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GENETIC VARIATION, POPULATION STRUCTURE, AND EVOLUTION OF CALIFORNIA QUAIL[1]

ROBERT M. ZINK
Museum of Zoology, Louisiana State University, Baton Rouge, LA 70803

DALE F. LOTT AND DANIEL W. ANDERSON
Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616

Abstract. We studied the genetic population structure of California Quail (*Callipepla californica*). This relatively sedentary gallinaceous species has differentiated geographically in ecological features and morphology. In California and Baja California, we obtained samples of quail (101 total birds) from a total of seven sites representing six of the eight recognized subspecies. We analyzed genetic variation at 37 protein-coding loci using starch gel electrophoresis. Levels of within population genetic variation, such as average heterozygosity per individual (3.2%), percentage of loci polymorphic (18.1%), and mean number of alleles per locus (1.32), are similar to values reported for other birds, both passerines and nonpasserines. Genotypic distributions did not differ significantly from Hardy-Weinberg expectations. Geographic partitioning of genetic variation was slight. F_{ST} (3.2%) and pairwise genetic distances among samples ($\bar{D} = 0.005$) indicated little among-sample divergence, although statistically significant geographic heterogeneity was detected at four loci. Using Slatkin's (1985a) method to estimate levels of gene flow, our data indicated that populations receive an average of 5.5 immigrants per generation. A UPGMA phenogram and a distance Wagner network indicated the existence of two weakly differentiated groups of samples, corresponding roughly to Baja California and California. However, a sample from California (Tule Lake) is genetically more similar to samples from Baja California than to its nearest geographic neighbors. We hypothesize that California Quail dispersed southward into Baja California subsequent to its junction three to five million years ago with southern California.

Key words: California Quail; electrophoresis; genetic variation; population structure; gene flow; geographic variation; taxonomy.

INTRODUCTION

The nature of genetic variation within and among natural populations is of fundamental evolutionary importance (Lewontin 1974). Electrophoretic analysis of enzyme loci has proven useful for documenting genetic variation. The relative ease of gathering data, the relatively simple genetic basis of electrophoretic patterns (allozymes), and the analytical tools of population genetics have resulted in a wealth of information about the geography and maintenance of genetic variation in many organisms (Avise and Aquadro 1982, Smith et al. 1982). Study of geographic variation at allozyme loci in birds has lagged behind that of other vertebrate groups (Barrowclough 1983, Zink and Remsen 1986). Most geographic studies of genetic variation in birds have been of north temperate passerines (Barrowclough et al. 1985), which presents a biased view of birds as a whole if passerines and nonpasserines differ in demography, population sizes, dispersal, and average ages, factors that affect the maintenance and geographic patterning of genetic variation. In this study, we assessed levels and patterns of intraspecific genetic variation in a nonpasserine bird, the California Quail (*Callipepla californica*).

The California Quail includes ecologically and morphologically distinct populations (Leopold 1977). These quail inhabit mixed woodlands, chaparral, and desert environments. Phenotypic variation in external morphological traits has been partitioned by taxonomists into seven (sometimes eight) subspecies (AOU 1957, Johnsgard 1973). The distribution of California Quail has been modified by man (Grinnell and Miller 1944, Leopold 1977, Leopold et al. 1981), but our samples are from areas that we believe have not received introductions that would bias our study. California Quail are sedentary, short-lived, and have a high reproductive potential (i.e., large clutch size, early age of first reproduction). An

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endemic subspecies on Santa Catalina Island (*C. c. catalinensis*) allowed us to describe effects of isolation on genetic divergence. Because the Baja California peninsula drifted from its previous location as part of central Mexico to its current site during the last 10 million years (see Murphy 1983), quail which live there currently are of biogeographic interest. Thus, aspects of the distribution, morphological variability, and life history of California Quail provide an important context in which to evaluate genetic variation within populations, gene flow, and the historical origin and maintenance of genetic differences between populations.

