

**INTERACTION BETWEEN ISLAND FOXES
(*UROCYON LITTORALIS*) AND INDIANS ON ISLANDS
OFF THE COAST OF SOUTHERN CALIFORNIA:
I. MORPHOLOGIC AND ARCHAEOLOGICAL EVIDENCE
OF HUMAN ASSISTED DISPERSAL**

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ABSTRACT.—The island fox, *Urocyon littoralis*, occurs on six widely separated islands off the coast of Southern California. Using cranial morphometrics, present day samples from each of the six island populations and archaeological samples from four of the islands were examined for patterns of geographic variation. Univariate and multivariate statistics were used to clarify evolutionary relationships. Morphometric analyses revealed that morphological divergence in the Northern Channel Island populations is consistent with their spatial distribution and known geological history, whereas the Southern Channel Island populations showed no such concordance. Phenetic affinities of archaeologically obtained island fox material, together with occurrence of island fox bone material only in Middle to Late Period sites on the Southern Channel Islands suggests that Indians were probably responsible for establishing foxes on San Clemente, Santa Catalina and San Nicolas Islands.

Data in the archaeological record were used to determine when Indians would have dispersed island foxes. Examination of the fox remains in Channel Island archaeological sites revealed that foxes were present on the Northern Channel Islands prior to the arrival of Indians 9,000–10,000 years ago. On the Southern Channel Islands foxes do not appear in the archaeological record until about 3,400–3,800 years ago on Santa Catalina and San Clemente Islands and 2,200 years ago on San Nicolas Island. Results of morphometric and archaeological analyses both support a fairly recent, post-Holocene introduction of foxes from the Northern Channel Islands to the Southern Channel Islands by Indians.

RESUMEN.—El zorro isleño, *Urocyon littoralis*, se encuentra distribuido en seis islas ampliamente separadas fuera de la costa del sur de California. Por medio del análisis de la morfometría craneal de especímenes actuales de cada una de las seis poblaciones isleñas, y también de ejemplares arqueológicos de cuatro de estas islas, se determinaron configuraciones de variación geográfica. Se realizaron estadísticas univariadas y multivariadas para clarificar las relaciones evolucionarias. Los análisis morfométricos han revelado que la divergencia morfológica en las poblaciones de las islas del canal del norte es consistente con su distribución espacial e historia geológica ya conocida, mientras que las poblaciones de las islas del canal del sur no demostraron tal concordancia. Afinidades fenéticas de materiales de zorros isleños obtenidos por métodos arqueológicos, junto con la ocurrencia de materiales osteológicos de estos zorros, encontrados solamente en

sitios de mediados hasta fines del período arqueológico en las islas del canal sur, sugieren que probablemente los indios fueron responsables de establecer a los zorros en las islas de San Clemente, Santa Catalina, y San Nicolas.

Información obtenida del récord arqueológico utilizado para determinar cuando los indios dispersaron a los zorros isleños. La examinación de los restos de zorros en sitios arqueológicos de las islas canales reveló que los zorros se encontraban presente en las islas del canal norte antes de la llegada de los indios hace 9,000-10,000 años. Los zorros no aparecen en la historia arqueológica de las islas canales del sur hasta hace alrededor de 3,400-3,800 años en las islas de Santa Catalina y San Clemente y hasta hace 2,200 años en la isla de San Nicolas. Los resultados de los análisis morfométricos tanto como los análisis arqueológicos apoyan la teoría que una introducción bastante reciente de los zorros, después del período Holocénico, fue llevada a cabo por los indios desde las islas canales del norte hacia las islas canales del sur.

RESUME.—Le renard insulaire, *Urocyon littoralis*, se trouve dans six îles bien séparées loin du côte du sud de la Californie. On a examiné avec des morphométriques craniaux des échantillons actuels de chacune de six îles et aussi des échantillons archéologiques de quatre îles pour des modèles de la variation géographique. On a utilisé des statistiques univariates et multivariates pour clarifier des parentés évolutives. Les analyses morphométriques ont révélés que la divergence morphologique dans les populations des îles du Canal du Nord est d'accord avec sa distribution spatiale et son histoire géologique connue, tandis que les populations des îles du Canal du Sud n'ont pas montré une concordance semblable. Les affinités phénétiques des échantillons archéologiques du renard insulaire, ensemble avec l'occurrence des échantillons des os du renard insulaire seulement dans les sites des Périodes Moyenne et Tardive dans les îles du Canal du Sud, suggèrent que les Natifs ont probablement établi le renard dans les îles San Clemente, Santa Catalina, et San Nicolas.

On a utilisé l'information archéologique pour déterminer l'année quand les Natifs auront dispersé le renard insulaire. L'examination des restes du renard dans les sites archéologiques des îles du Canal a révélé que le renard s'est trouvé dans les îles du Canal du Nord avant de l'arrivée des Natifs il y a 9000-10,000 années. Le renard paraît pour la première fois dans le registre archéologique il y a 3400-3800 années dans l'île Santa Catalina et il y a 2200 années dans l'île San Nicolas. Les résultats des analyses morphométriques et archéologiques soutiennent l'idée que les Natifs l'ont introduit récemment, après du Holocène, des îles du Canal du Nord jusqu'aux îles du Canal du Sud.

INTRODUCTION

Humans have played a significant role in directly or indirectly spreading animals into many new areas. Prehistoric peoples have had an especially profound effect on the zoogeography of many islands via transport and introduction of semidomesticates (e.g. canids, felids, suids, mustelids, viverrids), domesticates (e.g. equids, bovids, camelids), and commensals (e.g. canids, rodents). Early humans are known to have carried many animals in their watercraft (Wallace 1869; Darlington 1957; Carlquist 1965). Polynesians introduced dogs, pigs, and rats to islands throughout the Pacific, which in turn contributed to the extinction of many

endemic land vertebrates on these islands (Olson and James 1982a; 1982b; 1984). Olson (1982) believes that Indians were responsible for the introduction of the extinct rodent *Isolobodon portoricensis* to Puerto Rico and the Virgin Islands. The Haida Indians may have been responsible for the occurrence of deer mice (*Peromyscus maniculatus*) on many of the Queen Charlotte Islands off the coast of British Columbia (Foster 1963; 1965).

Considering their seafaring abilities and trading activities, it is not at all surprising that maritime Chumash and Gabrielino Indians, who occupied the California Channel Islands and adjacent mainland coast, were capable of transporting animals to some of the offshore islands (King 1971; Tartaglia 1976; Hudson *et al.* 1978). It is definitely known that they transported dogs in plank canoes (Schumacher 1877; Bowers 1890; McKusick and Warren 1959; Orr 1968). Native Americans may also have been responsible for intentionally or inadvertently introducing several species of terrestrial vertebrates from the mainland to islands off the coast of Southern California (Wenner and Johnson 1980; Johnson 1983), or for moving species between islands (Gill 1980; Wenner and Johnson 1980; Collins 1982; Johnson 1983). Indian transport in canoes has been used to explain patterns of variation observed in Channel Island populations of deer mice (Gill 1980; Ashley and Wills 1987; 1989), western harvest mice (*Reithrodontomys megalotis*) (Ashley 1989; Collins and George 1990), and island fox (Collins 1982).

The island fox (*Urocyon littoralis*) which is found on the six largest islands off the Southern California coast (i.e., San Miguel, Santa Rosa, Santa Cruz, San Nicolas, Santa Catalina, and San Clemente Islands; Fig. 1), is a diminutive form of the mainland gray fox (*U. cinereoargenteus*) (Grinnell *et al.* 1937). Fritzwell and Haroldson (1982) and Hall (1981) have given subspecific recognition (i.e., *littoralis*, *santarosae*, *santacruzae*, *dickeyi*, *catalinae*, and *clementae*) to fox populations on each island. Superficially there is little morphological variability among populations but the species is markedly different from the gray fox (Grinnell *et al.* 1937).

The distribution of island foxes has elicited considerable debate over how such a poor over-water disperser could colonize six widely separated islands (Wenner and Johnson 1980; see review in Collins 1982). One hypothesis suggests that present-day populations represent a relict form of a previously widespread, smaller, continental race which reached exposed offshore landmasses via land-bridges resulting from eustatic sea level changes during the Pleistocene (Stock 1943; von Bloeker 1967; Remington 1971). A second, more widely accepted hypothesis states that original colonizing foxes were similar in size to those on the adjacent mainland, but unique selective pressures on the islands led to a reduction in size (Grinnell *et al.* 1937; Vedder and Norris 1963; Case 1978; Johnson 1978; 1983; Wenner and Johnson 1980; Collins 1982). Accordingly, gray foxes probably reached one of the Northern Channel Islands through chance by rafting or swimming (Wenner and Johnson 1980) and during an initial period of isolation evolved to their present small body size. Eustatic sea level change during the late Pleistocene could have permitted subsequent dispersal, via interisland land-bridges, of small-sized island foxes across the Northern Channel Island chain (i.e., San Miguel, Santa Rosa and Santa Cruz Islands). Following arrival of Native Americans, this hypothesis concludes, island foxes were then transported to the

three largest Southern Channel Islands in Indian watercraft (Norris 1951; Vedder and Norris 1963; Johnson 1972; 1983; Wenner and Johnson 1980; Collins 1982; in press).

