.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0		
W4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	
G1	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0
G2	4.0	1.0	3.0	3.0	2.0	3.0	3.0	3.0	3.0	2.0	1.0	2.0
G3	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	2.0	0	1.0	0.0
G4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
M1	2.0	0.0	0.0	2.0	0.0	1.0	1.0	1.0	3.0	1.0	1.0	1.0
M2	1.0	0.0	0.0	2.0	0.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0
M3	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0
M4	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	2.0	0.0	1.0	0.0
P1	35.0	31.0	29.0	36.0	32.0	32.0	36.0	32.0	35.0	32.0	32.0	33.0
P2	3.0	3.0	2.0	4.0	3.0	2.0	3.0	3.0	5.0	2.0	3.0	3.0
P3	30.0	27.0	25.0	31.0	27.0	27.0	31.0	27.0	29.0	27.0	26.0	28.0
P4	4.0	2.0	0.0	4.0	1.0	3.0	4.0	1.0	5.0	2.0	3.0	2.0
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

Appendix 9 continued.

G2	3.0										
G3	0.0	2.0									
G4	0.0	2.0	0.0								
M1	0.0	2.0	1.0	0.0							
M2	0.0	2.0	1.0	0.0	0.0						
M3	0.0	3.0	0.0	0.0	1.0	1.0					
M4	0.0	4.0	0.0	0.0	1.0	0.0	0.0				
P1	27.0	37.0	35.0	29.0	26.0	26.0	35.0	31.0			
P2	1.0	7.0	3.0	1.0	2.0	2.0	3.0	2.0	17.0		
P3	22.0	32.0	30.0	24.0	21.0	22.0	30.0	26.0	0.0	13.0	
P4	2.0	5.0	4.0	1.0	2.0	0.0	4.0	1.0	21.0	2.0	18.0
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

Appendix 10: Matrix of Rogers' (1972) genetic distances (X 10^2) for all 24 sites.

C2	2.0											
C3	2.5	1.9										
C4	2.2	1.9	1.6									
T1	1.7	1.2	1.5	1.6								
T2	1.1	1.1	1.8	1.4	1.0							
T3	2.0	1.9	2.3	1.2	1.7	1.4						
T4	2.5	1.8	1.5	1.8	1.1	1.9	2.3					
W1	1.9	2.1	3.0	2.6	1.8	1.6	2.3	2.8				
W2	1.6	1.5	2.2	1.9	1.0	1.3	1.8	1.7	2.1			
W3	2.5	2.2	2.8	2.6	1.9	2.1	2.8	2.3	2.1	1.8		
W4	1.7	1.2	2.1	1.9	1.1	0.9	1.7	1.9	2.0	1.0	1.9	
G1	1.6	1.7	2.1	2.5	1.5	1.3	2.2	1.8	2.0	1.8	2.3	1.6
G2	2.9	2.4	3.7	3.1	2.5	2.9	2.9	3.2	2.7	2.7	2.4	2.6
G3	1.3	1.1	2.0	1.3	0.9	0.8	1.3	1.5	1.6	1.4	2.0	1.1
G4	1.8	1.5	1.6	1.6	0.6	1.2	1.7	1.4	2.0	1.2	1.8	1.4
M1	2.8	1.7	2.2	2.4	1.5	2.1	2.6	2.0	2.8	2.2	2.8	2.2
M2	2.0	1.8	1.9	2.8	1.5	1.7	2.6	1.9	2.0	2.0	2.3	2.0
M3	1.4	1.4	2.3	1.4	1.2	1.1	1.0	1.8	1.8	1.2	2.3	1.1
M4	1.7	1.6	1.5	1.7	0.7	1.0	1.7	1.3	2.2	0.9	2.2	1.1
P1	5.7	4.7	5.4	5.8	4.9	4.8	5.6	5.7	5.6	5.2	5.4	5.0
P2	2.1	2.6	2.9	2.7	2.0	1.7	2.5	2.8	2.8	2.0	2.9	2.3
P3	5.2	4.8	5.4	5.7	4.5	4.8	5.5	5.3	4.9	4.5	4.5	4.6
P4	3.0	2.3	2.3	3.0	1.8	2.2	3.2	2.4	3.2	2.2	3.0	1.9
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

Appendix 10 continued.