METHODS

We collected 101 California Quail from a total of seven sites (Fig. 1). A maximum of three individuals were taken from a single covey, to minimize sampling of the same families. Voucher study skins are preserved at the Department of Wildlife and Fisheries Biology, University of California, Davis, California 95616 USA. Samples of heart, liver, kidney, and muscle tissue were excised from specimens within 4 hr of collection and stored in liquid nitrogen in the field. Tissue samples were transferred to an ultra-cold freezer (−70°C) upon return from the field. Voucher tissue specimens are preserved in the Frozen Tissue Collection at the Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803 USA. Acronyms for loci follow Harris and Hopkinson (1976). Electrophoretic methods are described in Selander et al. (1971), Gutiérrez et al. (1983), and Johnson et al. (1984). (Upon request RMZ will provide precise conditions for electrophoretic experiments.) We assume that electromorphs at a locus are genetically distinct; therefore, we refer to electromorphs as alleles. Different alleles were identified by letters. We used the computer package BIOSYS-1 (Swofford and Selander 1981) for the computation of allelic and genotypic frequencies, observed (direct count) and expected (based on Hardy-Weinberg equilibrium) heterozygosities (and their standard errors), Nei's (1978) and Rogers' (1972) genetic distances, heterogeneity chi-square values for each locus, chi-square tests for departures from Hardy-Weinberg genotypic expectations within each sample, Wright's (1978) measures of population subdivision (*F*-statistics), and patterns of genetic similarity (UPGMA phenogram and distance Wagner networks). These two methods of constructing branching diagrams are essentially "phenetic" and can be interpreted as estimates of evolutionary history if rates of allozymic change are uniform (UPGMA) or heterogeneous (distance Wagner; see Farris 1981; Felsenstein 1978, 1982). To test for departures from expected Hardy-Weinberg distributions of genotype proportions within samples, we used the chi-square test with pooling of all uncommon alleles (Swofford and Selander 1981). This procedure prevents the inflation of chi-square values if cells have expected frequencies of less than one. We used Slatkin's (1985a) formula for estimating levels of gene flow, namely $\ln(p(1)) = a \ln(Nm) + b$, where $p(1)$ is the average frequency of private polymorphisms, Nm is the product of the population size and the immigration rate, and a and b are constants (−0.505 and −2.44, respectively) appropriate for use when the number of individuals analyzed per sample is 25. Because our average sample size per locality is less than 25, we performed the correction advocated by Slatkin (1985a). The value of Nm is an estimate of gene flow, namely the average number of immigrants into the average deme per generation. We followed Slatkin's suggestion of sequentially deleting samples and computing Nm based on subsets of samples to determine whether or not a genetically divergent sample might influence Nm.

RESULTS

Of the 37 presumptive genetic loci examined, 16 (43.2%) exhibited at least one heterozygous genotype in at least one population sample. Allelic frequencies at these 16 loci are given in Table 1. The 21 remaining loci were monomorphic and fixed for the same allele in all samples: Est-D, Est-1, Lap, Mdh-1, Mdh-2, Icd-2, αGpd, Got-2, Gsr, Adh, Fum, Ldh-1, Ldh-2, Ck-heart, Ck-muscle, "general proteins" 1 and 2, Gpt, Gdh, Sod-2, and Acp.

The observed and expected average heterozygosities (H), percentage of loci polymorphic (P), and the mean number of alleles per locus (A) are given in Table 1. H-values range from 0.022 (Santa Catalina Island) to 0.051 (Ensenada); the mean across all quail sampled is 0.032. P-values range from 13.5% (Santa Catalina Island and Willits) to 32.4% (Ensenada); the average over

all individuals is 43.2% and the average of population values is 18.1%. A-values range from 1.16 (Santa Catalina Island and Willits) to 1.46 (Ensenada); the average over loci and samples is 1.32.

Observed and expected genotypic proportions within population samples did not differ significantly ($P > 0.05$) from Hardy-Weinberg expectations. Values of F_{IS}, a measure of deviation from the expected number of heterozygous genotypes per locus (averaged over localities), ranged from 0.35 to −0.14, and averaged (over loci and localities) 0.13. Ten of 16 values were negative, indicating no trend toward heterozygote excess or deficiency. The F_{IS} values are thus consistent with results of the chi-square analyses.

