Origins and antiquity of the island fox (*Urocyon littoralis*) on California's Channel Islands

Torben C. Rick [a,*], Jon M. Erlandson [b,c], René L. Vellanoweth [d], Todd J. Braje [e], Paul W. Collins [f], Daniel A. Guthrie [g], Thomas W. Stafford Jr. [h]

[a] *Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20013-7012, USA*
[b] *Museum of Natural and Cultural History, University of Oregon, Eugene 97403-1224, USA*
[c] *Department of Anthropology, University of Oregon, Eugene, OR 97403-1218, USA*
[d] *Department of Anthropology, California State University, Los Angeles, CA 90032, USA*
[e] *Department of Anthropology, Humboldt State University, Arcata, CA 95521, USA*
[f] *Department of Vertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara, CA 93105, USA*
[g] *Joint Science Department, Claremont Colleges, Claremont, CA 91711-5916, USA*
[h] *Stafford Research, Inc., 200 Acadia Avenue, Lafayette, CO 80026, USA*

ARTICLE INFO

ABSTRACT

The island fox (*Urocyon littoralis*) is one of few reportedly endemic terrestrial mammals on California's Channel Islands. Questions remain about how and when foxes first colonized the islands, with researchers speculating on a natural, human-assisted, or combined dispersal during the late Pleistocene and/or Holocene. A natural dispersal of foxes to the northern Channel Islands has been supported by reports of a few fox bones from late Pleistocene paleontological localities. Direct AMS ^{14}C dating of these "fossil" fox bones produced dates ranging from ~6400 to 200 cal yr BP, however, postdating human colonization of the islands by several millennia. Although one of these specimens is the earliest securely dated fox from the islands, these new data support the hypothesis that Native Americans introduced foxes to all the Channel Islands in the early to middle Holocene. However, a natural dispersal for the original island colonization cannot be ruled out until further paleontological, archaeological, and genetic studies (especially aDNA [ancient DNA]) are conducted.
Published by University of Washington.

Introduction

The endangered island fox (*Urocyon littoralis*), a diminutive relative of the gray fox (*U. cinereoargenteus*), has been an important apex predator on California's Channel Islands for millennia (Collins, 1993; Moore and Collins, 1995; Roemer et al., 2004). While a great deal is known about island fox ecology, biogeography, and conservation, questions remain about when and how these animals first colonized the Channel Islands (Johnson, 1975, 1983; Wenner and Johnson, 1980; Collins, 1991a; Vellanoweth, 1998; Agenbroad, 2002a). Most research-ers agree that Native Americans introduced the island fox to the southern Channel Islands, probably during the middle to late Holocene (Collins, 1991a,b; Vellanoweth, 1998; Shelley, 2001). Based partly on reports of fox remains from late Pleistocene sediments of the Upper Tecolote Formation on Santa Rosa Island, however, foxes were thought to have reached the northern Channel Islands naturally during the late Pleistocene by rafting across a Santa Barbara Channel narrowed by lower sea levels (Wenner and Johnson, 1980; Collins, 1991a,b, 1993).

Recent AMS (Accelerator Mass Spectrometry) ^{14}C dating of the Upper Tecolote Formation fox specimen to the late Holocene raised questions about the natural dispersal of foxes to the northern islands (Shelley, 2001), but several fox bones from San Miguel Island fossil localities continued to support a possible Pleistocene age for the origins of the island fox (Guthrie, 1993:409). All the San Miguel specimens were found on eroded surfaces where faunal remains of paleontological, archaeological, or recent biological origin could have become mixed.

To help clarify the origins, antiquity, and evolution of island foxes, we obtained direct AMS ^{14}C dates for three island fox bones from the late Pleistocene San Miguel Island fossil localities (Fig. 1). These are the only known specimens that could predate the earliest definitive evidence for human colonization of the northern Channel Islands, approximately 13,000 cal yr BP (Johnson et al., 2002).

Context and background

Divided into northern (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) and southern (San Clemente, Santa Catalina, San Nicolas, and Santa Barbara) groups, California's eight Channel Islands range in size from about 2.6–249 km². Currently between 20–98 km offshore, the islands have not been connected to the mainland during the