G2	3.1										
G3	1.3	2.1									
G4	1.3	2.7	1.2								
M1	1.9	2.3	1.7	1.5							
M2	1.4	2.5	1.6	1.5	1.7						
M3	1.5	2.3	0.5	1.3	2.1	1.9					
M4	1.5	3.0	1.1	1.0	1.9	1.5	1.1				
P1	4.8	6.0	5.1	4.8	5.0	4.6	5.4	5.0			
P2	1.8	3.9	2.0	1.7	2.4	2.1	2.0	1.6	4.0		
P3	4.5	5.4	4.7	4.5	4.7	4.4	5.0	4.5	1.0	3.6	
P4	2.5	3.5	2.5	2.0	2.3	2.0	2.7	1.8	4.1	2.3	4.0
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

APPENDIX 11: Matrix of between-site Mahalanobis distances using eight external characters. Site codes are as indicated in Appendix 1.

C2	1.55											
C3	2.65	2.41										
C4	1.62	1.55	2.33									
T1	1.66	2.51	3.19	1.67								
T2	2.44	2.58	3.27	1.26	1.75							
T3	2.91	2.83	4.02	2.04	2.28	1.78						
T4	2.03	2.46	3.18	1.24	1.57	1.26	1.86					
W1	2.17	1.99	3.63	1.80	2.05	2.07	1.70	2.26				
W2	2.49	2.17	3.90	1.87	2.41	1.82	2.37	2.25	1.77			
W3	3.13	3.33	3.96	2.14	2.20	1.89	2.49	1.70	2.74	2.38		
W4	3.28	3.41	3.97	2.19	2.28	1.70	2.60	1.85	2.90	2.28	0.65	
G1	4.13	3.77	5.44	3.82	4.08	3.90	3.75	4.32	2.51	2.78	3.99	4.12
G2	3.53	3.23	4.09	2.66	3.04	2.65	2.85	3.35	2.15	2.38	2.93	2.91
G3	3.09	3.16	3.85	2.12	2.02	1.91	2.06	2.29	1.98	2.33	1.65	1.75
G4	3.80	3.66	3.85	2.52	2.75	2.01	2.97	2.70	3.13	2.67	1.83	1.38
M1	5.04	4.32	5.38	4.07	4.46	3.94	3.96	4.66	3.43	3.23	3.85	3.71
M2	4.93	4.43	4.75	3.60	3.99	3.16	3.57	4.02	3.66	3.42	3.17	2.84
M3	4.73	3.96	4.58	3.41	4.04	3.15	3.32	3.94	3.47	3.08	3.34	3.03
M4	4.50	3.97	4.34	2.98	3.69	2.52	2.99	3.16	3.46	2.99	2.42	2.09
P1	6.74	6.05	7.34	6.10	6.27	6.02	5.76	6.67	4.97	5.05	5.88	5.82
P2	6.13	5.51	6.84	5.43	5.73	5.32	5.21	5.97	4.40	4.31	5.13	5.10
P3	6.32	5.55	6.77	5.82	6.01	5.92	5.58	6.57	4.68	4.99	6.05	6.00
P4	5.67	5.24	6.46	4.96	5.13	4.78	4.55	5.39	3.79	4.09	4.62	4.66
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

APPENDIX 11 continued.

G2	2.34										
G3	3.18	1.63									
G4	4.15	2.46	1.72								
M1	2.74	2.11	2.93	3.02							
M2	4.04	2.38	2.44	1.68	2.02						
M3	4.00	2.47	2.70	2.12	1.92	1.21					
M4	4.32	2.85	2.41	1.43	2.87	1.51	1.56				
P1	3.29	3.91	4.86	5.27	2.38	4.20	4.19	5.16			
P2	2.48	3.24	4.25	4.68	1.96	3.78	3.82	4.55	1.22		
P3	3.45	3.74	4.82	5.37	2.61	4.35	4.14	5.34	1.53	2.27	
P4	2.08	2.75	3.58	4.28	2.12	3.50	3.77	4.25	2.00	1.31	2.75
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

APPENDIX 12: Matrix of between-site Mahalanobis distance matrices using twelve skeletal characters. Site codes as indicated in Appendix 1.