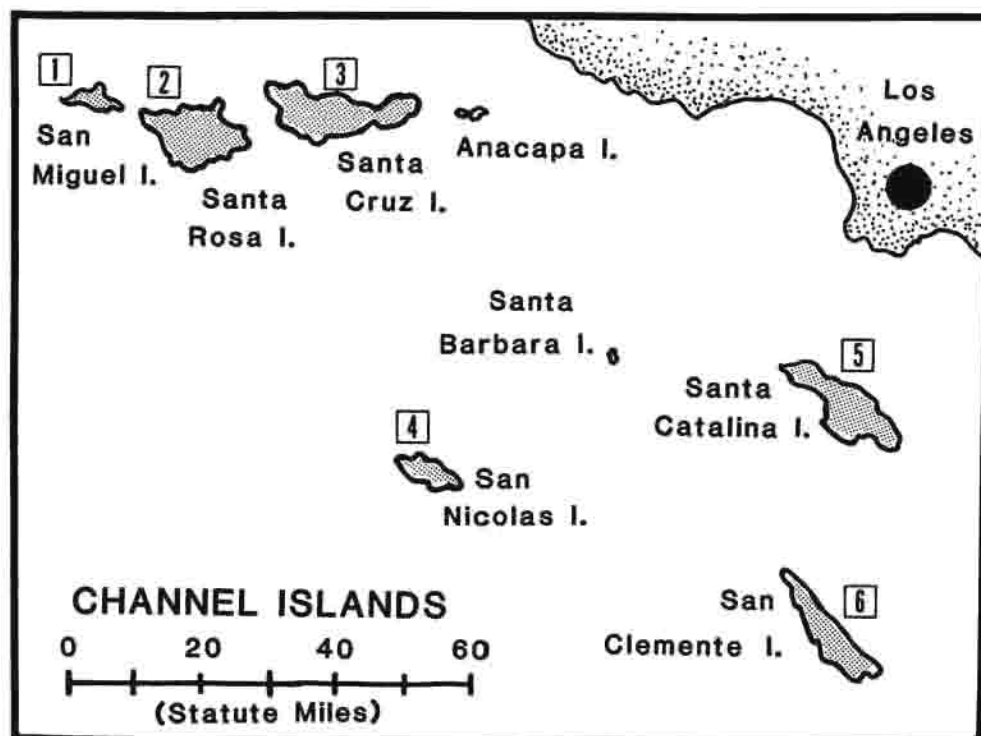


FIG. 1.—Map showing present-day sample localities. Numbers refer to the following samples: 1—SMI; 2—SRI; 3—SCrI; 4—SNI; 5—SCaI; 6—SCII. Acronyms are defined in Table 1.

If Native Americans were responsible for transporting foxes to some of the Southern California islands, then evidence to support this hypothesis should be present in phenetic similarities between present-day populations and archaeological samples. Examination of faunal remains recovered from Channel Island archaeological sites should: (1) provide evidence about whether island foxes were present on each of the islands throughout the period of human occupation, 9,000-10,000 years B.P.; (2) determine whether any fox populations were established as a result of Indian transport; and (3) determine the approximate time when foxes were first introduced to some islands.

The primary objectives of this paper are to: (1) clarify evolutionary relationships of island fox populations by examining morphological variability within and among present-day and archaeological samples; (2) document the role that Native Americans played in introducing island foxes to some islands on which they presently occur; and (3) based on the occurrence of fox remains in Channel Island

archaeological sites, determine sequence and timing for establishment of foxes on each island.

MATERIALS AND METHODS

Morphometric Analysis.—To examine interisland phenetic affinities of present-day and prehistoric island fox populations, I recorded twenty-nine measurements (Fig. 2; described in Collins 1982) from 497 present-day and 96 archaeologically recovered island fox skulls. All measurements were taken with dial calipers accurate to 0.01 mm. Before investigating patterns of geographic variation, I examined the extent of nongeographic, intraspecific variation from factors such as sexual, ontogenetic, and intra-locality character variation. Only present-day specimens were used in the analysis of nongeographic variation. To look at variation within and between populations, specimens were assigned to six *a priori* designated population samples (Fig. 1).

Univariate statistics (mean, standard deviation, standard error, and coefficient of variation) were calculated for each sample and all characters using PROC MEANS (Helwig and Council 1979). See Collins (1982:215-227) for a summary of these statistics. To give all variables more equal weight (regardless of their magnitude) and to make their variances more homogeneous across locality samples, I transformed all linear measurements to logarithms (\log_e). All further statistical procedures were performed on the transformed data.

Secondary sexual dimorphism was assessed for each of the 29 cranial measurements from one island sample (Santa Cruz Island), using *t*-tests (BMDP3D; Dixon 1983). Significant differences between the sexes ($P \leq 0.01$) were recorded for 27 of the 29 variables; therefore the remainder of the statistical analyses were run separately for each sex.

Ontogenetic variation was examined using a sample composed of all present-day island foxes. I assigned specimens to one of six age categories based on a combination of cranial suture closures, tooth eruptions, and molar tooth wear patterns described for the gray fox (Wood 1958). See Collins (1982: 141 and 169) for a diagram of molar wear patterns and a description of the characters used to distinguish each age category. Because of small sample sizes in the youngest and oldest age categories, the original six age classes were reduced to four: (1) juvenile (original age category 1-2); (2) subadult (age 3); (3) adult (original age category 4); (4) old adult (original age category 5-6). A one-way analysis of variance (F test) and Duncan's multiple range test were used to determine significant differences among means and maximal nonsignificant subsets (SAS; Helwig and Council 1979). As a result, specimens in age categories 2-4 were pooled for subsequent statistical analyses while specimens in age category 1 were excluded from further treatment. These results tend to agree with Wood's (1958) demarcation of adults in gray foxes.

Since only a few of the archaeological specimens possessed both skulls and lower mandibles, I only used 22 cranial characters (Fig. 2) for further statistical analyses. To use archaeological specimens in any further analyses, it was necessary to determine the sex of each specimen. To do this I ran a separate canonical variates

analysis (CVA) for each island sample. Archaeological specimens from an island were entered into a CVA analysis for that island as unidentified. These specimens were then evaluated with the discriminant equation generated from the reference sample to determine their sex. If the probability of classification to a particular