Across localities and loci, the significant heterogeneity chi-square (94.6; df = 32; $P < 0.005$) indicated the existence of geographic differentiation. For polymorphic loci, the chi-square values (locus, df, P) were: 32.9 (La, 6, $P < 0.005$), 19.5 (Lgg, 6, $P < 0.005$), 23.1 (Np, 6, $P < 0.005$), 3.3 (Ada, 3, NS), 6.8 (Mpi, 6, NS), 0.08 (Got-1, 3, NS), and 8.87 (Pap, 3, $P < 0.05$). The following polymorphic loci were excluded because no degrees of freedom remained after pooling allelic classes with expected values of less than one: Sod-1, Eap, Icd-1, Acon, Gpi, 6Pgd, Sdh, Me, and Gda. Of the four loci exhibiting significant geographic heterogeneity (La, Lgg, Np, Pap), only La shows a geographically structured pattern of variation (Fig. 1). The patterns at La and Lgg (not shown; see Table 1) have a geographic anomaly, namely the similarity of the Tule Lake sample to that from Ensenada, instead of to its geographically more proximate sample (Willits). At La, there is a suggestion of a north to south cline in the frequency of the B allele (excluding Santa Catalina Island and Tule Lake samples).

The commonly used measure of population subdivision, Wright's (1978) F_{ST}, ranged from 0.213 (La) to 0 (six loci). The mean of these values, 0.032, indicates that only 3.2% of the variance in allelic frequencies among populations is "explained" by the geographic site of the sample. That is, over 96% of the genetic variance is contained within samples or demes. Consistent with the low F_{ST} values, pairwise genetic distance (Table 2) are very low. The average Nei's genetic distance among localities is 0.005, and the range is from 0 (3 comparisons) to 0.016 (La Paz versus Santa Catalina Island). Rogers' genetic distances are of a similar magnitude (0.016 to 0.045; Table 2).

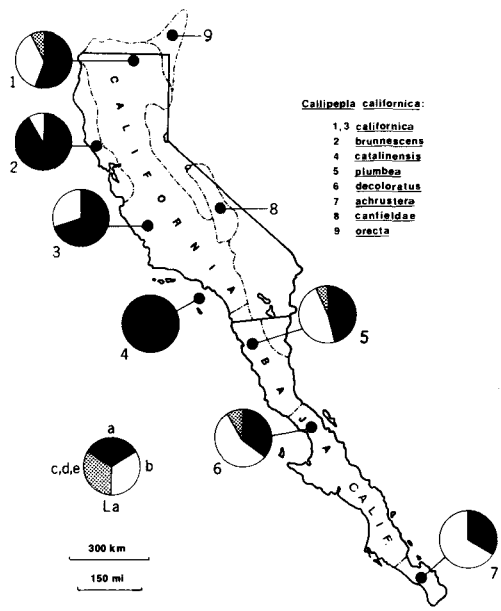

FIGURE 1. Distribution of subspecies (see Grinnell and Miller 1944, Johnsgard 1973) of California Quail and sampling sites. Samples are: 1 (Tule Lake, $n = 17$), 2 (Willits, $n = 5$), 3 (McMillan, $n = 13$), 4 (Santa Catalina Island, $n = 20$), 5 (Ensenada, $n = 17$), 6 (Catavina, $n = 17$), and 7 (La Paz, $n = 12$). Variation at the La (leucyl-alanine peptidase) locus is shown. For clarity, three allelic classes are depicted, a, b, and the pooled class for alleles c, d, and e. Frequencies of each allelic class are implied by the percentage of the circle shaded appropriately for that class. Allele c occurs only in samples 3 and 4, allele d only in sample 4, and allele e only in sample 6.