* Corresponding author. Fax: +1 (202)357 2208.
E-mail address: rickt@si.edu (T.C. Rick).
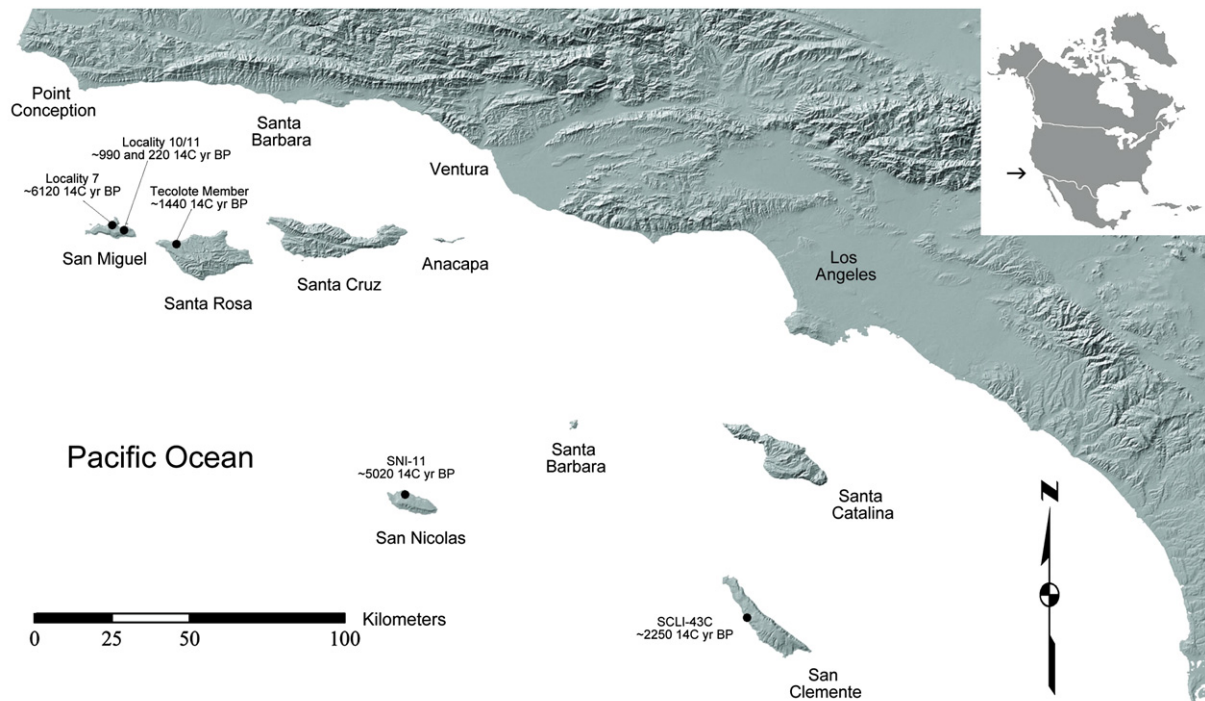
Figure 1. Southern California and the Channel Islands showing the location of directly dated fox specimens and approximate ages (^{14}C yr BP). Tecolote Member, SNI-11, and SCLI-43C are archaeological specimens dated by Shelley (2001).

Quaternary (Johnson, 1983). During glacial periods of the Pleistocene, lower sea levels caused the northern islands to coalesce into a single, larger island (Santarosae), the eastern end of which was only 6–8 km from the mainland (see Porcasi et al., 1999; Kennett et al., 2008). Considerably more dispersed and isolated, the southern islands have remained farther from the mainland and were more difficult for terrestrial animals to colonize.

Island foxes are about the size of a house cat (Fig. 2), with subspecies found on all the islands except Anacapa and Santa Barbara (each ~2.6–3 km^2 in area). Other endemic island terrestrial mammals appear to have been limited primarily to the deer mouse (*Peromyscus maniculatus*), western spotted skunk (*Spilogale gracilis*), western harvest mouse (*Reithrodontomys megalotis*), San Miguel Island vole (*Microtus miguelensis*), and ornate shrew (*Sorex ornatus*; Guthrie, 1998; Schoenherr et al., 1999). Pygmy (*Mammuthus exilis*) and full-sized (*M. columbi*) mammoths lived on the northern islands during the

Pleistocene (Agenbroad, 1998; Thaler, 1998). Mammoths are generally good swimmers that colonized the islands naturally, while foxes are poor over-water dispersers (Wenner and Johnson, 1980; Johnson, 1983; Collins, 1991a).

The focus of extensive conservation, including a captive breeding program, four subspecies of island fox are currently critically endangered due to predation by golden eagles (*Aquila chrysaetos*) and possibly canine diseases (Coonan et al., 2002, 2005; Roemer et al., 2002, 2004; Clifford et al., 2006). Foxes are omnivorous, consuming insects, fruits, mice, small reptiles, marine invertebrates, and other foods, and they prey on deer mice and ground nesting birds (Moore and Collins, 1995). Island foxes are generally docile, show little fear of humans, and are easily tamed (Moore and Collins, 1995).

Island foxes played an important role in the spiritual lives of native Channel Island peoples—the Island Chumash and Tongva (Gabrielino). Island foxes have been found in numerous archaeological sites, were likely semi-domesticates or pets, were harvested for their pelts, and probably served other functions like pest/rodent control (Collins, 1991b). The Chumash and Tongva had extensive exchange networks with the mainland and islands, including trade of a variety of beads, subsistence items, other goods, and likely island foxes (Collins, 1991b; Vellanoweth, 2001; Kennett, 2005).

Despite research at several Channel Island fossil localities (Lipps, 1964; Orr, 1968; Guthrie, 1993, 1998, 2005; Agenbroad, 1998, 2002b; Thaler, 1998; Agenbroad et al., 2005), foxes are rare or absent in paleontological deposits, with bones known from just four localities. The method of accumulation (carnivore dens, owl roosts, etc.) can influence the types of animals found in a fossil deposit. Guthrie (2005:37–38) suggested that many of the fossil localities he has analyzed may have been deposited by bald eagles (*Haliaeetus leucocephalus*), with at least one historic bald eagle nest known to contain a small number (*n* = 10) of island fox bones (Collins et al. 2005). The few fossil specimens are all morphologically similar to modern island foxes with no documented gray foxes or intermediaries. The "Pleistocene" Santa Rosa fox remains consist of three bones from one individual now known to date to 1480–1280 cal yr BP

Figure 2. Adult island fox on San Nicolas Island (photo by R. L. Vellanoweth).

(Shelley, 2001). Once thought to have been lost, there are limited notes available for these bones.