C2	2.09											
C3	2.32	2.11										
C4	1.69	1.97	1.98									
T1	2.39	2.07	2.68	2.40								
T2	2.90	1.47	2.72	2.61	1.81							
T3	1.91	1.86	2.00	1.93	1.57	1.85						
T4	2.67	2.67	2.88	3.09	1.65	2.32	1.83					
W1	3.06	2.47	3.85	3.21	2.04	2.09	2.77	2.75				
W2	2.80	1.95	3.30	2.48	1.84	1.73	2.48	2.88	1.09			
W3	3.38	2.13	3.45	3.21	2.49	1.49	2.61	2.84	1.68	1.58		
W4	2.75	2.42	2.67	2.50	1.79	1.81	1.54	2.01	2.21	2.04	1.84	
G1	4.57	3.57	4.97	4.61	3.39	2.86	3.91	3.63	1.89	2.43	1.98	3.13
G2	3.86	3.15	4.34	3.93	2.71	2.37	3.19	3.09	1.59	2.04	1.61	2.27
G3	3.86	3.05	3.81	3.62	2.64	2.32	2.80	3.39	2.22	2.10	1.83	1.92
G4	3.57	2.54	3.03	3.13	2.61	1.63	2.30	2.77	2.53	2.34	1.69	1.52
M1	4.43	3.69	4.74	4.56	3.26	2.65	3.55	3.45	2.30	2.83	2.15	2.63
M2	4.18	3.04	3.59	3.94	3.38	2.13	3,16	3.32	3.30	3.15	2.14	2.51
M3	4.80	4.09	4.39	4.14	4.00	3.03	3.57	4.20	3.86	3.63	3.00	2.64
M4	3.93	3.31	3.70	3.55	3.60	2.61	3.01	3.78	3.29	3.10	2.37	2.19
P1	7.41	6.20	7.28	7.69	6.36	5.78	6.89	6.36	5.22	5.71	4.85	6.11
P2	6.03	5.25	6.61	6.17	4.98	4.50	5.53	5.00	3.39	4.05	3.41	4.50
P3	6.98	6.04	7.09	7.44	5.98	5.65	6.47	5.81	4.85	5.54	4.77	5.70
P4	6.24	5.33	6.79	6.45	5.03	4.45	5.50	5.18	3.59	4.29	3.62	4.67
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

APPENDIX 12 continued.

G2	1.64										
G3	2.50	1.78									
G4	2.76	2.27	1.90								
M1	2.17	1.28	2.06	2.38							
M2	3.28	2.50	2.64	1.68	2.38						
M3	4.03	3.24	2.86	2.28	2.94	2.52					
M4	3.70	2.85	2.49	2.05	2.74	2.30	1.47				
P1	4.03	4.58	5.18	5.57	4.62	5.20	6.68	6.16			
P2	2.14	2.58	3.89	4.26	2.80	4.24	4.85	4.66	3.72		
P3	3.68	4.30	5.06	5.35	4.38	5.27	6.68	6.14	1.66	3.45	
P4	2.39	2.76	3.71	4.29	2.41	4.26	4.78	4.69	3.84	1.73	3.54
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

APPENDIX 13: Matrix of between-site Mahalanobis distance matrices using three song frequency and one temporal character. Site codes as indicated in Appendix 1.

C2	1.46											
C3	2.32	1.06										
C4	4.49	4.84	4.64									
T1	3.26	2.01	1.77	5.34								
T2	2.22	1.60	2.24	5.15	1.76							
T3	0.93	0.83	1.51	4.50	2.78	2.13						
T4	1.76	0.80	1.47	4.87	1.59	0.83	1.44					
W1	2.43	1.80	1.31	4.52	3.06	3.31	1.64	2.50				
W2	3.09	1.95	1.84	5.78	2.63	2.68	2.27	2.23	2.37			
W3	1.83	1.57	1.86	4.97	3.39	2.93	1.10	2.26	1.49	1.89		
W4	4.41	3.35	2.95	6.58	3.85	4.20	3.54	3.73	3.06	1.53	2.82	
G1	2.11	1.63	1.54	4.69	3.24	3.09	1.27	2.35	0.92	1.91	0.65	2.69
G2	3.17	2.45	2.25	5.69	3.72	3.73	2.35	3.08	1.84	1.51	1.39	1.61
G3	3.66	2.92	2.61	5.87	4.04	4.14	2.81	3.52	2.17	1.75	1.86	1.38
G4	3.71	3.27	3.45	6.20	4.44	3.89	3.12	3.59	3.46	1.97	2.35	2.13
M1	3.13	2.42	1.86	4.98	3.55	3.87	2.27	3.10	0.96	2.18	1.66	2.38
M2	3.87	3.47	3.12	4.96	4.63	4.59	3.13	4.00	2.51	2.66	2.30	2.43
M3	4.24	3.94	3.96	6.51	5.31	4.96	3.62	4.47	3.48	2.79	2.57	2.38
M4	3.94	3.81	4.17	5.92	4.79	3.83	3.62	3.83	4.43	2.99	3.27	3.55
P1	3.83	2.72	2.21	6.04	3.31	3.77	2.92	3.18	2.24	1.26	2.27	0.87
P2	3.39	3.77	4.19	5.52	5.39	4.40	3.21	4.12	3.88	3.46	2.61	3.93
P3	3.32	3.23	3.20	4.96	4.70	4.28	2.74	3.75	2.63	2.66	1.88	2.80
P4	1.67	1.97	2.55	5.01	3.86	2.99	1.35	2.49	2.30	2.37	0.89	3.36
	C1	C2	C3	C4	T1	T2	T3	T4	W1	W2	W3	W4