A UPGMA phenogram was used to examine patterns of genetic variation across all loci simultaneously. Its structure (Fig. 2) resembled the estimate of evolutionary history portrayed by the distance Wagner network (Fig. 3). Two groups of samples emerged from the branching diagrams, Willits–McMillan–Santa Catalina Island, and Ensenada–Tule Lake–Catavina–La Paz. In both analyses, the Tule Lake sample is most closely allied to samples from Baja California. Within the first group, the extent of differentiation on both the phenogram and distance Wagner network is too small to permit further interpretation. On the phenogram, the second group consists of two pairs of samples, Ensenada–Tule Lake, and Catavina–La Paz, the latter group linking geographically proximate samples. In contrast,

TABLE 1. Allelic frequencies, heterozygosity values, percentage of loci polymorphic, and mean number of alleles per locus for samples of California Quail. Population codes: 1 (Tule Lake), 2 (Willits), 3 (McMillan), 4 (Santa Catalina Island), 5 (Ensenada), 6 (Catavina), and 7 (La Paz); see Figure 1 for locations of these samples.

Locus (allele)	Population						
	1	2	3	4	5	6	7
La							
A	0.529	0.900	0.731	1.000	0.471	0.294	0.333
B	0.441	0.100	0.269		0.441	0.618	0.667
C					0.088	0.029	
D						0.059	
E	0.029						
Lgg							
A	0.824	0.900	1.000	0.975	0.676	0.882	0.833
B	0.176				0.176	0.059	
C		0.100		0.025	0.147	0.059	0.167
Np							
A	0.882	1.000	0.846	0.700	0.912	1.000	1.000
B			0.038				
C			0.115	0.275	0.088		
D				0.025			
E	0.118						
Sod-1							
A	1.000	1.000	1.000	1.000	1.000	1.000	0.958
B							0.042
Eap							
A	1.000	1.000	1.000	1.000	0.941	1.000	1.000
B					0.059		
Icd-1							
A	1.000	1.000	1.000	1.000	0.971	1.000	1.000
B					0.029		
Ada							
A	1.000	0.900	0.923	0.950	0.941	1.000	1.000
B		0.100	0.077	0.050	0.059		
Mpi							
A	0.971	0.900	0.808	0.825	0.853	0.941	0.833
B			0.038	0.175	0.059		
C	0.029	0.100	0.154		0.029	0.029	0.125
D					0.029	0.029	
E							0.042
F					0.029		
Got-1							
A	0.971	1.000	1.000	1.000	0.971	0.971	0.875
B					0.029		0.042
C						0.029	
D	0.029						
E							0.083
Acon							
A	1.000	1.000	1.000	1.000	0.971	1.000	1.000
B					0.029		
Gpi							
A	1.000	1.000	1.000	1.000	1.000	0.971	1.000
B						0.029	

TABLE 1. Continued.

Locus (allele)	Population 1	2	3	4	5	6	7
Pap							
a	1.000	0.900	0.962	0.900	1.000	1.000	1.000
b			0.038	0.100			
c		0.100					
6Pgd							
a	1.000	1.000	1.000	1.000	0.971	1.000	0.958
b					0.029		0.042
Sdh							
a	1.000	1.000	1.000	1.000	1.000	1.000	0.917
b							0.083
Me							
a	1.000	1.000	0.923	1.000	0.941	0.971	1.000
b			0.077		0.059		
c						0.029	
Gda							
a	0.912	1.000	1.000	1.000	0.941	1.000	1.000
b	0.088				0.059		
H_{obs}	0.029	0.032	0.027	0.022	0.051	0.024	0.038
(SE)	0.014	0.015	0.012	0.011	0.017	0.012	0.015
H_{exp}	0.036	0.032	0.038	0.029	0.060	0.029	0.044
(SE)	0.018	0.014	0.016	0.015	0.022	0.016	0.018
P^a	16.2	13.5	16.2	13.5	32.4	16.2	18.9
A^b	1.19	1.16	1.22	1.16	1.46	1.27	1.24

[a] P = Percentage of loci polymorphic.
[b] A = Average number of alleles per locus.

the distance Wagner network portrays the Tule Lake sample as a sister taxon to the La Paz–Catavina samples. Because the level of difference is slight, we decline additional interpretation.

The analysis of the level of gene flow (Table 3) indicates that the estimated number of immigrants received by each "population" is between 4.52 and 6.31 per generation; *Nm* considering all samples is 5.55. The effect of sequentially removing samples is not great. Therefore, level of gene flow seems consistent throughout the range.