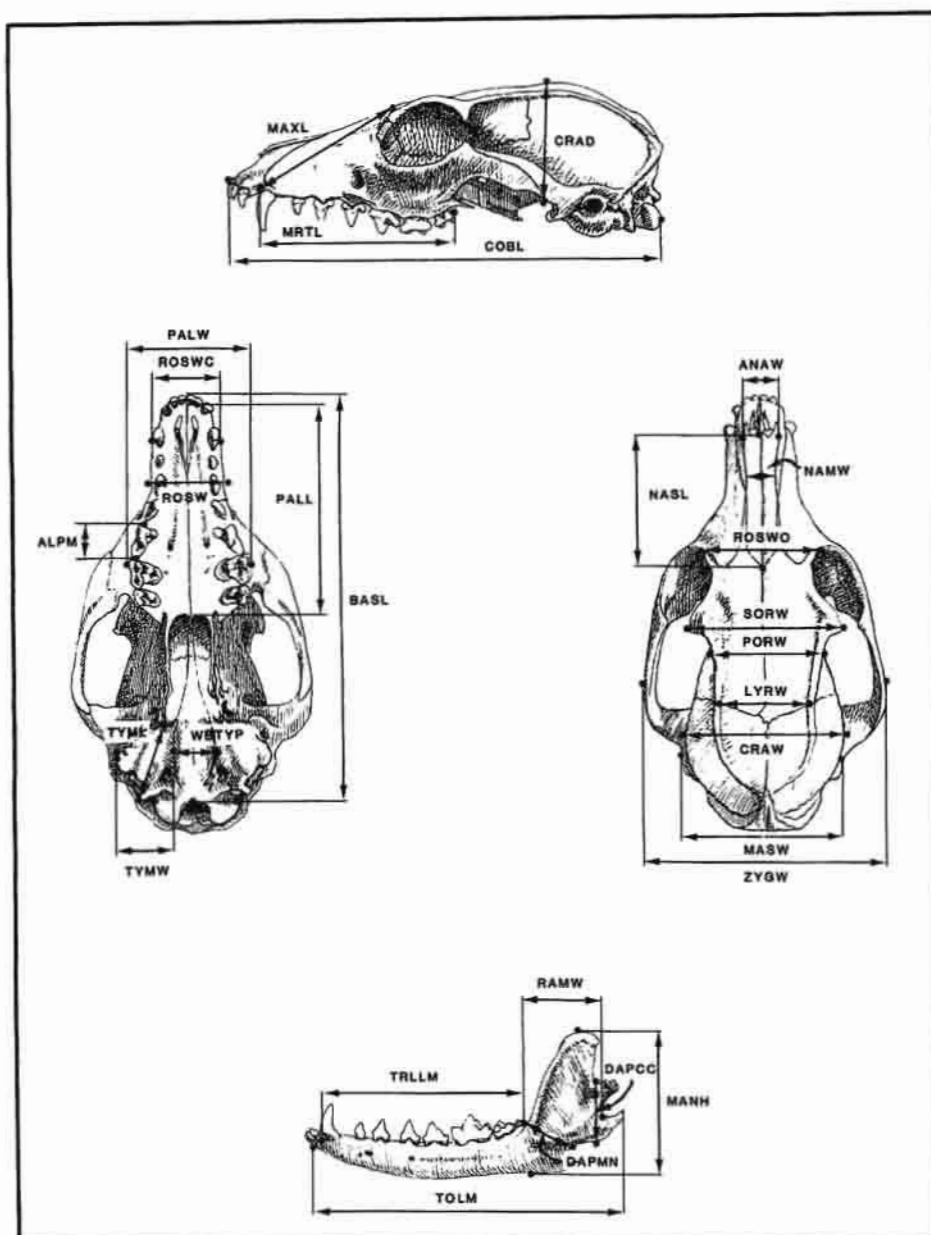


FIG. 2.—Twenty-nine cranial measurements used in this study; acronyms are defined and measurements are described in Collins (1982).

sex was 90% or above, then I assigned the specimen to that sex and included it in further multivariate analyses; otherwise it was removed from all further analyses.

Multivariate analysis of variance (MANOVA; Helwig and Council 1979) was used to determine if significant morphometric variation existed among *a priori* designated present-day samples. I assessed morphologic divergence and phenetic overlap among present-day and historic island fox populations using multigroup discriminant function analysis (BMDP7M; Dixon 1983). I analyzed males and females separately, using present-day fox samples as targets for classification of archaeological material. A set of canonical discriminant functions were calculated for each CVA and the centroid for each sample was plotted on the first two vectors. Minimum polygons enclosing all individuals in each population sample were drawn to illustrate the degree of phenetic overlap in present-day fox populations, and to clarify phenetic affinities of the archaeological specimens.

Archaeological Analysis.—I examined faunal material recovered from Channel Island archaeological sites for the occurrence of island fox bone and recorded type and quantity of fox bone found at each site, and when present, noted the provenience of each occurrence. In addition, I examined each bone for evidence of possible cultural modifications such as butchering, burning, unusual breakage and/or manufacturing marks, to determine whether a bone was derived from cultural or natural depositional processes. Intact skulls were measured and used in canonical variates analyses to clarify phenetic affinities between present-day and prehistoric fox populations.

RESULTS

Results-Morphologic Variation.—F-tests for both male and female samples detected statistically significant ($P \leq 0.05$) differences among the six present-day and four archaeological samples (Table 1), thus invalidating the null hypothesis of no statistically significant geographic variation among populations. While all of the F-tests for present-day samples were significant ($P \leq 0.0001$), some of the comparisons between present-day and archaeological samples were either insignificant ($P > 0.05$) or were at higher probability values (Table 1). Small size of archaeological samples probably contributed to higher P values obtained from comparisons with present-day samples (Table 1). Multivariate analysis of variance (MANOVA) disclosed that statistically significant differences (F transformation of Wilk's lambda statistic = 27.87; d.f. = 145, 1793, $P < 0.001$) exist among samples. Based upon the F-test and MANOVA results, I concluded that it was appropriate to investigate dispersion of these samples within discriminant space.

Mean centroids for each of six present-day and three to four archaeological male and female island fox samples are plotted on the first two canonical variate (CV) axes (Figs. 3 and 4 respectively). The variance-covariance matrices yielded a total of 13 canonical variates for males and 17 variates for females (Table 2). Thirteen and 17 of the variables exhibit statistically significant ($P \leq 0.01$) morphological variation (Table 2). The first three CV axes account for a combined total

of 89.8% and 87.6% of the total morphologic variation (Table 2). Although canonical variates 4 through 13 and 17 are significant ($P \leq 0.01$), each provides little additional discrimination between localities; axes 4-5 account for the remaining 10.2% and 12.5% of the between-sample morphological variation (Table 2). Therefore, there is little distortion of the phenetic distances between populations if the character space is reduced from 22 dimensions to only two.

TABLE 1.—Matrix of probability values¹ for F-tests for significant differences among the island fox samples. These tests are based on 22 cranial characters and the sexes were analyzed separately. Probability values of F-tests for the males are on the upper diagonal, females on the lower diagonal. Degrees of freedom for these tests were 13 and 194 for males and 17 and 190 for females.

Locality ²	Number		SMI	SRI	SCrI	SNI	SCaI	SCII	SRII	SCrII	SNII
	Females	Males									
SMI	20	25		S	S	S	S	S	.01	S	S
SRI	32	30	S		S	S	S	S	.05	S	S
SCrI	67	68	S	S		S	S	S	S	.05	S
SNI	61	46	S	S	S		S	S	S	.01	.01
SCaI	16	21	S	S	S	S		S	S	.01	S
SCII	17	22	S	S	S	S	S		S	S	S
SRII	5	8	.05	NS	S	S	S	S		.05	.01
SCrII	1	6	.05	.05	.05	.01	.01	.05	.05		.01
SNII	12	10	s	s	s	s	s	s	s	.05	
SCIII	1	0	0.5	.05	.05	.05	.05	NS	.05	.05	.05
TOTAL	232	236									

¹Probability notations used in this table are: S = significant ($P < 0.001$), NS = nonsignificant ($P > 0.05$), and intermediate P values are listed (i.e. $P \leq 0.05 = .05$).

²Locality acronyms are as follows: PRESENT-DAY SAMPLES: (SMI = San Miguel Island; SRI = Santa Rosa Island; SCrI = Santa Cruz Island; SNI = San Nicolas Island; SCaI = Santa Catalina Island; SCII = San Clemente Island; ARCHAEOLOGICAL SAMPLES: (SCrII = Santa Cruz Island; SRII = Santa Rosa Island; SNII = San Nicolas Island; SCIII = San Clemente Island).

For male foxes, samples cluster into three groups (Fig. 3): San Miguel (SMI) and Santa Rosa (SRI) Islands; Santa Cruz (SCrI), Santa Catalina (SCaI) and San Nicolas (SNI) Islands; and San Clemente Island (SCII). For both males and females, there is general correspondence between the position of present-day island samples in multivariate space and their actual geographic locations (Figs. 3 and 4). For males, island samples are distributed counter-clockwise from north to south starting with San Miguel in the upper right and ending with San Clemente in the lower right (Fig. 3). For females, present-day populations are similarly distributed north to south but are in a clockwise pattern (Fig. 4). In both CVAs degree of overlap among present-day Northern Channel Island populations (SMI, SRI, SCrI) appears to correspond to length of time that these islands have been isolated from each other (Figs. 3 and 4). Santa Cruz Island last separated from

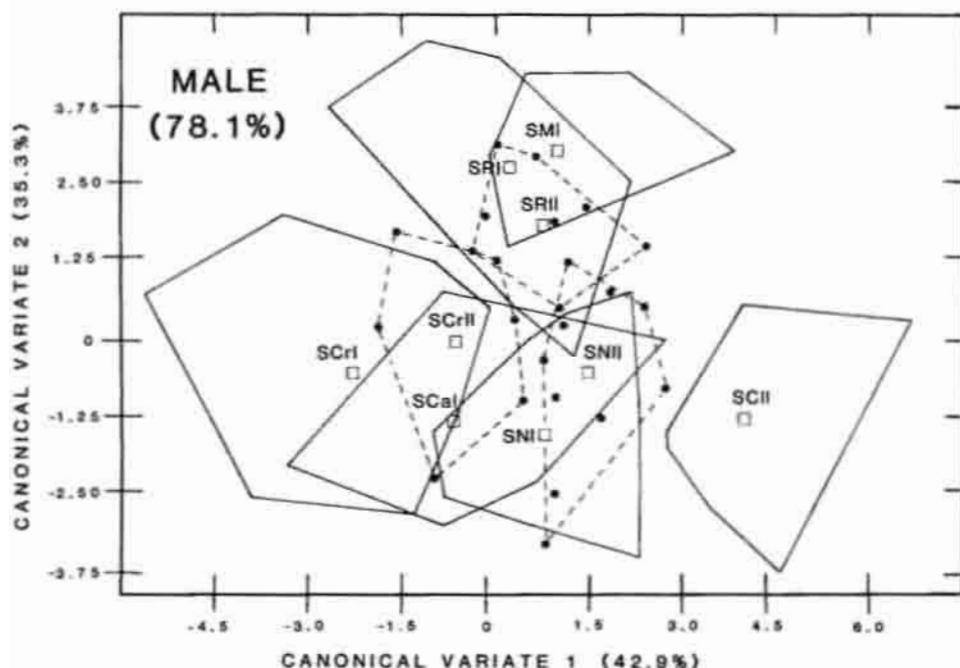


FIG. 3.—Discriminant function plot of the first two canonical vectors for male island foxes. Polygons enclose all of the individuals of each sample with solid lines used to denote present-day samples and dashed lines to denote archaeological samples. Open squares are used for sample mean centroids and solid black dots are used to note the location of archaeological specimens. Acronyms refer to samples described in Figure 1 and the Appendix.