APPENDIX 13 continued.

G2	1.28										
G3	1.69	0.52									
G4	2.63	1.94	1.96								
M1	1.08	1.24	1.39	3.03							
M2	2.05	1.69	1.47	2.30	1.82						
M3	2.74	1.84	1.66	1.47	2.82	1.88					
M4	3.60	3.39	3.49	1.71	4.24	3.33	2.93				
P1	2.02	1.15	1.09	2.41	1.63	2.24	2.58	3.79			
P2	3.01	3.02	3.15	2.03	3.70	2.74	2.26	2.00	3.93		
P3	1.90	1.76	1.76	1.85	2.19	1.02	1.56	2.73	2.64	1.76	
P4	1.47	2.03	2.44	2.24	2.48	2.63	2.61	2.82	2.96	1.96	1.88
	G1	G2	G3	G4	M1	M2	M3	M4	P1	P2	P3

LITERATURE CITED

Aldrich, J.W. 1984. Ecogeographical variation in size proportions of the Song Sparrow (*Melospiza melodia*). Ornithol. Monogr. 35: 1-134.

Aquadro, C.F. and J.C. Avise. 1982. Evolutionary genetics of birds. VI. A reexamination of protein divergence using varied electrophoretic conditions. Evolution 36: 1003-1019.

Avise, J.C., J.C. Patton and C.F. Aquadro. 1982a. Evolutionary genetics of birds I. Relationships among North American thrushes and allies. Auk 97:135-147.

Avise, J.C., J.C. Patton and C.F. Aquadro. 1982b. Evolutionary genetics of birds II. Conservative protein evolution in North American sparrows and relatives. Syst. Zool. 29: 323-334.

Bailey, R.C. and J. Byrnes. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Syst. Zool. 39: 124-130.

Baker, A.J., M.D. Dennison, A. Lynch and G. LeGrand. 1990. Genetic divergence in peripherally isolated populations of chaffinches in the Atlantic Islands. Evolution 44: 981-999.

Baker, M.C. 1974. Genetic structure of two populations of White-crowned Sparrows with different song dialects. Condor 76: 351-356.

Baker, M.C. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). Evolution 29: 226-241.

Baker, M.C. 1982. Genetic population structure and vocal dialects in *Zonotrichia* (Emberizidae). Pp. 209 -235 *in* Acoustic communication in birds, vol. 2 (D.E. Kroodsma and E.H. Miller, Eds.). New York, Academic Press.

Baker, M.C., A.E.M. Baker, M.A. Cunningham, D.B. Thompson and D.F. Tomback. 1984a. Reply to "Allozymes and song dialects: A reassessment." Evolution 38: 449-451.

Baker, M.C. and M.A. Cunningham. 1985. The biology of bird-song dialects. Behav. Brain Sci. 8: 85-133.

Baker, M.C., M.A. Cunningham and D.B. Thompson. 1984b. Cultural and genetic differentiation of two subspecies of White-crowned Sparrow. Condor 86: 359-367.

Baker, M.C. and L.R. Medwalt. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*. Evolution 32: 712-722.

Baker, M.C., D.B. Thompson, G.L. Sherman, M.A. Cunningham and D.F. Tomback. 1982.

Allozyme frequencies in a linear series of song dialect populations. Evolution 36: 1020-1029.

Balaban, E. 1988. Cultural and genetic variation in Swamp Sparrows (*Melospiza georgiana*) I. Song variation, genetic variation, and their relationship. Behaviour 105: 250-291.