DISCUSSION

LEVELS OF GENETIC VARIATION

Although protein-coding loci comprise a small fraction of the genome of eukaryotes (Lewontin

TABLE 2. Nei's (1978) unbiased genetic distances (below diagonal) and Rogers' (1972) genetic distances (above diagonal) between pairs of samples of California Quail.

Sample	1	2	3	4	5	6	7
1. McMillan	—	0.021	0.026	0.027	0.033	0.026	0.020
2. Santa Catalina	0.002	—	0.039	0.038	0.045	0.035	0.021
3. Ensenada	0.003	0.009	—	0.024	0.029	0.020	0.034
4. Catavina	0.005	0.015	0.001	—	0.016	0.017	0.028
5. La Paz	0.005	0.016	0.001	0.000	—	0.026	0.034
6. Tule Lake	0.002	0.009	0.000	0.001	0.002	—	0.029
7. Willits	0.000	0.002	0.005	0.008	0.008	0.004	—

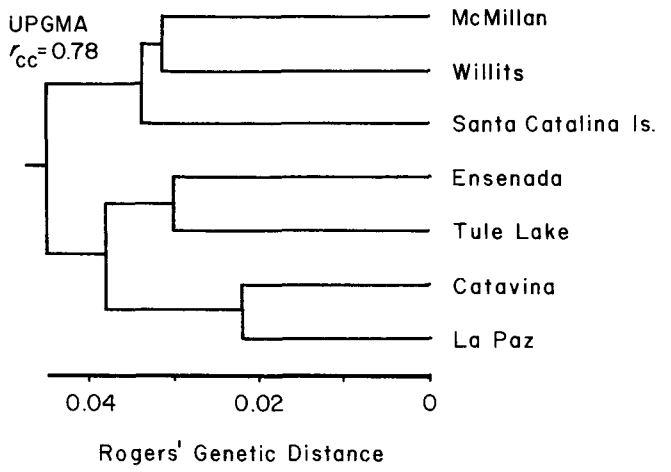

FIGURE 2. UPGMA phenogram (Sneath and Sokal 1973) using Rogers' genetic distances. r_{cc} = cophenetic correlation coefficient.

1974), and although these loci may or may not contribute to the expression of phenotypic traits that vary geographically, such as color or bill size (Zink et al. 1985), analyses of genetic variation at these loci contribute to our understanding of genetic structuring of natural populations (Barrowclough 1983).

The relatively few intraspecific surveys of avian allozymic variation deal mostly with passerine birds (Johnson and Zink 1983), which may differ from nonpasserines in aspects that influence the accrual and patterning of genetic variation, such as potentially greater age of nonpasserine species, fluctuations in population size (e.g., see Barrowclough and Shields 1984), time of isolation of populations, and levels and patterns of gene flow.

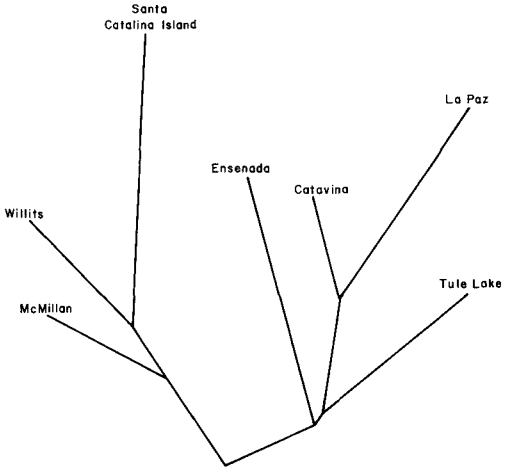

FIGURE 3. Optimized distance Wagner network, rooted at the midpoint of the longest inter-taxon distance, based on Rogers' genetic distance. The low Farris' *f*, 0.027, and the high cophenetic correlation coefficient, 0.98, suggest that this diagram is an accurate summary of the genetic distance matrix. The length of the Tule Lake branch corresponds to 0.01 units of Rogers' distance.