The other fox remains were recovered from three late Pleistocene fossil localities (SMI-V-7, V-10, and V-11) on San Miguel Island (Guthrie, 1993). For SMI-V-7 on Simonton Cove, Guthrie obtained ^{14}C dates of 25,160±380 and >38,000 ^{14}C yr BP for bird (*Fratercula* sp.) bones from the surface. For SMI-V-10 on Cuyler Harbor, he reported a date of 32,143±787 ^{14}C yr BP for a bird (*Chendytes lawi*) bone from the surface. SMI-V-11 has not been dated but is located near SMI-V-10. Archaeological sites are located in the immediate vicinity of all three localities and extensive erosion may have mixed paleontological, archaeological, and recent biological materials on these surfaces. Consequently, these San Miguel Island fox remains could date anywhere from the late Pleistocene (~38,000 ^{14}C yr BP) to the Historic period.

Methods

The three San Miguel localities produced a total of nine fox bones (long bones, vertebrae, and skull fragments) from three individuals (one at each locality). We selected one relatively large bone from each locality for AMS dating, including an ulna from locality SMI-V-7 and femur fragments from localities V-10 and V-11 housed at the Santa Barbara Museum of Natural History (SBMNH). The bones are generally well preserved with two of the specimens (SBMNH 138 and 397) etched and pitted on the surface, probably from being digested by another animal and/or sand blasting. The bones were sampled and analyzed at Stafford Laboratories with protocols outlined in Waters and Stafford (2007); XAD purified collagen was dated from all three bones. During collagen extraction, protein preservation was similar to that expected for recent bones rather than Pleistocene material. Graphite targets were analyzed at the Keck Carbon Cycle AMS Facility in the Earth System Science Department, University of California-Irvine.

Results

Calibrated ^{14}C dates for the three island fox specimens range from ca. 6400 cal yr BP to the Historic period—much younger than the late Pleistocene dates available for other bones from the same localities (Table 1). The locality V-7 ulna produced a date of 6120±25 ^{14}C yr BP (6400–6210 cal yr BP; UCIAMS-40173), currently the oldest securely dated fox from the Channel Islands. The locality V-10 and V-11 femora were dated to 990±15 ^{14}C yr BP (950–800 cal yr BP; UCIAMS-38253) and 220±15 ^{14}C yr BP (300–0 cal yr BP; UCIAMS-38252), respectively. Like the ^{14}C dates reported here, direct AMS dating of the Santa Rosa fossil fox remains provided a date of 1440±50 ^{14}C yr BP (1480–1280 cal yr BP; UCR-3563; Shelley, 2001).

AMS measured $\delta^{13}C$ values were also obtained for the three San Miguel Island fox specimens, with the preliminary values ranging from −11.6‰ for the ca. 6400 yr old specimen to −18.4‰ and −19.5‰ for the two late Holocene specimens. Several studies have shown that stable carbon and nitrogen isotopes from bone collagen are a reliable proxy of general dietary patterns, especially the degree of marine or terrestrial contributions to the diet (Chisholm et al., 1982; Schoeninger et al., 1983; Walker and DeNiro, 1986; Goldberg, 1993; Newsome et al., 2004). The oldest fox specimen in our sample, with a value of −11.6‰, is enriched in marine carbon and comparable to values obtained from marine mammals (see Walker and DeNiro, 1986; Newsome et al., 2004), suggesting the complete proteins this animal consumed came almost exclusively from marine foods. The other two values (−18.4‰ and −19.5‰) suggest a diet considerably higher in terrestrial foods, and are comparable to land mammal values reported by Walker and DeNiro (1986) and values reported for two modern island fox (−18.3‰ and −16.0‰) specimens from San Clemente Island (Goldberg, 1993:181).

These preliminary data suggest that at least some island foxes were consuming large amounts of marine foods. It is possible that foxes were scavenging marine carrion on beaches, as modern foxes are known to do (Moore and Collins, 1995), scavenged marine foods around Native American villages, or were fed marine foods by Native Americans. Given the high marine signature for the 6400 yr old fox, the two latter possibilities seem probable, especially if foxes were semi-domesticates or pets. Because of the relatively small size of our preliminary sample, however, more stable isotope studies of fox bones are needed to assess their ancient diet.

Discussion

Prior to our study, several researchers speculated that island foxes evolved from gray foxes that arrived on the northern islands by chance-rafting during the Pleistocene, with Native Americans later transporting island foxes to the southern islands (Wenner and Johnson, 1980; Collins, 1991a; Vellanoweth, 1998). Others speculated on human-assisted dispersal of foxes to all the islands (Vellanoweth, 1998; Kennett, 2005:49). Through analysis of island fox and mainland gray fox skeletons, Collins (1991a, 1993) suggested that gray foxes may have first colonized the islands just prior to the Wisconsin glaciation (~25,000 ^{14}C yr BP), and under selective pressure and inbreeding rapidly dwarfed into the small-sized island fox in 10,000 yr or less. This proposition was supported by morphometric and genetic data interpreted in light of the "fossil" Santa Rosa Island fox specimen now known to be of late Holocene age (see Collins, 1991a, 1993; Wayne et al., 1991; Goldstein et al., 1999; Aguilar et al., 2004). These dates were also based on the timing of the breakup of Pleistocene Santarosae with foxes thought to have arrived while the northern islands were still connected and closer to the mainland, an event now thought to have occurred between about 10,000 and 9000 cal yr BP, some 4000 to 3000 yr after human colonization (see Porcasi et al., 1999; Kennett et al., 2008). Because the genetic and

Table 1
AMS ^{14}C dates on paleontological island fox bones

Locality/provenience	Museum catalog number[a]	AMS lab number[b]	Material dated	$\delta^{13}C$ ‰ VPDB	Conventional radiocarbon age, ^{14}C yr BP±1 SD	cal yr BP age range (2 sigma)[d]
San Miguel Island Locality V-7c	SBMNH-127	UCIAMS-40173	Bone collagen[c]	−11.6	6120±25	6400–6210
San Miguel Island Locality V-10c	SBMNH-397	UCIAMS- 38253	Bone collagen[c]	−18.4	990±15	950–800
San Miguel Island Locality V-11	SBMNH-138	UCIAMS- 38252	Bone collagen[c]	−19.5	220±15	300–0
Santa Rosa Island Upper Tecolote Member[e]	SBMNH-2327	UCR-3563	Bone collagen	n/a	1440±50	1480–1280

[a] SBMNH— Santa Barbara Museum of Natural History.