Barrowclough, G.F. 1980. Genetic and phenotypic differentiation in a wood warbler (Genus *Dendroica*) hybrid zone. Auk 97:655-668.

Barrowclough, G.F. 1983. Biochemical studies of microevolutionary processes. Pp. 223-261 *in* Perspectives in ornithology (A.H. Brush and G.A. Clark, Eds.). New York, Cambridge Univ. Press.

Barrowclough, G.F. and K.W. Corbin. 1978. Genetic variation and differentiation in the Parulidae. Auk 95: 691-702.

Berlocher, S.H. and G.L. Bush. 1982. An electrophoretic analysis of *Rhagoletis* (Diptera: Tephritidae) phylogeny. Syst. Zool. 31: 136-155.

Boag, P.T. and P.R. Grant. 1981. Intense natural selection in a population of Darwin's finches (*Geospizinae*) in the Galapagos. Science 214: 82-85.

Bogart, J.P. 1982. Ploidy and genetic diversity in Ontario salamanders of the *Ambystoma jeffersonianum* complex revealed through an electrophoretic examination of larvae. Can. J. Zool. 60: 848-855.

Bowen, B.S. 1982. Temporal dynamics of microgeographic structure of genetic variation in *Microtus californicus* . J. Mamm. 63: 625-638.

Bowman, R.I. 1979. Adaptive morphology of song dialects in Darwin's finches. J. Ornithol. 120: 353-389.

Bowman, R.I. 1983. The evolution of song in Darwin's finches. Pp. 237-538 *in* Patterns of evolution in Galapagos organisms (R.I. Bowman, M. Berson and A.E. Leviton, Eds.). San Francisco, AAAS, Pacific Division.

Bryant, E.H. 1986. On the use of logarithms to accommodate scale. Syst. Zool. 35: 552-559.

Campbell,N.A. and W.R. Atchley. 1981. The geometry of canonical variate analysis. Syst. Zool. 30: 268-280.

Chapman, F.M. 1940. The post-glacial history of *Zonotrichia capensis* . Bull. Amer. Mus. Nat. Hist. 77: 381-438.

Clayton, J.W. and D.N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Bd. Canada 29: 1169-1172.

Corbin, K.W. 1981. Genic heterozygosity in the White-crowned Sparrow: a potential index to boundaries between subspecies. Auk 98: 669-680.

Corbin, K.W. 1987. Geographic variation and speciation. Pp. 321-353 *in* Avian genetics A population ecology approach. (F. Cook and P.A. Buckley, Eds.). New York, Academic Press.

Corbin, K.W., C.G. Sibley and A. Ferguson. 1979. Genic changes associated with the establishment of sympatry in orioles of the genus *Icterus*. Evolution 33: 624-633.

Cunningham, M.A. and M.C. Baker. 1983. Vocal learning in White-crowned Sparrows: sensitive phase and song dialects. Behav. Ecol. Sociobiol. 13: 259-269.

Douglas, M.E. and J.A. Endler. 1982. Quantitative matrix comparisons in ecological and evolutionary investigations. J. Theor. Biol. 99: 777-795.

Egli, W. 1971. Investigaciones sobre el canto de *Zonotrichia capensis chilensis* (Meyen) (Aves, Passeriformes) Boi. Mus. Nac. Hist. Nat. Chile 32: 173-190.

Elston, R.C. and R. Forthofer. 1977. Testing for Hardy-Weinberg equilibrium in small samples. Biometrics 33: 536-542.

Endler, J.A. 1976. Natural selection in the wild. Monogr. Pop. Biology. 21. 336 pp., Princeton, New Jersey, Princeton Univ. Press.

Endler, J.A. 1977. Geographic variation, speciation, and clines. Princeton, New Jersey, Princeton Univ. Press.

Evans, P.G.H. 1987. Electrophoretic variability of gene products. Pp. 105-162 *in* Avian genetics A population ecology approach. (F. Cook and P.A. Buckley, Eds.). New York, Academic Press.

Glover, D.G., M.H. Smith, L. Ames, J. Joule and J.M. Dubach. 1972. Genetic variation in pika populations. Can. J. Zool. 55: 1841-1845.

Gorman, G.C. and Y.J. Kim. 1976. *Anolis* lizards of the Eastern Caribbean: A case study in evolution. II. Genetic relationships and genetic variability of the *bimaculatus* group. Syst. Zool. 25: 62-77.

Grant, B.R. 1985. Selection on bill characters in a population of Darwin's finches: *Geospiza conirostris* in Isla Genovesa, Galapagos. Evolution 39: 523-532.