In our study of California Quail, the percentage of loci that were polymorphic, the average number of alleles per locus and the lack of significant departures from Hardy-Weinberg expected genotypic proportions are consistent with results of other genetic surveys of passerine and nonpasserine birds (e.g., Johnson and Zink 1983, Zink 1986). The range of H among populations, 2.2 to 5.1%, and heterozygosity over all individuals, 3.2%, are slightly lower than values reported for most birds (H = 5.3%; Barrowclough 1983) but similar to those reported by Gutiérrez et al. (1983) for other quail species. For example, the interspecific average genetic distance among avian congeners (but confamilial) is greater in nonpasserines than in passerines (Barrowclough et al. 1981: Gutiérrez et al. 1983; Zink, Hackett, and Gerwin, unpubl. data). However, this greater degree of differentiation is not reflected at the population level within nonpasserine species (Barrett and Vyse 1982, Johnson and Zink 1983, Zink and Winkler 1983), including the California Quail (this study). Thus, there is no evidence that the particular life history and demographic at-

TABLE 3. Average frequencies of private alleles in samples and subsamples, number of private alleles and estimate of (Nm), corrected for sample size; sample from Willits was omitted because sample size was too small ($n = 5$).

Location	1	2	3	4	5	6	All samples
No. birds	13	20	17	17	12	17	16[a]
No. private alleles[b]	18/1	17/1	19/4	15/4	15/4	15/3	17
$p(1)$	0.050	0.047	0.049	0.046	0.042	0.044	0.046
$(Nm)_{est}$[c]	4.52	5.59	4.95	5.62	6.31	6.12	5.55

[a] Average for the six population samples.
[b] (Number of private alleles after removal of sample)/(number of private alleles in sample).
[c] Corrected for sample size, $Nm_{est} = Nm(N_i/25)^{-1}$, where $N_i = (\Sigma N_i/6)$.

tributes of California Quail influence levels of within or among-deme genetic variation, relative to many passerines.

POPULATION STRUCTURE AND GENE FLOW

The significant chi-square values for four loci indicate geographic heterogeneity, suggesting that the 101 quail were not sampled from a single panmictic unit. However, the significance of this population structure is unclear. The low F_{ST}-value (3.2%) and average pairwise genetic distance (0.005) reveal that the degree of population structuring is slight. These values are similar to those obtained for other birds (Barrowclough 1983; Barrowclough and Johnson, in press). Thus, although there is evidence of significant genetic structure among populations of California Quail, the high level of genetic similarity also stands out as important.

Alleles segregating at allozyme loci in avian demes are most likely selectively neutral (Barrowclough et al. 1985). Slatkin's (1985a) method (with a correction for sample size) of estimating gene flow, based on the frequency of "rare" selectively neutral alleles, applied to the data for California Quail, yielded an estimate (Nm) of 5.5 immigrants per generation. This value is similar to other species for which a "moderate" level of gene flow is indicated (Slatkin 1985a). Other estimates of Nm for birds fall within a range of from 2 to 10 (Zink and Remsen 1986). Using a different method of estimation, Barrowclough (1980) suggested that high levels of gene flow typify many avian species.

The hypothesis of moderate gene flow requires scrutiny, in view of the significant geographic heterogeneity at four loci and the sedentary nature of California Quail (Leopold 1977). Slatkin (1985a) noted that if a particular sample is genetically divergent, it can bias estimation of the overall $p(1)$, and as a result, lower the estimate of Nm. In this study of quail, sequential removal of samples and recalculation of Nm had little effect on the magnitude of Nm (Table 3). For example, although the Santa Catalina Island sample is fixed for the A allele at La (Fig. 1), removal of this sample had no marked effect on Nm (5.59; Table 3). Therefore, the value of 5.5 is not influenced by a single genetically divergent sample, and lends confidence to our conclusion that gene flow among quail populations could be moderate (Slatkin 1985b). However, this conclusion needs corroboration from mark-recapture studies, and other direct and indirect methods. If gene flow is high, the slight but significant geographic heterogeneity might erode over time.