Santa Rosa and San Miguel Islands about 2000 years before the latter two islands separated from each other (Johnson 1983).

Another prominent feature of both CVA plots (Figs. 3 and 4) is that archaeological samples are phenetically closer to the present-day sample from their island of origin. This can best be seen in the relative degree of overlap in present-day and archaeological samples from San Nicolas Island (Fig. 3). It is also apparent that group centroids for archaeological samples (SRII, SCrII, SNII) are situated, in multivariate character space, closer to each other than are group centroids for present-day samples (Figs. 3 and 4). The San Clemente Island sample is divergent in size (CV-1) but not in shape (CV-2) from other island samples (Fig. 3). Despite the size difference exhibited by San Clemente Island foxes, this population manifests the same basic skull shape as the other present-day populations, which suggests that foxes on San Clemente Island may have been isolated for a relatively short period of time, and as such, may not have had sufficient time to evolve substantive shape differences. This population may still be under constraints of a morphologic and genetic bottleneck. With the exception of Northern Channel Island samples, there does not appear to be a relationship between location of

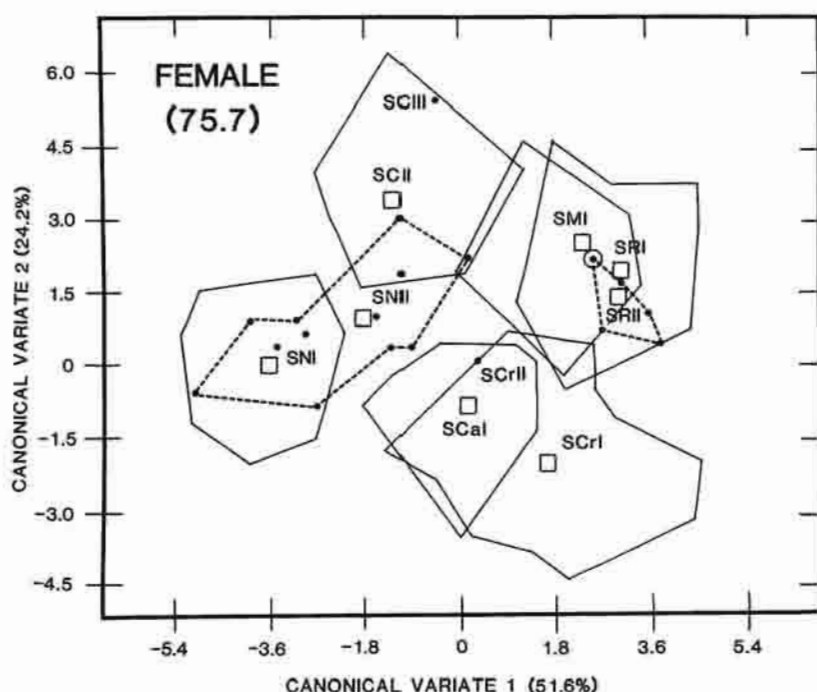


FIG. 4.—Discriminant function plot of the first two canonical vectors for female island foxes. Polygons enclose all of the individuals of each sample with solid lines used to denote present-day samples and dashed lines to denote archaeological samples. Open squares are used for sample mean centroids and solid black dots are used to note the location of archaeological specimens. Acronyms refer to samples described in Figure 1 and the Appendix. The fossil island fox specimen from the Upper Tecolote Member on Santa Rosa Island is represented by a circled black dot.

present-day island samples in multivariate space and actual geographic distances between islands. The Santa Catalina Island sample is phenotypically closer to Santa Cruz Island than to its geographically closest neighbor San Clemente Island (Figs. 3 and 4). Degree of divergence observed in present-day and archaeological island fox samples suggests that gene exchange was probably occurring between fox populations during the time of Indian occupation.

The female CV analysis differed from the male CVA in several ways. The San Nicolas Island sample was divergent in size (CV-1) but not shape (CV-2) from other island samples (Fig. 4). Overlap was evident between the San Nicolas Island archaeological sample (SNII) and the present-day San Clemente Island sample

TABLE 2.—*Logarithmized variables which were significant ($P \leq 0.01$) in distinguishing among the island fox samples. Character acronyms are the same as in Figure 2.*

Step Number	Variable	Wilk's lambda U-Statistic	Approx. F Value	df	Percent of ¹ Inter OTU Variance
MALE					
1	WBYP	0.5230	37.58	5,206	42.9
2	MASW	0.2961	34.35	10,410	35.3
3	SORW	0.1666	34.34	15,564	11.7
4	NAMW	0.1035	33.09	20,674	6.4
5	MAXL	0.0705	31.35	25,752	3.8
6	NASL	0.0448	31.54	30,806	
7	PALW	0.0341	29.70	35,844	
8	CRAW	0.0266	28.26	40,870	
9	BASL	0.0213	26.94	45,889	
10	CRAD	0.0179	25.55	50,902	
11	ROSWC	0.0150	24.47	55,911	
12	TYML	0.0132	23.21	60,917	
13	ZYGW	0.0118	22.09	65,921	
FEMALE					
1	WBYP	0.3814	67.16	5,207	51.6
2	MASW	0.1953	52.03	10,412	24.2
3	SORW	0.0925	51.66	15,566	11.8
4	MAXL	0.0527	48.39	20,678	8.9
5	NAMW	0.0349	44.37	25,756	3.6
6	BASL	0.0262	40.13	30,810	
7	CRAD	0.0200	37.15	35,848	
8	ANAW	0.0161	34.55	40,875	
9	NASL	0.0130	32.60	45,893	
10	CRAW	0.0107	30.92	50,906	
11	ROSWO	0.0088	29.62	55,915	
12	MRTL	0.0075	28.36	60,922	
13	PALL	0.0065	27.16	65,925	
14	ROSWC	0.0056	26.12	70,928	
15	PALW	0.0049	25.15	75,929	
16	ZYGW	0.0043	24.47	80,929	
17	PORW	0.0038	23.68	85,928	

¹This is the percentage of the between sample variance which is accounted for by the first five canonical vectors of interlocality phenetic variation.

(SCII) (Fig. 4). The present-day San Clemente Island sample was phenetically closer to San Miguel Island than to other Southern Channel Islands. Of particular interest in Figure 4 is the location of an apparent fossil fox specimen recovered from the Upper Tecolote geological formation on Santa Rosa Island, which has been estimated to date between 10,400 and 16,000 years of age (Orr 1968). This specimen, noted by the double circle in Figure 4, is situated between the SMI and SRI group centroids, which suggests that a small sized fox was present on Santa Rosa Island prior to currently accepted dates (about 9,000-10,000 years B.P.) for arrival of Native Americans to the Northern Channel Islands (Erlandson 1988). It also indicates that foxes have changed very little, at least in overall size and shape, during the last 16,000 years. Thus, foxes must have reached the Northern Channel Islands on their own prior to the arrival of Native Americans. As with the male CVA results, the broad overlap of SCAI and SCrI as well as the slight overlap of SNII and SCII, and proximity of SCII to SMI all suggest that gene interchange was probably occurring between these islands during Indian occupation.

Degree of phenetic overlap in present-day and historic island fox samples was further assessed by comparing the proportion of individuals from each locality that were misclassified in the discriminant function analyses. For males, 189 of 212 present-day specimens (89%) were correctly classified to their *a priori* designated samples by the classification procedure of the discriminant function analysis (Table 3). The most distinctive locality samples were SNI (95.7% correctly classified), SCII (95.5% correctly classified), and SMI (92.0% correctly classified), whereas the least distinctive locality samples were SCAI (71.4% correctly classified) and SCrI (86.8% correctly classified). In the female analysis, 199 of 213 present-day specimens (93%) were correctly classified to their *a priori* designated samples (Table 3). The most distinctive samples for females were SNI and SCAI (100% correctly classified), and SCrI and SCII (94% correctly classified), whereas the least distinctive samples were SMI (80% correctly classified) and SRI (84.4% correctly classified).

Of fourteen SMI and SRI specimens that were misclassified by the discriminant function, all but two were classified to one of the adjacent Northern Channel Islands (Table 3). The degree of phenetic overlap between Santa Cruz, San Nicolas and Santa Catalina Islands is suggested by the 15 specimens which misclassified among these three islands (Table 3). The high proportion of correctly classified individuals in both of the CVAs suggests that present-day island fox populations have begun to diverge morphologically from one another. Given the high proportion of correct classifications in both the male and female analyses, it appears that these two discriminant functions should classify the archaeological samples with a high degree of precision.