Hafner, D.J. and K.E. Petersen. 1985. Song dialects and gene flow in the White-crowned Sparrow, *Zonotrichia leucophrys nuttalli*. Evolution 39: 687-694.

Handford, P. 1980. Aspects of the annual cycle in highland populations of the Rufous-collared Sparrow, *Zonotrichia capensis* . Auk 97: 400-403.

Handford, P. 1981. Vegetational correlates of variation in the song of *Zonotrichia capensis*. Behav. Ecol. Sociobiol. 8: 203-206.

Handford, P. 1983. Continental patterns of morphological variation in a South American sparrow. Evolution 37: 920-930.

Handford, P. 1985. Morphological relationships among subspecies of the Rufous-collared Sparrow, *Zonotrichia capensis* . Can. J. Zool. 63: 2383-2388.

Handford, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis* , in northwestern Argentina, Can. J. Zool. 66: 2658-2670.

Handford, P. and S.C. Lougheed. 1991. Variation in length and pitch characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis* , with respect to habitat, trill dialects and body size. Condor. in press.

Handford, P. and F. Nottebohm. 1976. Allozymic and morphological variation in population samples of Rufous-collared Sparrows, *Zonotrichia capensis* , in relation to vocal dialects. Evolution 30: 802-817.

Harris, H. and D.A. Hopkinson. 1976. Handbook of enzyme electrophoresis in human genetics. Amsterdam, North-Holland Publ. Co.

Harris, M.A. and R.E. Lemon. 1972. Songs of Song Sparrows (*Melospiza melodia*): individual variation and dialects. Can. J. Zool. 50: 301-309.

Hartl, D.L. 1988. A primer of population genetics. 2nd ed. Sinauer, Sunderland, Mass.

Hubby, J.L. and R.C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura.* Genetics 54: 577-594.

International Union of Biochemistry. 1984. Enzyme nomenclature. 2nd ed. New York, Academic Press.

Johnson, N.K. and J.A. Marten. 1988. Evolutionary genetics of flycatchers II. Differentiation in the *Empidonax difficilis* complex Auk 105: 177-191.

Johnson, N.K. and R.M. Zink. 1983. Speciation in sapsuckers (*Sphyrapicus*): I. Genetic differentiation. Auk 100: 871-884.

Jones, J.S., R.K. Selander and G.D. Schnell. 1980. Patterns of morphological and molecular polymorphism in the land snail *Cepaea nemoralis* . Biol. J. Linn. Soc. 14: 359-387.

Kilpatrick, C.W. 1981. Genetic structure of insular populations. Pp. 28-59 *in* Mammalian population genetics (M.H. Smith and J. Joule, Eds.) . Athens, Georgia, Univ. Georgia Press.

King, J.R. 1972. Variation in the song of the Rufous-collared Sparrow, *Zonotrichia capensis* , in northwestern Argentina. Z. Tierpsychol. 30: 344-373.

Kroodsma, D.E. and J.R. Baylis. 1982. Appendix: a world survey of evidence for vocal learning in birds. Pp. 311-337 *in* Acoustic communication in birds, vol. 2 (D.E. Kroodsma and E.H. Miller, Eds.). New York, Academic Press.

Kruskal, J.B. and M. Wish. 1976. Multidimensional scaling. London, Sage Publications.

Lagercrantz, U. and N. Ryman. 1990. Genetic structure of Norway Spruce (*Picea abies*): concordance of morphological and allozymic variation. Evolution 44: 38-53.

Legendre, P. and A. Vaudor. 1985. R-package. Universite de Montreal, Montreal.

Lewontin, R.C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Nat. 123: 115-124.

Lewontin, R.C. and J.L. Hubby. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura* . Genetics 54: 595-609.

Lougheed, S.C., T.W. Arnold and R.C. Bailey. 1991. Measurement error of external and skeletal variables in birds and its effect on principal components. Auk 108: 432-436.

Lougheed, S.C. and P. Handford. 1989. Night songs in the Rufous-collared Sparrow. Condor 91: 462-465.

Lougheed, S.C., A.J. Lougheed, M. Rae and P. Handford. 1989. Analysis of a dialect boundary in chaco vegetation in the Rufous-collared Sparrow. Condor 91: 1002-1005.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Canc. Res. 27: 209-220.

Marcus, L. 1986. LESSOFT software. Amer. Mus. Nat. Hist. New York.