Larson et al. (1984) noted situations in which Nm reflects historical rather than current patterns of gene flow. Indeed, we doubt that at present gene flow is moderate between Santa Catalina Island and the mainland. Similarly, we doubt that immigrants are directly exchanged between Tule Lake and La Paz (i.e., the pattern of dispersal and subsequent breeding is a stepping stone and not an island one). Hence, although our data indicate moderate levels of gene flow, they may only reflect historical patterns of gene flow, not current ones. As Slatkin noted, if populations are not in genetic and demographic equilibrium, the distribution of rare alleles will not be an index of gene flow (Slatkin 1985a, 1985b). Maruyama and Fuerst (1984) predict that a characteristic of nonequilibrium populations will be an excess of rare, neutral alleles. Although we cannot speculate on whether quail populations are in equilibrium, Barrowclough et al. (1985) noted that a characteristic of many avian populations was an excess of rare alleles. These rare alleles, if found segregating in nonequilibrium populations, yield inflated or inaccurate estimates of gene flow. Therefore, genetic similarity among populations

of quail is potentially a result of gene flow, but our estimate of *Nm* may be biased by sampling of populations that are not in genetic and demographic equilibrium. Further research on the genetic characteristics of avian populations, and the applicability of Slatkin's model to them, is warranted (Rockwell and Barrowclough, in press).

PATTERNS OF GENETIC DISTANCE AND POTENTIAL EFFECTS OF INTRODUCTIONS

The absence of consistent geographic patterns of variation among loci and the low level of differentiation, suggest that the evolutionary history of California Quail has not been typified by long periods of extended isolation, which should lead to greater levels of population subdivision (i.e., higher F_{ST}) and affect all loci similarly. Inspection of the pattern of genetic similarity across all polymorphic loci (Table 2; Fig. 2) and the estimate of evolutionary history (Fig. 3) reveals two groups of samples. Although the samples from Baja California occur in the same cluster in both branching diagrams, the two major groups (as represented in our samples) do not correspond closely to geographic proximity, or any obvious environmental or ecological factors. The Tule Lake sample, taken near the interface of the Great Basin and the Cascade Range, is genetically most similar (Nei's $D = 0$; Table 2) to the Ensenada sample, although the two sites show no obvious ecological similarities and are widely separated geographically. Possibly a relatively more ancient reduction in gene flow initiated divergence of the Willits, McMillan, and Santa Catalina Island samples, a result being that more easterly samples (e.g., Tule Lake) are allied with those from Baja California via an interior gene flow route. We lack samples of nonintroduced (e.g., Sierra Nevada) interior quail to examine this proposition. In our scenario, some interior populations died out; current populations in western Nevada, and possibly the Owens Valley, were introduced (Grinnell and Miller 1944, Leopold et al. 1981, Ryser 1985). Sources of introduced birds are uncertain.

We considered the possibility that the similarity of samples from Tule Lake and Baja California was a result of past introductions and reintroductions of California Quail (Leopold 1977). California Quail are sometimes transferred, at least on a local scale, by persons interested in augmenting local stocks for hunting; these introductions often are unrecorded (R. J. Gutiérrez, in litt.). Between 1934 and 1943, game managers introduced approximately 65,000 quail in California (Richardson 1941), most coming from the Ensenada area. Most introductions occurred in southern California, although a number were kept as breeding stock for game farms and these birds could have been used for later introductions elsewhere (True 1934). We were unable to find any records or recollections of introductions from local game managers familiar with quail in the Tule Lake area at least since the 1950s. Our specimens from Tule Lake showed no obvious color or morphological similarities to other California or Baja California specimens. Thus, we have no evidence that the genetic composition of the Tule Lake sample reflects introductions in the recent past. In addition, we cannot rule out an east–west and separate historical occupation of northern California in the more distant past or a random chance similarity. Because the level of differentiation (F_{ST}) is consistent with other intraspecific surveys of birds (Barrowclough and Johnson, in press) without histories of introductions, we suggest that our data on population structure are not compromised by introductions. As found for other birds (Barrowclough and Johnson, in press) there is no strong geographic pattern of genetic differentiation at protein-coding loci.