[b] UCIAMS— University of California-Irvine Accelerator Mass Spectrometry Facility; UCR— University of California-Riverside Radiocarbon Laboratory.

[c] The chemical fraction dated is the XAD-purified hydrolyzed gelatin hydrolyzate of KOH-Collagen (see Waters and Stafford, 2007). AMS measured $\delta^{13}C$ values have an error of roughly 2‰.

[d] All dates were calibrated using CALIB 5.0.2 (Stuiver and Reimer, 1993; Stuiver et al., 2005). UCIAMS-38253, UCIAMS-38252, and UCR-3563 were calibrated as terrestrial samples. Because UCIAMS-40173 was enriched in marine carbon we calibrated this sample as a marine sample applying a ΔR of 225±35. Calibrating UCIAMS-40173 as a terrestrial sample makes it roughly 600 yr older with a 2 sigma range of 7160–6910 cal yr BP.

[e] Date obtained from Shelley (2001:30).

morphologic data do not provide absolute ages, the fossil and archaeological records supply the most direct means of documenting the chronology of island fox dispersal.

Numerous paleontological projects have been conducted on the Channel Islands, including research in paleontological and archaeological deposits at Daisy Cave (CA-SMI-261) on San Miguel (Guthrie, 1980; Walker, 1980; Erlandson et al., 1996), late Pleistocene and Holocene deposits at Arlington Springs (CA-SRI-173) on Santa Rosa (Johnson et al., 2002), late Pleistocene localities on San Miguel and Santa Rosa (Guthrie, 1993, 1998, 2005), late Pleistocene deposits on Anacapa (Lipps, 1964), and several mammoth localities on Santa Rosa, San Miguel, and Santa Cruz (Orr, 1968; Cushing et al., 1984; Gray and Harz, 1998; Agenbroad 1998, 2002b; Thaler, 1998; Agenbroad et al., 2005). These projects have yielded faunal assemblages that include abundant avian materials, extant and extinct micro-mammals, reptiles and amphibians, and mammoths (Guthrie, 1980, 1993; Walker, 1980; Agenbroad, 1998). Orr (1968) estimated that a minimum of 200 mammoths had been identified by the early 1960s. Agenbroad's (1998, 2002b) surveys on Santa Rosa, San Miguel, and Santa Cruz identified over 140 new mammoth localities.

In contrast, island foxes are rare or absent in fossil deposits and the few that have been found are all Holocene in age. Moreover, at Daisy Cave, pre-human deposits lack island foxes, yet post-human archaeological deposits contain them (Walker, 1980). If island foxes originated from a small founding population prior to human arrival, finding the remains of those presumably full-sized foxes in the fossil or archaeological records would be difficult. However, the complete absence of island foxes in pre-human age deposits is peculiar, especially given the large samples of birds, micro-mammals, and mammoths that have been recovered in Quaternary deposits.

Island fox remains occur in at least 40 island archaeological sites, but many of these are from fairly poorly dated multi-component sites (Table 2). A few of the foxes identified in island sites (e.g., SRI-1, SRI-3, SMI-261, and SCLI-43c) could conceivably predate the ca. 6400 cal yr BP date reported here. Recent excavation of several sites dated between 11,000 and 8000 cal yr BP on San Miguel, Santa Rosa, and Santa Cruz islands has produced few mammal bones and no foxes (see Erlandson et al., 2007), however, suggesting that foxes may have arrived on the islands sometime after about 10,000–9000 cal yr BP. The ca. 6400–6200 cal yr BP fox dates reported here are about the same age as the earliest securely dated Channel Island dog remains (Rick et al., 2008).

Recent studies from elsewhere around the world lend support to a human-assisted dispersal of foxes to all the Channel Islands. For example, White (2004) described the translocation of the northern common cuscus (*Phalanger orientalis*) to New Ireland by hunter-gatherers as early as 20,000 yr ago. Ancient human translocation of animals has also been documented on islands in the Caribbean, North Atlantic, Mediterranean, and Pacific (Grayson, 2001). Researchers have also suggested that most of the extant mammalian fauna on the Channel Islands and some reptiles were intentionally or unintentionally introduced by Native Americans, including skunks, harvest mice, deer mice, shrews, ground squirrels, rattlesnakes, dogs, and foxes (Walker, 1980; Wenner and Johnson, 1980; Johnson, 1983; Collins and George, 1990; Guthrie, 1998; Rick et al., 2008). When the late Holocene Santa Rosa fox specimen was still thought to be late Pleistocene in age, Wenner and Johnson (1980:515–516) argued that foxes likely rafted out accidentally to the northern islands during storms, but they noted that "it is also conceivable that the early aborigines initially brought the first fox to one or another of the superislands," a proposition now supported by the fossil and archaeological records.