Mayr, E. 1942. Systematics and the origin of species. New York, Columbia University Press.

Mayr, E. 1963. Animal species and evolution. Cambridge, Mass., Harvard University

Press.

Miller, A.M. and V.D. Miller. 1968. The behavioral ecology and breeding biology of the Andean Sparrow, *Zonotrichia capensis* . Caldasia 10: 83-154.

Morton, E.S. 1975. Ecological sources of selection on avian sounds. Amer. Nat. 109: 17-34.

Morton, E.S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behavior 99: 65-86.

Morton, E.S., S.L. Gish and M. van der Voort. 1986. On the learning of degraded and undegraded songs in the Carolina Wren. Anim. Behav. 34: 815-820.

Mundinger, P.C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations in birds. Pp. 147-208 *in* Acoustic communication in birds, vol. 2 (D.E. Kroodsma and E.H. Miller, Eds.). New York, Academic Press.

Murphy, R.W., J.W. Sites, D.G. Buth and C.H. Haufler. 1990. Proteins I: isozyme electrophoresis. Pp. 45-126 *in* Molecular systematics (D.M. Hillis and C. Moritz,Eds.) Sunderland, Mass., Sinauer Assoc. Inc.

Nei, M. 1972. Genetic distance between populations. Amer. Nat. 106: 283-292.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

Nottebohm, F. 1969. The song of the Chingolo, *Zonotrichia capensis* , in Argentina: description and evaluation of a system of dialects. Condor 71: 299-315.

Nottebohm, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. Amer. Nat. 109: 605-624.

Nottebohm, F. 1985. Sound transmission, signal salience and song dialects. Behav. Brain Sci. 8: 112-113.

Nottebohm, F. and R.K. Selander. 1972. Vocal dialects and gene frequencies in the Chingolo sparrow (*Zonotrichia capensis*). Condor 74: 137-143.

Olrog, C.C. 1979. Nueva lista de la avifauna Argentina. Opera Lilloana 27. Tucuman, Argentina, Inst. Miguel Lillo.

Patton, J.L. and S.Y. Yang. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. Evolution 31: 697-720.

Payne, R.B. 1981. Population structure and social behavior: models for testing ecological significance of song dialects in birds. Pp. 108-120 *in* Natural selection and social behavior: recent research and new theory (R.D. Alexander

and D.W. Tinkle, Eds.). New York, Chiron Press.

Paytner, R.A. (Ed.) 1970. Checklist of the birds of the world. vol. 13. Mus. Comp. Zool. Cambridge, Mass.

Paytner, R.A. 1985. Ornithological gazetteer of Argentina. Harvard Univ. Cambridge, Mass.

Penny, D.F. and E.G. Zimmerman. 1976. Genic divergence and local population differentiation by random drift in the pocket gopher genus *Geomys*. Evolution 30: 473-483.

Pimentel,R.A. 1979. Morphometrics. Dubuque, Iowa, Kendall/ Hunt Co.

Richardson, B.J., P.R. Baverstock and M. Adams. 1986. Allozyme electrophoresis. A handbook for animal systematics and population studies. New York, Academic Press.

Rising, J.D. 1988. Patterns and evolutionary significance of geographic variation in the schistacea group of Fox Sparrow (*Passerella iliaca*). R.M. Zink 1986. A review. Auk 105: 217-219.

Rising, J.D. and K.M. Sommers. 1989. The measurement of overall body size in birds. Auk 106: 666-674.

Robins, J.D. and G.D. Schnell. 1971. Skeletal analysis of the *Ammodramus -Ammospiza* grassland sparrow complex: a numerical taxonomic study. Auk 88: 567-590.

Rockwell, R.F. and G.F. Barrowclough. 1987. Gene flow and the genetic structure of populations. Pp. 223-255 *in* Avian genetics A population ecology approach. (F. Cook and P.A. Buckley, Eds.). New York, Academic Press.

Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. 7213: 145-153.

Rothstein, S.I. and R.C. Fleischer. 1987. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. Condor 89: 1-23.

SAS Institute Inc. 1985. SAS statistical software version 5. Cary, NC.

Schnell, G.D., N.L. Kennedy and T.L. Best. 1978. Interspecific morphological variation in kangaroo rats (*Dipodomys*): Degrees of concordance with genic variation. Syst. Zool. 27: 34-48.