HISTORICAL BIOGEOGRAPHY

Although only slight geographic differentiation was observed among California Quail populations, the results have biogeographic implications. First, the sample from Santa Catalina Island, although phenotypically distinct, is not more divergent genetically from mainland samples than mainland samples are from one another. This result suggests relatively recent isolation, because one might expect island samples to be more divergent. In other words, factors causing divergence (period of isolation, fluctuation in effective population size) of the island quail have been of similar magnitude to those causing genetic divergence of mainland samples from each other. Johnson (1972) argued persuasively that California Quail were introduced to Santa Catalina Island approximately 12,000 years ago by man. This length of time probably is insufficient to cause extensive genetic differentiation by genetic drift. However, possible results of such an introduction, namely a bottleneck in population size and/or isolation from gene flow, are potentially

a cause of the relatively low heterozygosity (2.2%), low number of alleles per locus (1.16), and the somewhat divergent allelic frequencies at La, Np, and Mpi. Although our data are consistent with Johnson's (1972) hypothesis, without knowledge of the long-term *Ne* it is impossible to determine if the genetic characteristics of the quail from Santa Catalina Island required 1,000 or 10,000 or more years to develop.

The geologic history of Baja California is well studied. Murphy (1983) summarizes geological information and provides a perspective on historical biogeographic patterns in the herpetofauna. After separation from the central Mexican mainland, Baja California began drifting northward and became connected to southern California approximately three to five million years ago. Thus, a fundamental question is whether California Quail arrived in Baja via dispersal from the north, or if they were present on Baja while it moved northward, and subsequently dispersed northward into California. In the latter scenario, California Quail would be nearest relatives (cladistically) with quail in Mexico, such as Elegant Quail (*C. douglasii*). Although we lack samples of Elegant Quail, we are impressed by the genetic similarity of our samples from southern Baja California and northern California. Of course, because the California Quail is genetically similar to the Gambel's Quail (*C. gambelii*; Gutiérrez et al. 1983), one might not expect differences between quail in Baja California and elsewhere. However, the period of time that Baja California was isolated is sufficient to allow considerable divergence (see calibration of genetic distances in Gutiérrez et al. 1983). California Quail in Baja California are not phenotypically intermediate between Gambel's and Elegant quail, which might be predicted if there was sympatry and hybridization between California and Elegant quail (or their ancestors). Therefore, we propose that there was no swamping of Elegant Quail genotypes in Baja California by flow of quail genes from the north, upon the connection of Baja California and southern California. We hypothesize that California Quail dispersed southward into Baja California subsequent to its connection to the southern California mainland. Quail present on the peninsula prior to its connection would have either gone extinct in the new climate or as a result of competition from California Quail. Also, breeding populations of the Brown Towhee (*Pipilo fuscus*) in Baja California are more similar genetically to conspecific populations in California than to populations on the Mexican mainland (Zink, unpubl. data). In addition, a sample of Leconte's Thrasher (*Toxostoma lecontei*) from Baja California is very similar genetically to samples from California (Zink, unpubl. data). Therefore, it seems likely that significant colonization of Baja California occurred subsequent to its connection with mainland California, in quail, towhees, and thrashers. Identity and affinities of quail, towhees, and thrashers on Baja California during its northward drift would be an interesting problem for paleornithologists.

PHENOTYPIC AND GENOTYPIC DIFFERENTIATION

Phenotypic differentiation among California Quail populations is of a level recognized by taxonomists as subspecies. The phenotypic characteristics upon which the subspecies are based (Grinnell and Miller 1944) lack strong correlates in our genetic data. Therefore, we only note that if the phenotypic markers which delimit subspecies have a genetic basis (e.g., James 1983), genetic divergence at allozyme loci probably is less extensive (see, however, Lewontin 1984, 1986). We lack sufficient samples to determine if genetic distances within subspecies are less than between subspecies. However, given the low genetic distances between subspecies, differences within subspecies, if present, must be very low (e.g., our Tule Lake versus McMillan *D*-value is 0.002). Although we have no quantitative measure of the among-sample component of morphologic differentiation, we hypothesize that it would exceed the 3.2% determined for our sample of allozyme loci. That is, if one quantified the phenotypic differences on which subspecies limits are based, the among-subspecies component would exceed 3.2%. A quantitative genetic approach (Price et al. 1984) might establish the geographic partitioning of genetic variation in morphological traits within and among populations.

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