Additional support for the antiquity of foxes on the Channel Islands may come from the extinction of *Chendytes lawi* (flightless scoter) and *Fratercula dowi* (a burrowing nesting alcid). Based on the abundance

Table 2
Archaeological and paleontological island fox remains from the Channel Islands[a]

Site or locality	Age (cal yr BP)	NISP	MNI	References
Archaeological specimens				
SMI-1	7140–3250	2	1	Collins (1991a)
SMI-87	4790–2340	1	1	–
SMI-261	11,600–640	13	1	Collins (1991a)
SMI-470	460–Historic	1	1	–
SMI-481	1410–920	n/a	1	–
SMI-525	3230–520	1	1	Collins (1991a)
SMI-603	4570–4260	1	1	–
SRI-1	9260–2110	9	6	Collins (1991a)
SRI-2	2030–Historic	>16	9	Collins (1991a,b)
SRI-3	8300–2360	3	2	Collins (1991a)
SRI-4	7410–2130	1	1	Collins (1991a)
SRI-25	n/a	2	1	Shelley (2001)
SRI-41	5470–3630	2	1	Collins (1991a)
SRI-365	n/a	n/a	1	–
SCRI-122	Late Holocene	2	2	Collins (1991a)
SCRI-131	Late Holocene	2	2	Collins (1991a)
SCRI-147	Late Holocene	>18	5	Collins (1991a)
SCRI-206	n/a	1	1	Collins (1991a)
SCRI-236 (aka SCRI-83)	Late Holocene	7	6	Collins (1991a)
SCRI-240	Historic	5	n/a	Noah (2005)
SCRI-306	670–410	n/a	n/a	Arnold (1987)
SCRI-328/330	Historic	9	n/a	Noah (2005)
SCRI-333 (aka SCRI-3)	6170–1260	>45	13	Collins (1991a)
SCRI-474 (aka SCRI-100)	Late Holocene	>46	11	Collins (1991a)
SNI-7	n/a	n/a	20	Collins (1991a,b)
SNI-11	5890–5660; 3840–510	>5	2	Collins (1991a)
SNI-25	740–Historic	n/a	10	–
SNI-39	3210–2780	11	5	Shelley (2001)
SNI-51	2840–1840	2	1	Collins (1991a)
SNI-102	2780–2150	n/a	n/a	Martz (2005)
SNI-119	n/a	4	1	Collins (1991a)
SNI-160	1710–930	n/a	n/a	Martz (2005)
SNI-161	5440–5270	1	1	Vellanoweth (1998)
SCAI-17	5920–3900; 1330–880	3	2	Collins (1991a)
SCAI-45	1450–1050	3	1	Collins (1991a)
SCAI-137	270–230	3	1	Collins (1991a)
SCLI-43	10,210–520	>28	4	Collins (1991a)
SCLI-48	n/a	1	1	Collins (1991a)
SCLI-1215	5300–460	>2	2	Collins (1991a)
SCLI-1524	2910–460	>20	9	Collins (1991a)
Paleontological specimens				
SRI-Tecolote member	1480–1280	3	1	Collins (1991a); Shelley (2001)
SMI-Locality 7c	6400–6210	1	1	Guthrie (1993)
SMI-Locality 10	950–800	6	1	Guthrie (1993)
SMI-Locality 11	300–0	1	1	Guthrie (1993)

[a] SMI = San Miguel, SRI = Santa Rosa, SCRI = Santa Cruz, SCAI = Santa Catalina, SNI = San Nicolas, SCLI = San Clemente. NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals) based on Collins (1991a,b) unless otherwise noted. For additional details see Collins (1991a), Shelley (2001), and sources cited therein. Fox bones from unknown sites or localities were excluded. An additional NISP of 30 fox bones presented in Colten (2001) could be from SCRI-191, –192, –240, –330, and/or –474.

of eggshells at some fossil localities, Guthrie (1993:410, 1998, 2005) argued that ground-nesting colonies of *Chendytes* existed on San Miguel Island in the late Pleistocene. *Chendytes* bones have also been identified in island archaeological sites as recent as the middle to late Holocene (Jones et al., 2008). Many of these later bones may be from birds that bred on offshore rocks, but the late Pleistocene specimens are from mainland portions of San Miguel where, if present, foxes would have had ready access to *Chendytes* nests, eggs, and fledglings. Because foxes prey on ground nesting bird eggs and chicks, if foxes had arrived prior to human arrival such breeding colonies seem unlikely. A modern analog may be the recent expansion of ground breeding northern harriers (*Circus cyaneus*), western gulls (*Larus occidentalis*), and Brandt's cormorants (*Phalacrocorax penicillatus*) on San Miguel Island after all foxes were incarcerated during captive breeding efforts beginning in the late 1990s (Coonan et al., 2002, 2005; Charles Drost, personal communication, 2008). The expansion of these birds to conspicuous breeding areas across the island is correlated with the fox removal.

If humans introduced foxes to all the Channel Islands, questions remain about the length of time necessary for dwarfing. Recent syntheses suggest that morphological evolutionary rates of change are significantly faster on islands than mainland regions, especially after initial colonization when the animals are undergoing significant selective pressure (Millien, 2006). Small colonizing populations can also result in inbreeding, which can accelerate the dwarfing process (Collins, 1993). Several studies demonstrate rapid dwarfing on islands, including red deer on Jersey Island in 6000 yr or less (Lister, 1989, 1995) and sloths (*Bradypus*) on Panamanian islands between about 8900 and 3400 yr (Anderson and Handley, 2002). Analysis of a small number of subfossil *Urocyon* sp. bones from Cozumel Island, Mexico suggested that dwarfing occurred between about 13,000 to 5000 yr (Gompper et al., 2006). Pergams and Ashley (1999) noted significant size reduction in island deer mice populations from three California Channel Islands in just 90 yr, however, a time frame that is far more rapid than anything in the fossil record and one not associated with a recent introduction or founder effect. Studies of island lizards also provide evidence of extremely rapid change with significant body size increases in just 100 yr (Case and Schwaner, 1993). Using a conservative estimate of 6000–5000 yr for dwarfing, the oldest secure ages for Channel Island foxes (~7000–6000 cal yr BP) fits with the oldest known dates for humans (~13,000 cal yr BP; Johnson et al., 2002). This assumes that we have the oldest dates for both humans and foxes, and that we have fairly rapid evolution, issues that need to be tested further.