Schnell, G.D. and R.K. Selander. 1981. Environmental and morphological correlates of genetic variation in mammals. Pp. 28-59 *in* Mammalian population genetics (M.H. Smith and J. Joule, Eds.). Athens, Georgia, Univ. Georgia Press.

Sene, F.M. and H.L. Carson. 1977. Genetic variation in Hawaiian *Drosophila* . IV Allozyme similarity between *D. silvestris* and *D. heteroneura* from islands of Hawaii. Genetics 86: 187-198.

Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson and J.B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus* -- I. variation in the old-field mouse (*Peromyscus polionotus*). Univ. Texas Publ. 7103: 49-90.

Shaw, C.R. and R. Prasad. 1070. Starch gel electrophoresis of enzymes -- a compilation of recipes. Biochem. Genet. 4: 297-320.

Seigel, S. 1956. Nonparametric statistics for the behavioural sciences. Tokyo, McGraw-Hill Kogakusha Ltd.

Slatkin, M. 1987. Gene flow and the geographic structure of populations. Science 236: 787-792.

Sokal, R.R. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool. 28: 227-232.

Sokal, R.R. and R.C. Rinkel. 1963. Geographic variation of the alate *Pemphigus populi -transversus* in eastern North America. Univ. Kans. Sci. Bull. 44: 467-507.

Stearns, S., G. de Jong and B, Newman. 1991. The effects of phenotypic plasticity on genetic correlations. Trends Ecol. Evol. 6: 122-126.

Swofford, D.L. and R.K. Selander. 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72: 281-283.

Thompson, D.B. 1990. Different spatial scales of adaptation in climbing behavior of *Peromyscus maniculatus* . Geographic variation, natural selection, and gene flow. Evolution 44: 952-965.

Tomback, D.F. and M.C. Baker. 1984. Assortative mating by White-crowned Sparrows at song dialect boundaries. Anim. Behav. 32: 465-469.

Tomback, D.F., D.B. Thompson and M.C. Baker. 1983. Dialect discrimination by White-crowned Sparrows: reactions to near and distant dialects. Auk 100: 452-460.

Tubaro, P.L. 1990. Aspectos causales y funcionales de las patrones de variacion del canto del chingolo (*Zonotrichia capensis*). Ph.D. thesis. University of Buenos Aires, Buenos Aires.

Turner, J.R.G. M.S. Johnson and W.F. Eanes. 1979. Contrasted modes of evolution in the same genome: Allozymes and adaptive change in *Heliconius* . Proc. Nat. Acad. Sci. U.S.A. 76: 1924-1928.

Verfoorst, F. 1982. Conservacion de la vegetacion natural en la Republica Argentina. Fund. Miguel Lillo Ser. Conserv. Nat. Nº1.

Wiley, R.H. and D.G. Richards. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 132-182 *in* Acoustic communication in birds, vol. 1 (D.E. Kroodsma and E.H. Miller, Eds.). New York, Academic Press.

Wilkinson, L. 1987. SYSTAT: The System for Statistics. Evanston, IL, SYSTAT Inc.

Workman, P.L. and J.D. Niswander. 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. Amer. J. Human Genet. 22: 24-49.

Wright, S. 1931. Evolution on Mendelian populations. Genetics 16: 97-159.

Wright, S. 1940. Breeding structure of populations in relation to speciation. Amer. Nat. 74: 232-248.

Wright, S. 1943. Isolation by distance. Genetics 28: 114-138.

Wright, S. 1978a. Evolution and the genetics of natural populations. IV. The theory of gene frequencies. Chicago, Univ. Chicago Press.

Wright, S. 1978b. Evolution and the genetics of natural populations. IV. Variability within and among natural populations. Chicago, Univ. Chicago Press.

Zink, R.M. 1982. Patterns of genic and morphological variation among sparrows in the genera *Zonotrichia* , *Melospiza* , *Junco* , and *Passerella* . Auk 99: 632-649.

Zink, R.M. 1986. Patterns and evolutionary significance of geographic variation in the Schistacea group of Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. 40: 1-119.

Zink, R.M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. Condor 90: 72-82.

Zink, R.M. and G.F. Barrowclough. 1984. Allozymes and song dialects: a reassessment. Evolution 38: 444-448.

Zink, R.M. and J.V. Remsen. 1987. Evolutionary processes and patterns of geographic variation in birds. Pp. 1-69 *in* Current ornithology, vol. 4 (R.H. Johnston, Ed.). New York, Plenum Press.