Classification analysis of archaeological material further suggests that Indians have played a major role in determining present island fox zoogeography. Eight of 13 Santa Rosa Island archaeological specimens (SRII) classified with the present-day SRI sample whereas the remaining five specimens classified with SMI (Table 3). The fossil specimen classified with the present-day SRI sample. Male archaeological specimens from Santa Cruz Island (SCrII) exhibited a much broader

TABLE 3.—*Jackknifed discriminant classification of individual island fox, based on 22 skull variables. Rows are actual groups and columns are predicted groups. The archaeological material is classified in relation to the discriminant equation established from the six present-day island samples. Samples acronyms are the same as those in Table 1.*

Actual Locality	N	Percent Classified Correctly	Predicted Locality					
			SMI	SRI	SCrI	SNI	SCaI	SCII
MALE								
SMI	25	92.0	23	2				
SRI	30	90.0	2	27		1		
SCrI	68	86.8		2	59	5	2	
SNI	46	95.7		1	1	44		
SCaI	21	71.4	1		2	3	15	
SCII	22	95.5	1					21
SRII	8	—	3	5				
SCrII	6	—	1	1	2	1	1	
SNII	10	—	1			9		
TOTAL	236							
FEMALE								
SMI	20	80.0	16	3	1			
SRI	32	84.4	3	27	1	1		1
SCrI	67	94.0		2	63	1		1
SNI	61	100.0				61		
SCaI	16	100.0					16	
SCII	17	94.1				1		16
SRII	5	—	2	3				
SCrII	1	—			1			
SNII	12	—	1	1		7	2	1
SCIII	1	—						1
TOTAL	232							

phenetic range, with specimens classifying to most of the island samples (Table 3). The San Nicolas Island archaeological material (SNII) showed overlap with present-day samples from San Miguel, Santa Catalina, and San Clemente Islands (Table 3). The archaeological specimen from San Clemente Island classified with the present-day San Clemente Island sample.

In summary, results of two canonical variates analyses showed that each of six present-day island fox populations exhibit a moderate degree of phenetic divergence. Small island foxes have been present on Santa Rosa Island for at least

10,400–16,000 years. The broad overlap observed between some island samples (i.e., SMI-SRI, SCrI-SCaI and SNI-SCaI), coupled with the occurrence of misclassifications between these overlapping samples, suggests that gene exchange has probably occurred in the past between these islands. Phenetic affinities of archaeological material from three of the islands (SNI, SCrI, SRI) suggests that Indians played a role in determining present island fox zoogeography.

Results-Archaeological Occurrences.—Although an examination of faunal remains recovered from Channel Island archaeological sites provides additional information which favors the hypothesis that Indians have played a role in the dispersal of island foxes, a number of problems were encountered with these samples. Since the majority of archaeologists prior to the late 1950s were not interested in recovering or documenting the occurrence of faunal remains, little faunal material was saved. Most early excavators used screens or mesh sizes which were too large to catch any small, and most medium-sized, faunal material. Most faunal remains which were saved lacked provenience data. Finally, most early archaeologists saved only the largest or most impressive faunal material (e.g. skulls and mandibles).

Despite these shortcomings, a number of observations can be made from the archaeological record. Island fox remains were found in 27 archaeological sites and one fossil locality on six of the eight islands (Table 4). These sites ranged in age from 7,500 years B.P. to historic times. Foxes have not been found in archaeological contexts on Anacapa or Santa Barbara Islands, but were present on Santa Cruz and Santa Rosa Islands throughout Indian occupation. Foxes do not appear in the archaeological record on the Southern Channel Islands until about 3,800–2,200 years B.P. The presence of fox remains only in the upper levels of Middle to Late Period sites on San Clemente, Santa Catalina and San Nicolas Islands suggests that they were probably introduced to these islands by Native Americans. Finally, the recovery of a fox skull from a late Holocene geologic formation on Santa Rosa Island leads me to conclude that small-sized island foxes were present on Santa Rosa Island prior to the arrival of Native Americans.

Unmodified remains. Unmodified fox remains are rare on San Miguel Island, and have been found at only three sites (Table 4). At SMI-525 a burned ulna was recovered from a stratum which was bracketed between corrected radiocarbon dates of 2,981–1,724 yrs. B.P. (Table 4). On Santa Rosa Island, unmodified fox remains have been recovered from one fossil locality and five archaeological sites (Table 4). The absence of adequate provenience data and detailed field notes hampered a more thorough analysis of fox material found in Santa Rosa Island archaeological sites. As a result, I can only say that foxes were present on Santa Rosa Island in Early (7,500 to 3,500 B.P.) through Late Period (800–120 B.P.) sites. Also, the occurrence of an island fox skull in the Upper Tecolote Member of the Santa Rosa Island Formation, which dates from 10,400 to 16,000 years B.P., suggests that foxes must have reached the Northern Channel Islands on their own prior to the arrival of Native Americans 9,000–10,000 years ago.

TABLE 4.—*Island fox skeletal remains recovered from Channel Island archaeological sites.*

Site ¹ Number	Provenience	Chronological Placement	Age (years before present) ² Radiocarbon Estimated		Skeletal elements present	Sources
SAN MIGUEL ISLAND (UCLA Archaeological Survey Site Numbers)						
SMI-1	12-18''	Early/Middle	6,270-3,240	7,000-3,000	1 R. radius and 1 R. hemi-mandible fragment	Erlandson (1989)
SMI-261	Unit E-3, 0-24''	Early/Middle	10,260-2,990	7,500-800	7 limb bones (may be from one individual)	Walker (1978), Collins (unpubl. data), Erlandson (1988)
	Unit F-2				1 pelvis, 1 R. humerus	
	Unit F-4, 12-18''				1 caudal vertebrae	
	Unit F-6, 36-42''				1 caudal vertebrae	
	Unit G-3, 18-24''				1 radius	
	Unit G-5, surface				1 pelvic fragment	
SMI-525	Profile-D, Stratum 14	Middle/Late	3,020-1,460	3,080-770	1 burned proximal end of ulna	Walker and Snethkamp (1984)
SANTA ROSA ISLAND (UCLA Archaeological Survey Site Numbers)						
SRI-1	Cemetery A, Burial 1	Early		7,500-3,500	4 skulls (3 with mandibles, 2 mandibles only)	Orr (1968)
SRI-2A		Middle/Late	1,910-800	1,600-1,200	1 ulna	Orr (1968) King (1981), Glas-sow et al. (1983)
	Cemetery A, Burial 4, Level 2				5 partial skulls (3 with mandibles), 1 complete skeleton	Orr (1968) King (1981)
SRI-2B	Cemetery A, Plot C-2 Cemetery B, Trench B	Late Late	600 ± 70	700-550	3 partial skulls (2 with mandibles, assorted postcranial elements)	Glassow et al. (1983), Orr (1968), King (1981)
SRI-3	none	Early	7,230-4,000	7,500-3,500	2 skulls, 1 ulna	Glassow et al. (1983), Orr (1968), King (1981), Erlandson (1988, 1989)

TABLE 4.—*Island fox skeletal remains recovered from Channel Island archaeological sites. (continued)*

Site ¹ Number	Provenience	Chronological Placement	Age (years before present) ²		Skeletal elements present	Sources
			Radiocarbon	Estimated		
SRI-4	none	Early/Middle	6,670-2,160	7,500-800	1 partial skull	Glassow et al. (1983), Orr (1968), King (1981)
SRI-41	Cemetery C, Sec. II	Late		800-120	1 skull with mandible	Orr (1968), King (1981)
Tecolote Cyn.	Upper Tecolote Member	Late Pleistocene	16,000-10,400+		1 skull with mandible	Orr (1968)
SANTA CRUZ ISLAND (University of California, Berkeley Site Numbers)						
SCrI-3	(Olson's excavations)	Early		4,300-3,300		Hoover (1971), Glassow (1980), Collins (unpubl. data)
SCrI-3	Pit A, 0-2' Pit F, 0-1' (Van Valkenburgh's excavations)	Early		5,400-4,300	1 R. mandible, 1 partial pelvis 1 humerus, 1 radius 1 complete skeleton found in a grave (burial)	Van Valkenburgh (1933), King (1981)
SCrI-3	(Wilcoxon's excavations) Unit 6A, Central, 70-80cm	Early/Middle	5,325-1,315	5,500-3,500 3,500	1 skull, 14 post cranial elements	Hoover (1971), Breschini et al. (1988), Wilcoxon (pers comm), Col- lins (unpubl. data)
	Unit 6A, Central, 100-110cm			3,500	4 metacarples	
	Unit 6B, North, 40-50 cm			5,500-3,500	fragments from 1 skull and pelvis	
	Unit 6B, North, 70-80cm			5,500-3,500	portion of left pelvis	
	Trench 6, 0-40cm			3,500	3 partial mandibles, 1 radius, 1 axis vertebrae, and 5 teeth	
	Trench 2A, Central, 60-70cm			5,500-3,500	1 right anterior portion of ramus (burnt)	
	Trench 2A, Central, 100-110cm			5,500-3,500 5,500-3,500	1 R. anterior portion of mandible 1 R. anterior portion of mandible	