Conclusions

Foxes and domestic dogs were present on California's Channel Islands since at least the middle Holocene, and their introduction by humans would have significantly altered island ecosystems. The purportedly pre-human-age island fox bones have now been directly ^{14}C dated to the Holocene, with island foxes on the northern islands for at least 6400 yr and on the southern islands (San Nicolas) for at least 6000–5000 yr (Vellanoweth, 1998; Shelley, 2001). Several lines of evidence support the hypothesis that Native Americans introduced foxes to all the islands where they are currently found, including: 1) the widespread occurrence of foxes in island archaeological sites and absence in pre-Holocene fossil/subfossil deposits; 2) deliberate translocation of foxes between islands by Native Americans; 3) significance of foxes in Native American religion and ceremony; 4) presence of late Pleistocene ground nesting colonies of *Chendytes and Fratercula*; and 5) rapid dwarfing of animals on other islands around the world. This is one of the few known animal translocations by hunter-gatherers (see Grayson, 2001) and demonstrates a significant Native American influence on the structure and functioning of Channel Island ecosystems.

A natural dispersal of foxes cannot be ruled out until additional paleontological and genetic (especially aDNA [ancient DNA]) research is conducted, however, with the aDNA research offering a chance to document and analyze the ancient genetic diversity of foxes, to investigate their relationship to modern fox populations, and to identify possible founder populations. These aDNA studies would also be an important complement to genetic studies of contemporary island foxes that document a small founding population (Wayne et al., 1991; Goldstein et al., 1999; Aguilar et al., 2004). Continued direct ^{14}C dating of island fox bones from Channel Island archaeological sites and interdisciplinary collaboration between researchers will also help elucidate the antiquity, evolution, and biogeography of the island fox, and the role of Native Americans in island ecology. Regardless of whether foxes were transported to the islands by humans during the Holocene or dispersed to the islands during the late Pleistocene prior to human arrival, they are unique animals that helped shape island ecosystems and cultures for at least 6500 yr.

References

Agenbroad, L.D., 1998. New pygmy mammoth (*Mammuthus exilis*) localities and radiocarbon dates from San Miguel, Santa Rosa, and Santa Cruz Islands. In: Weigand, P. (Ed.), Contributions to the Geology of the Northern Channel Islands, Southern California. Pacific Section American Association of Petroleum Geologists, Bakersfield, pp. 169–175.

Agenbroad, L.D., 2002a. California's Channel Islands: a one way trip in the tunnel of doom. In: Browne, D., Mitchell, K., Chaney, H. (Eds.), Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 1–6.

Agenbroad, L.D., 2002b. New localities, chronology, and comparisons for the pygmy mammoth (*Mammuthus exilis*): 1994–1998. In: Browne, D., Mitchell, K., Chaney, H. (Eds.), Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 518–524.

Agenbroad, L.D., Johnson, J.R., Morris, D., Stafford Jr., T.W., 2005. Mammoths and humans as late Pleistocene contemporaries on Santa Rosa Island. In: Garcelon, D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01. Institute for Wildlife Studies, Arcata, pp. 3–7.

Aguilar, A., Roemer, G., Debenham, S., Binns, M., Garcelon, D., Wayne, R.K., 2004. High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mammal. Proceedings of the National Academy of Sciences 101, 3490–3494.

Anderson, R.P., Handley Jr., C.O., 2002. Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. Evolution 56, 1045–1058.

Arnold, J.E., 1987. Craft specialization in the prehistoric Channel Islands, California. University of California Publications in Anthropology 18. University of California Press, Berkeley.

Case, T.J., Schwaner, T.D., 1993. Island/mainland body size differences in Australian varinid lizards. Oecologia 84, 102–109.

Chisholm, B.S., Nelson, D.E., Schwarcz, H.P., 1982. Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science 216, 1131–1132.

Clifford, D.L., Mazet, J.A.K., Dubovi, E.J., Garcelon, D.K., Coonan, T.J., Conrad, P.A., Munson, L., 2006. Pathogen exposure in endangered island fox (*Urocyon littoralis*) populations: implications for conservation management. Biological Conservation 131, 230–243.

Collins, P.W., 1991a. Interaction between island foxes (*Urocyon littoralis*) and Indians on islands off the coast of southern California: I. Morphological and archaeological evidence of human assisted dispersal. Journal of Ethnobiology 11, 51–81.

Collins, P.W., 1991b. Interaction between island foxes (*Urocyon littoralis*) and Native Americans on islands off the coast of southern California: II. Ethnographic, archaeological, and historical evidence. Journal of Ethnobiology 11, 205–229.

Collins, P.W., 1993. Taxonomic and biogeographic relationships of the island fox (*Urocyon littoralis*) and gray fox (*U. cinereoargenteus*) from western North America. In: Hochberg, F.G. (Ed.), Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, pp. 351–390.