	Unit 11-B, Central, 210-220cm		5,500	fragments of R. mandible, ½ of a pelvis	
	Unit 32-B, South, 50-60cm		3,500	2 mandibles, piece of skull	
SCrI-83	(Roger's/Olson's excavations) Site 3, Pit A, Sec 2, 2-4' Site 3, Pit A, Sec 3, 2'-4'2'' Site 3, Pit DD-1, 3' Site 3, C-21, 18'' Site 3, X3/X2, 3'9''	Middle	3,500-800	1 R. mandible 2 partial skulls, 1 R. mandible	Hoover (1971), King (1981), Col- lins (unpubl. data)
			750-650	complete skull (ritual burial) skull 1 partial cranium (posterior portions)	
SCrI-100	(Olson's excavations)	Middle/Late	900-700		Hoover (1971), King (1981), Col- lins (unpubl. data), Fisher (1930)
	Pit B-9, Casual Pit C-11, 3' Pit C-14, 5' Pit D-5			partial cranium lower premolar 3 1 femur, 1 thoracic vertebrae 2 skulls (Associated with a human burial)	
	Pit D-8			1 femur, 1 tibia, 1 complete pelvis, 1 crushed cranium	
	Pit E-2 Pit H, 3'3'6''			posterior portion of the cranium 3 femurs, 2 partial pelvis, 2 ulna, 1 tibia, 2 radius, 2 vertebrae, fragments of skull	
	Pit H, 3'6''-4'			1 pelvis, 1 femur, 1 ulna, 1 radius, pieces of a skull	
	Pit H, 4'6''-5' Pit H, 5'-5'6''			1 lumbar vertebrae posterior portion of skull, 1 lumbar vertebrae	
	Pit H, 6'6''-7'			3 postcranial elements, fragments of skull and lower mandible	
	Pit H, 7'-7'6''			partial pelvis	

TABLE 4.—Island fox skeletal remains recovered from Channel Island archaeological sites. (continued)

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Site ¹ Number	Provenience	Chronological Placement	Age (years before present) ²		Skeletal elements present	Sources
			Radiocarbon	Estimated		
SCrI-122	Pit H, 7'6"-8' Casual				1 atlas vertebrae 4 partial skulls, 1 L. mandible	
	(Olson's excavations) Pit A, Level I, 2' Pat A, Level II, 1'4"	Late		800-120	1 partial skull 1 skull	Hoover (1971), King (1981), Collins (unpubl. data)
SCrI-131	Pit 4, 3'-5'2"	Late		800-120	2 skulls (associated with human burials)	Hoover (1971), King (1981)
SCrI-147	(Olson's excavation) Pit A, 1'-2'	Late		800-120	5 postcranial elements, fragments of juv. skull	Hoover (1971), King (1981)
SCrI-147	(Spaulding's excavation) Unit 1, E. Trench, Cut 6, Sec. N.	Middle/Late	2,975-425 1,065 ± 110	3,500-700	1 lower canine	Breschini et al. (1988), Collins (unpubl. data)
	Unit 1, W. Trench, Cut 23, Sec. L.				1 L. mandible	
	Unit 1, Entire Trench, Cut 30				1 radius, 1 ulna (butcher marks present)	
	Unit 1, Central Block, Cut 9				1 juvenile humerus	
	Column Sample, Level J Unit 2, Cut 18				skull 2 femurs, 1 ulna, 1 radius, 1 humerus, posterior portion of skull	
SCrI-206	Level J				posterior elements of skull	Collins (unpubl. data)

SAN NICOLAS ISLAND (UCLA Archaeological Survey Site Numbers)

COLLINS

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SNI-7	none				20 complete/partial skeletons (20 skulls)	Orr (1948 Field Notes)
SNI-II	Mound A, upper component Base of midden	Middle/Late	2,220-573 ± 110		1 R. mandible, 1 proximal epiphysis of R. tibia partial skull and skeleton eroding out of base of midden (SBMNH 2304)	Bleitz-Sanburg (1987) Kovach (pers. comm.)
SNI-51	18-30"	Late		800-120	1 skull, 1 mandible	Rozaire (1959)
SNI-119	Pit 2, 4-18"				1 mandible, 1 L & R humerus, 1 femur	Collins (unpubl. data)
Unspecified "Indian Midden"					30 whole/partial skulls, 9 mandibles	Collins (unpubl. data)
SANTA CATALINA ISLAND (UCLA Archaeological Survey Site Numbers)						
SCal-17	none	Early/Middle	3,880 ± 250	3,880-800	2 mandibles and fragment of 1 pelvis	Meighan (1959), Drover et al. (1979)
SCal-45	10-40cm	Middle		1,450-1,050	2 radius, 1 scapula	Rosen (1980)
SCal-137	Unit 2, level 2 and 3	Late	270-330 ± 100		1 L. and 1 R. tibia, distal end of humerus	Rosenthal (1988), Cottrell et al (1980)
SAN CLEMENTE ISLAND (UCLA Archaeological Survey Site Numbers)						
Pyramid Cove	(Test Pit) 18"	Late		800-120	1 tibia	Woodward (unpubl. notes)
SCI-43C	Eel Point Area C, Unit 4, Feature D, 160-175cm Area C, Unit 6, Feature 0, 175-190cm Area C, Test Pit 2, (Ext. A), 120-135cm	Early/Middle	4,300-3,005		2 complete pup skeletons (burials) partial adult skeleton (burial)	Salls (1988)
			3,400		25 miscellaneous postcranial bones representing one individual	
SCI-48	0-29'	Historic		800-120	1 humerus	McKusick and Warren (1959)

TABLE 4.—Island fox skeletal remains recovered from Channel Island archaeological sites. (continued)

Site ¹ Number	Provenience	Chronological Placement	Age (years before present) ²		Skeletal elements present	Sources
			Radiocarbon	Estimated		
SCI-1215	Nursery Site Unit 4-5, W10, 50-60cm N69-70, W13, 30-40cm	Middle/Late	1,490 ± 30	3,500-800	partial adult skeleton (burial ?) 1 miscellaneous bone	Salls (1988), Bleitz (pers. comm.)
SCI-1524	Lemon Tank Unit O-N, 18E, 40-50cm Unit O-N, 22E, 20-30cm Unit O-N, 26E, 0-10cm Unit O-N, 34E, 0-10cm Unit 7S, 15E, 20-30cm, Feature R6 Unit 7S, 17E, 10-20cm, Feature 125 Unit 8S, 17E, 10-20cm, Feature 96 Unit 13S, 15E, 30-40, Feature 48 Unit 13S, 19E, 30-40cm, Feature 140 Unit 17S, OW, 20-30cm, Feature 109	Late		800-120	1 broken tooth 2 miscellaneous bones Burial ? 1 pup (10 bones) 1 miscellaneous bone fragment Burial 1 pup with 8 beads Burial 1 adult Burial 1 pup Burial 1 pup with numerous artifacts Burial 1 pup Burial 1 pup	Rabb (pers. comm.), Bleitz (pers. comm.)

¹For site concordance of Northern Channel Island Sites with other numbering systems see Glassow (1977).²Unless otherwise noted the radiocarbon dates listed here are all uncorrected dates and most of the estimated ages used in this table are taken from King (1981:Table 1) Early: 7500-3500 B.P., Middle: 3500-800 B.P., Late: 800-120 B.P.

+ The one fossil island fox specimen was excavated by Orr from the upper Tecolote member in Tecolote Canyon on Santa Rosa Island. This geological stratum was dated to 10,400-16,000 radiocarbon years B.P. (Orr 1968). This particular fossil was not found to be associated with any archaeological material.

Seven Santa Cruz Island sites contained unmodified island fox remains (Table 4). Most of the material recovered from these sites had provenience data. Fox remains were recovered from Early, Middle and Late Period sites, which suggests that they were present on Santa Cruz Island for at least as long as Native Americans. Fox remains were found throughout all levels of SCrI-3 and were dated, using temporally diagnostic artifacts, at 5,500–3,500 years B.P. At SCrI-147, a Late Period site, fox remains were recovered from levels that were radiocarbon dated at 970 to $1,100 \pm 100$ yrs. B.P. (Table 4).

While fox remains are common in archaeological sites on San Nicolas Island, most of the material lacks provenience or site data and is listed only as having come from "Indian middens." Unmodified fox remains with site data have been recovered from four Late Period sites on San Nicolas Island (Table 4). Orr (1948, unpubl. field notes) collected twenty partial and/or complete fox skeletons from SNI-7 but did not record any provenience data for this material. The earliest record of foxes on San Nicolas Island comes from SNI-11 where two fox bones were found in the upper stratum of mound A, which has been radiocarbon dated at $2,220-573 \pm 110$ yrs. B.P. (Bleitz-Sandburg 1987). Occurrence of fox material only in the upper levels of San Nicolas Island archaeological sites, coupled with the large proportion of specimens recovered from the surface of "midden" sites, implies that island foxes are a fairly recent (i.e., post 2,200 yrs. B.P.) introduction to the island.

Fox remains are rare in archaeological sites on Santa Catalina Island. They have been recovered from one Middle and two Late Period sites (Table 4). Fox bones from the Little Harbor site (SCaI-17) lack provenience data. Therefore, it is possible to say only that foxes first appear in the archaeological record on Santa Catalina Island sometime between 3,880 to 800 years B.P., which is believed to be the length of time that the Little Harbor Site was inhabited (Meighan 1959). The absence of fox from Early Period sites on Santa Catalina Island suggests that they were probably introduced to the island by Indians sometime between 3,880 and 800 years B.P.

On San Clemente Island, unmodified fox remains have been found in four Late Period/Historic sites, and one Early/Middle Period site (Table 4). The occurrence of fox remains at the Eel Point Site (SCII-43C) below a level that had a reservoir-adjusted radiocarbon shell date of 3,400 yrs. B.P. (Salls 1988) suggests that foxes first reached San Clemente Island sometime between 4,300 and 3,400 years B.P. when this portion of the Eel Point Site was believed to have been occupied (Salls 1988).

Intentional burials. A total of 39 intentional burials of island foxes have been recovered from Santa Rosa, Santa Cruz, San Nicolas and San Clemente Islands (Table 4). On the Northern Channel Islands several fox burials have been directly associated with human remains; this has not been the case on the Southern Channel Islands. Nearly all of the fox material recovered by Orr from Santa Rosa Island sites was found during cemetery excavations (Orr 1968). However, lack of detailed field records and adequate provenience data prevented further analysis. Occurrence of fox remains in human cemeteries on Santa Rosa Island suggests possible existence of ritual/ceremonial customs associated with foxes.

Well-documented excavations on Santa Cruz Island provide evidence of seven direct human-island fox burial associations. Three fox burials recovered by Olson suggest ceremonial or ritualistic practices (Olson unpubl. Field Notebook 3). In the first, two fox skulls were associated with a child burial. In the second, a fox skull was situated between the pelvises of an adult man and woman. In the third, a fox skull was found wrapped in a mat fragment with two bone tubes which were coated with asphalt and wrapped with string (Hoover 1971). Several other investigators have observed foxes in burial contexts on Santa Cruz Island. According to Moodie, the burial of a fox skull (LACM-30754) between two abalone shells could represent burial of personal belongings, charms and/or a pet (Moodie unpubl. Field Notes). A complete fox skeleton was found in a human grave at SCRI-3 while two human burials at SCRI-131 each contained a fox skull (Van Valkenberg 1933). The island fox/human burial associations recorded in the archaeological record on Santa Cruz Island suggest that Chumash on Santa Cruz Island assigned some religious or ceremonial significance to island foxes and thus gave them special mortuary treatment.

Although a number of island fox burials have been recorded for San Nicolas Island, none were directly associated with human remains or with artifacts. Perhaps the most notable find was the recovery of 20 partial and/or complete island fox skeletons from SNI-7 (Orr 1948, unpubl. Field Notes). Given the large number of specimens and their proximity to one another within the site, I believe that these foxes were probably buried for disposal after having been skinned for their pelts. Butcher marks on some of the specimens are consistent with this interpretation. The archaeological record on San Nicolas Island suggests that foxes were not given any special ceremonial or ritual status by the Gabrielino (Nicoleño) Indians.

Although eleven fox burials have been recovered from three San Clemente Island sites (Table 4), none were found in direct association with human remains. At the Eel Point Site (SCII-43C) a dual burial of two fox pups was associated with ritual offerings of hematite and beads whereas the partial skeleton of an adult female fox was recovered without artifacts. The skeleton of an adult fox was found at the Nursery Site (SCII-1215). Recent excavations at the Lemon Tank site (SCII-1524) have uncovered a total of 20 ritual animal burials (Salls and Hale in litt.). Seven of these were foxes. Six were very young pups and two were associated with ritual offerings. The pup recovered from Unit 13S 15E was buried with a large abalone shell which contained a scraper, 22 beads, a bowl, a pendant, and drilled abalone shell (Table 4). Fox burials found at the Lemon Tank site probably represent ritual burials that were associated with canid killing or mourning ceremonies (Salls and Hale in litt.).

DISCUSSION

Geologic and Eustatic Evidence of Landbridges in the Southern California Borderland.—Geologists have not found evidence to suggest that there were any mainland-to-island landbridges connecting the California Channel Islands to the mainland during the Pleistocene (Junger and Johnson 1980; Vedder and Howell 1980; Johnson

1983). To produce landbridges, the present sea level would have had to have been 232 meters lower than it is at present. This is much lower than current estimates of -120 to -165 m for glacially controlled lowering of sea level during the Pleistocene (Johnson 1978).

The Southern Channel Islands were never connected to one another, to the mainland, nor to any of the Northern Channel Islands during the Pleistocene (Johnson 1983). The only islands that were connected then were the four Northern Channel Islands, which coalesced a number of times during the glacial episodes of the Pleistocene to form the superisland known as Santarosae. Santarosae last existed during the maximum Wisconsin glaciation of 24,000-14,000 B.P. Sea level began dropping about 28,000 B.P. and rapidly declined to a low of -120 m by 17,000-18,000 B.P. (Johnson 1978; 1983). The Santarosae landmass began to break up when sea level began rising about 16,000-17,000 B.P. (Vedder and Howell 1980; Johnson 1983). Anacapa Island was the first to separate from the Santarosae landmass about 12,000 B.P., followed by Santa Cruz Island about 11,500 B.P., and finally by San Miguel and Santa Rosa Islands about 9,500 B.P. (Johnson 1978; 1983). The present sea level was reached about 6,000 to 7,000 years ago. Thus, Santa Cruz Island has been isolated from the other Northern Channel Islands for about 2,000 years longer than San Miguel and Santa Rosa Islands have been isolated from each other. The recent geological record is important for understanding the origin and dispersal of island foxes because longer isolation could theoretically be evidenced by greater morphological divergence and because landbridges cannot be used to explain the dispersal of island foxes to the Southern Channel Islands.

Biotic Dispersal Mechanisms.—In the absence of landbridges, alternative explanations are needed to explain the dispersal of foxes to all six of the islands on which they presently occur. Overwater dispersal, which could occur by swimming, rafting or transport via human watercraft, offers the only plausible mechanism to explain present distribution of foxes on six widely separated islands. There is no evidence to suggest that foxes are good swimmers or that they could swim a distance of 6 km, which was probably the narrowest distance to occur during the Pleistocene between the mainland and any of the islands. Wenner and Johnson (1980) present a persuasive argument that overwater dispersal via debris rafts was probably the mechanism by which mainland foxes first colonized one of the Channel Islands. The fact that an already small-sized island fox was present on Santarosae at least 16,000 years B.P., coupled with the occurrence of small-sized fox bones throughout Indian occupation on Santa Rosa and Santa Cruz Islands, infers that Native Americans were not responsible for the initial transport of foxes from the mainland.

Dispersal of foxes to the Southern Channel Islands on rafts of floating debris, either directly from the mainland or from the Northern Channel Islands, is far more difficult to accept since this would require three independent successful colonization events. Evidence from both the archaeological record and the phenetic analyses reported here suggests that Indians were probably responsible for moving foxes from the Northern to the Southern Channel Islands.

Hypotheses on island colonizations. Although questions persist relative to how and when island foxes colonized the islands, morphological similarities observed between present-day and archaeological fox samples, coupled with the record of island foxes in archaeological sites provide clues relative to the role which Indians played in establishing foxes on some of the islands, and infer probable scenarios for the historical colonization sequence of the islands. Misclassification of archaeological specimens to islands other than where they were excavated from provides evidence of possible gene flow and routes for colonization.

Several lines of evidence refute a human assisted dispersal of gray foxes from the mainland to the Channel Islands. The recovery of a small fossil island-fox-sized skull from Santa Rosa Island, dated at 10,400 to 16,000 radiocarbon years B.P. (Orr 1968), coupled with the occurrence of island fox remains in middens on Santa Cruz and Santa Rosa Islands throughout the time of Indian occupancy (Table 4), suggest that gray foxes reached the Northern Channel Islands on their own accord by chance overwater dispersal prior to the arrival of Native Americans 9-10,000 years B.P. Several lines of evidence argue against a pre-Holocene colonization of the Southern Channel Islands by foxes. The absence of large gray-fox-sized fossils, along with the occurrence of island fox remains only in Middle and Late Period archaeological sites on the Southern Channel Islands (Table 4), infers that foxes from the mainland were probably not used by Native Americans to establish fox populations on San Nicolas, Santa Catalina and San Clemente Islands.