Collins, P.W., George, S.B., 1990. Systematics and taxonomy of island and mainland populations of western harvest mice (*Reithrodontomys megalotis*) in southern California. Natural History Museum of Los Angeles County Contributions in Science 420, 1–26.

Collins, P.W., Guthrie, D.A., Rick, T.C., Erlandson, J.M., 2005. Analysis of prey remains from an historic bald eagle nest site on San Miguel Island, California. In: Garcelon, D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01. Institute for Wildlife Studies, Arcata, pp. 103–120.

Colten, R.H., 2001. Ecological and economic analysis of faunal remains from Santa Cruz Island. In: Arnold, J.E. (Ed.), The Origins of a Pacific Coast Chiefdom: The Chumash of the Channel Islands. University of Utah Press, Salt Lake City, pp. 199–219.

Coonan, T.J., Schwemm, C.A., Roemer, G.W., Austin, G., 2002. Population decline of island foxes (*Urocyon littoralis littoralis*) on San Miguel Island. In: Browne, D., Mitchell, K., Chaney, H. (Eds.), Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 289–297.

Coonan, T.J., Rutz, K., Garcelon, D.K., Latta, B.C., Gray, M.M., Ashehoug, E.T., 2005. Progress in island fox recovery efforts on the northern Channel Islands. In: Garcelon, D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01. Institute for Wildlife Studies, Arcata, pp. 263–273.

Cushing, J., Daily, M., Noble, E., Roth, L., Wenner, A., 1984. Fossil mammoths from Santa Cruz Island, California. Quaternary Research 21, 376–384.

Erlandson, J.M., Kennett, D.J., Ingram, B.L., Guthrie, D.A., Morris, D.P., Tveskov, M.A., West, G.J., Walker, P.L., 1996. An archaeological and paleontological chronology for Daisy Cave (CA-SMI-261), San Miguel Island, California. Radiocarbon 38, 355–373.

Erlandson, J.M., Rick, T.C., Jones, T.L., Porcasi, J., 2007. One if by land, two if by sea: who were the first Californians? In: Jones, T.L., Klar, K.A. (Eds.), California Prehistory: Colonization, Culture, and Complexity. Altamira Press, Walnut Creek, pp. 53–62.

Goldberg, C.F., 1993. The Application of Stable Carbon and Nitrogen Isotope Analysis to Human Dietary Reconstruction in Prehistoric Southern California. Ph.D. Dissertation. University of California, Los Angeles.

Goldstein, D.B., Roemer, G.W., Smith, D.A., Reich, D.E., Bergman, A., Wayne, R.K., 1999. The use of microsatellite variation to infer population structure and demographic history in a natural system model. Genetics 151, 797–801.

Gompper, M.E., Petrites, A.E., Lyman, R.L., 2006. Cozumel Island fox (Urocyon sp.) dwarfism and possible divergence history based on subfossil bones. Journal of Zoology 270, 72–77.

Gray, R.S., Harz, W.H., 1998. Pygmy mammoths from San Miguel Island, California. In: Weigand, P. (Ed.), Contributions to the Geology of the Northern Channel Islands, Southern California. Pacific Section American Association of Petroleum Geologists, Bakersfield, pp. 177–184.

Grayson, D.K., 2001. The archaeological record of human impacts on animal populations. Journal of World Prehistory 15, 1–68.

Guthrie, D.A., 1980. Analysis of avifauna and bat remains from midden sites on San Miguel Island. In: Power, D.M. (Ed.), The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 689–702.

Guthrie, D.A., 1993. New information on the prehistoric fauna of San Miguel Island, California. In: Hochberg, F.G. (Ed.), Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, pp. 405–416.

Guthrie, D.A., 1998. Fossil vertebrates from Pleistocene terrestrial deposits on the northern Channel Islands, Southern California. In: Weigand, P. (Ed.), Contributions to the Geology of the Northern Channel Islands, Southern California. Pacific Section American Association of Petroleum Geologists, Bakersfield, pp. 187–192.

Guthrie, D.A., 2005. Distribution and provenance of fossil avifauna from San Miguel Island. In: Garcelon, D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01. Institute for Wildlife Studies, Arcata, pp. 35–42.

Johnson, D.L., 1975. New evidence on the origin of the fox, Urocyon littoralis clementae, and feral goats on San Clemente Island, California. Journal of Mammalogy 56, 925–928.

Johnson, D.L., 1983. The California continental borderland: land bridges, watergaps, and biotic dispersals. In: Masters, P.M., Flemming, N.C. (Eds.), Quaternary Coastlines and Marine Archaeology: Towards the Prehistory of Land Bridges and Continental Shelves. Academic Press, London, pp. 481–527.

Johnson, J.R., Stafford Jr., T.W., Ajie, V., Morris, D.P., 2002. Arlington springs revisited. In: Browne, D., Mitchell, K., Chaney, H. (Eds.), Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 541–545.

Jones, T.L., Porcasi, J.F., Erlandson, J.M., Dallas Jr., H., Wake, T.A., Schwaderer, R., 2008. The protracted Holocene extinction of California's flightless sea duck (Chendytes lawi) and its implications for the Pleistocene overkill hypothesis. Proceedings of the National Academy of Sciences 105, 4105–4108.

Kennett, D.J., 2005. The Island Chumash: Behavioral Ecology of a Maritime Society. University of California Press, Berkeley.

Kennett, D.J., Kennett, J.P., West, G.J., Erlandson, J.M., Johnson, J.R., Hendy, I.L., West, A., Culleton, B.J., Jones, T.L., Stafford Jr., T.W., 2008. Wildfire and abrupt ecosystem disruption on California's Northern Channel Islands at the Ållerød-Younger Dryas Boundary (13.0–12.9 ka). Quaternary Science Reviews 27, 2528–2543.

Lipps, J.H., 1964. Late Pleistocene history of west Anacapa Island, California. Geological Society of America Bulletin 75, 1169–1176.

Lister, A.M., 1989. Rapid dwarfing of red deer on Jersey Island in the last interglacial. Nature 342, 539–542.

Lister, A.M., 1995. Sea-levels and the evolution of island endemics: the dwarf red deer of Jersey. Geological Society, 96. Special Publications, London, pp. 151–172.

Martz, P.C., 2005. Prehistoric subsistence and settlement on San Nicolas Island. In: Garcelon, D., Schwemm, C. (Eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01. Institute for Wildlife Studies, Arcata, pp. 65–82.

Millien, V., 2006. Morphological evolution is accelerated among island mammals. PLoS Biology 4 (10), doi:10.1371/journal.pbio.0040321.

Moore, C.M., Collins, P.W., 1995. Urocyon littoralis. Mammalian Species 489, 1–7.

Newsome, S.D., Phillips, D.L., Culleton, B.J., Guilderson, T.P., Koch, P.L., 2004. Dietary reconstruction of an early to middle Holocene human population from the central California Coast: insights from advanced stable isotope mixing models. Journal of Archaeological Science 31, 1101–1115.

Noah, A.C., 2005. Household Economies: The Role of Animals in a Historic Period Chiefdom on the California Coast. PhD Dissertation. University of California, Los Angeles.

Orr, P.C., 1968. Prehistory of Santa Rosa Island. Santa Barbara Museum of Natural History, Santa Barbara.

Pergams, O.R.W., Ashley, M.V., 1999. Rapid morphological change in Channel Island deer mice. Evolution 53, 1573–1581.

Porcasi, P., Porcasi, J.F., O'Neill, C., 1999. Early Holocene coastlines of the California Bight: the Channel Islands as first visited by humans. Pacific Coast Archaeological Society Quarterly 35 (2 & 3), 1–24.

Rick, T.C., Walker, P.L., Willis, L.M., Noah, A.C., Erlandson, J.M., Vellanoweth, R.L., Braje, T.J., Kennett, D.J., 2008. Dogs, humans, and island ecosystems: the antiquity, distribution, and ecology of domestic dogs (Canis familiaris) on California's Channel Islands. The Holocene 18, 1077–1087.

Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proceedings of the National Academy of Sciences 99, 791–796.

Roemer, G.W., Coonan, T.J., Munson, L., Wayne, R.K., 2004. The island fox, In: Sillero-Zubiri, C., Hoffman, M., MacDonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals, and Dogs, Status Survey and Conservation Action Plan, 2nd Edition. IUCN/SSC Canid Specialist Group, The World Conservation Unit, Gland, pp. 97–105.

Schoenherr, A.A., Feldmath, R.C., Emerson, M.J., 1999. Natural History of the Islands of California. University of California Press, Berkeley.

Schoeninger, M.J., DeNiro, M.T., Tauber, H., 1983. Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. Science 220, 1381–1383.

Shelley, S.D., 2001. Archaeological Evidence of the Island Fox (Urocyon littoralis) on California's Channel Islands. Technical Report 98–12. Statistical Research Inc, Tucson.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C data base and revised Calib 3.0 ^{14}C age calibration program. Radiocarbon 35, 215–230.

Stuiver, M., Reimer, P.J., Reimer, R. 2005. Calib 5 Manual. http://calib.qub.ac.uk/calib/.

Thaler, P.F., 1998. Mammoth remains on the Channel Islands of southern California. In: Weigand, P. (Ed.), Contributions to the Geology of the Northern Channel Islands, Southern California. Pacific Section American Association of Petroleum Geologists, Bakersfield, pp. 161–167.

Vellanoweth, R.L., 1998. Earliest island fox remains on the Southern Channel Islands: evidence from San Nicolas Island, California. Journal of California and Great Basin Anthropology 20, 100–108.

Vellanoweth, R.L., 2001. AMS radiocarbon dating and shell bead chronologies: middle Holocene trade and interaction in western North America. Journal of Archaeological Science 28, 941–950.

Walker, P.L., 1980. Archaeological evidence for the recent extinction of three terrestrial mammals on San Miguel Island. In: Power, D.M. (Ed.), The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 703–717.

Walker, P.L., DeNiro, M.J., 1986. Stable nitrogen and carbon isotope ratios in bone collagen as indices of prehistoric dietary dependence on marine and terrestrial resources in Southern California. American Journal of Physical Anthropology 71, 51–61.

Waters, M.R., Stafford Jr., T.W., 2007. Redefining the age of Clovis: implications for the peopling of the Americas. Science 315, 1122–1126.

Wayne, R.K., George, S.B., Gilbert, D., Collins, P.W., Kovach, S.D., Girman, D., Lehman, N., 1991. A morphologic and genetic study of the island fox, Urocyon littoralis. Evolution 45, 1849–1868.

Wenner, A.M., Johnson, D.L., 1980. Land vertebrates on the islands: sweepstakes or landbridges? In: Power, D.M. (Ed.), The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp. 497–530.

White, J.P., 2004. Where the wild things are: prehistoric animal translocation in the Circum New Guinea Archipelago. In: Fitzpatrick, S.M. (Ed.), Voyages of Discovery: The Archaeology of Islands. Praeger, Westport, pp. 147–164.