Determining the time of initial colonization of the Northern Channel Islands by gray foxes is extremely difficult given the poor fossil record for these islands. However, the morphologic data leads me to conclude that gray foxes probably first reached the Northern Channel Islands in the late Pleistocene (i.e. 40,000-25,000 B.P.) just prior to the period of maximum Wisconsin glaciation of 24,000-14,000 B.P. During a relatively short period of isolation (i.e. 10,000 yrs.) these foxes rapidly evolved to their present small body size as a result of unique selection factors such as inbreeding and resource limitations. This rapid rate of change could account for the absence of fossil evidence of intermediate forms between gray foxes and island foxes, since the principal size change probably took place in a relatively short time frame. Island foxes weigh 31 to 46% less than mainland gray foxes. That such a significant reduction could occur in less than 40,000 years is not too surprising. Evidence from elsewhere in the world suggests that changes in body size in small allopatric populations of mammals on islands occurs very rapidly (Sondaar 1977; Marshall and Corruccini 1978). Red deer (*Cervus elaphus*) on Jersey Island off the coast of France, for example, showed a sixfold weight reduction in less than 6,000 years (Lister 1989). The presence of a moderate amount of morphologic divergence (Figs. 3 and 4) in present-day island fox populations, which range in age from 2,200 to 11,500 years old, is further proof that island foxes are capable of a fairly rapid rate of evolution.

Small-sized island foxes would have dispersed to the remainder of the Northern Channel Islands during the late Quaternary when these islands last coalesced to form the superisland known as Santarosae around 24,000 to 18,000 B.P. (Johnson 1983). As the glaciers began receding at the end of the last Wiscon-

sin Glacial epoch, 16,000 to 17,000 years ago, Santarosae began to break up. Island foxes became isolated on Santa Cruz Island about 11,500 B.P. and then on San Miguel and Santa Rosa Islands at 9,500 B.P. The degree of morphological divergence observed in present-day Northern Channel Island fox populations correlates with the recent geologic history as evidenced by the slight divergence in the Santa Cruz Island population and the broad overlap in the San Miguel and Santa Rosa Island populations (Figs. 3 and 4). Following the arrival of Native Americans 9,000-10,000 B.P., genetic interchange of island foxes among the Northern Channel Islands probably occurred via Indian transport. Misclassification of present-day foxes between these three islands (Table 3) indicates that Indians may have been moving foxes between the Northern Channel Islands.

Setting exact times for the colonization of the Southern Channel Islands is more difficult since the fossil and subfossil records are incomplete. If foxes were present on any of the Southern Channel Islands prior to the arrival of Native Americans, then I would have expected their remains to be present in middens throughout Indian occupation like they are on the Northern Channel Islands. This is not the case. Rather, foxes do not appear in an archaeological context until about 3,400 B.P. on San Clemente Island and 2,200 B.P. on San Nicolas Island (Table 4). Island foxes show up on Santa Catalina sometime between 3,880 and 800 B.P. (Table 4). Thus, island foxes probably reached the Southern Channel Islands via transport in Indian watercraft well after the arrival of Native Americans.

The morphometric analyses also support a fairly recent, post-Holocene introduction of island foxes from the Northern Channel Islands to the Southern Channel Islands by Native Americans. Morphologic overlap between present-day San Nicolas, Santa Catalina and Santa Cruz island fox populations (Figs. 3 and 4), along with the misclassification of specimens between these three islands (Table 3), suggests that foxes from Santa Cruz Island may have been used to establish the San Nicolas and Santa Catalina populations. Classification of archaeological specimens from San Nicolas Island to four other island samples (Table 3) indicates that island foxes were probably occasionally being transported between the islands by Indians through the Late Period (800-120 yrs. B.P.).

Determining the origin and setting an exact time for the colonization of San Clemente Island by island foxes is problematic. Grinnell *et al.* (1937) mention that Salvador Ramirez claimed to have introduced a pair of island foxes from Santa Catalina Island to San Clemente Island in 1875. However, W.E. Greenwell observed foxes on San Clemente Island in 1860 (Johnson 1975). This, along with J.G. Cooper's capture of an island fox on San Clemente Island in July 1863, establishes that island foxes were present on San Clemente Island prior to Ramirez's efforts. The occurrence of island foxes in five archaeological sites on San Clemente Island offers further evidence to suggest that foxes were present on this island prior to 1875. The recovery of island fox bone material from the Eel Point Site (SCII-43C) below a level which has been radiocarbon dated at 3,400 yrs. B.P. suggests that island foxes were introduced to this island by Indians sometime after 4,300 B.P. but before 3,400 B.P., which is the length of time that this portion of the SCII-43C site is believed to have been inhabited (Salls 1988).

Whether the population on San Clemente Island resulted from a single or multiple colonizations from one of the other Southern Channel Islands or from

one of the Northern Channel Islands remains problematical. Multiple discriminant function analysis of present-day island fox populations does indicate slight divergence of the San Clemente population from all other island fox populations. This, coupled with the high proportion of correctly classified individuals (94–96%) in the Jackknifed classification procedure of the discriminant function analyses (Table 3), suggest that the San Clemente Island population may still be under the constraints of a founder effect resulting in low intra-population variability and high self-fidelity in Jackknifed classification. Small population size coupled with founder effects may have acted to limit morphological variability in the fox population on San Clemente Island. Further work is needed on this population, including examination of allozymic variability, to shed additional light on its origin.

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APPENDIX

List of Specimens Examined

The following is a list of island fox (*Urocyon littoralis*) specimens examined in the morphometric analyses. This list is arranged according to present day samples and archaeological samples. Sample acronyms along with sample size for each locality sample are noted in parentheses. For the present day samples (localities 1-6) only adult specimens (age classes 3-6) and specimens with complete data sets are included in this listing, while all specimens measured for the archaeological analyses are listed. A listing of the complete names for collections in which specimens are housed can be found in the Acknowledgments. All localities listed are from southern California and are indicated on Figure 1.

Locality 1 (SMI; N=37). Santa Barbara Co., San Miguel Island: 3 (CSULB), 4 (LACM), 9 (MVZ), 15 (SBMNH), 4 (SDMNH), 2 (USNM).

Locality 2 (SRI; N=59). Santa Barbara Co., Santa Rosa Island: 16 (LACM), 1 (MPM), 8 (MVZ), 14 (SBMNH), 12 (UCLA), 1 (UILL), 7 (USNM).

Locality 3 (SCrI; N=128). Santa Barbara Co., Santa Cruz Island: 2 (CSULB), 13 (LACM), 7 (MVZ), 40 (SBMNH), 1 (SDMNH), 56 (UCLA), 5 (UCSB), 3 (USNM).

Locality 4 (SMI; N=104). Ventura Co., San Nicolas Island: 1 (CSULB), 1 (KU), 44 (LACM), 6 (MVZ), 23 (SBMNH), 5 (SDMNH), 18 (UCLA), 4 (UCSB), 2 (USNM).

Locality 5 (SCaI; N=37). Los Angeles Co., Santa Catalina Island: 1 (FMNH), 14 (LACM), 6 (MVZ), 1 (SBMNH), 5 (SDMNH), 1 (UCD), 1 (UCLA), 8 (USNM).

Locality 6 (SCII; N=39). Los Angeles Co., San Clemente Island: 13 (LACM), 1 (MCZ), 1 (MVZ), 7 (SBMNH), 5 (SDMNH), 4 (UCLA), 8 (USNM).

SRI Archaeological Sample (SRII; N=20). Santa Barbara Co., Santa Rosa Island: Site 1 (N=2, SBMNH); Site 2, trench B (N=1, SBMNH); Site 2 (N=5, SBMNH); Site 3 (N=2, SBMNH); Site 4 (N=1, SBMNH); Site 25 (N=1, SBMNH); Site 41 (N=2, SBMNH); Site unspecified (N=5, SBMNH); "Indian Midden on Santa Rosa," Site 106 (N=1, LACM).

SCrI Archaeological Sample (SCrII; N=21). Santa Barbara Co., Santa Cruz Island: Christie's, Site 3 (N=5, SBMNH); Cochie Prietos (N=2, SBMNH); Site 3 (N=1, LOWM); Site 83 (N=1, LOWM); Posa Landing, Site 100 (N=6, LOWM); Prisoner's Harbor, Site 240 (N=2, UCSB-AC); Site 333 (N=1, UCSB-AC); Willows, Site 2 (N=2, SBMNH); "Santa Cruz Island Kitchen Middens" (N=1, LACM).

SNi Archaeological Sample (SNII; N=53). Ventura Co., San Nicolas Island: Site 7 (N=20, SBMNH); Thousand Springs, Site 11 (N=1, SBMNH); Site 51 (N=2, LACM); Site 119 (N=1, UCLA); "Indian Shell Mound" (N=10, LACM); "2 mounds on the summit of San Nicolas Island" (N=7, UCLA); No site specified (N=8, LOWM; N=3, UCLA; N=1, UCSB).

SCII Archaeological Sample (SCIII; N=1). Los Angeles Co., San Clemente Island: Site 43C (N=1, UCLA-AC).