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Tracking the origins and diet of an endemic island canid (*Urocyon littoralis*) across 7300 years of human cultural and environmental change

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ABSTRACT

Understanding how human activities have influenced the foraging ecology of wildlife is important as our planet faces ongoing and impending habitat and climatic change. We review the canine surrogacy approach (CSA)—a tool for comparing human, dog, and other canid diets in the past—and apply CSA to investigate possible ancient human resource provisioning in an endangered canid, the California Channel Islands fox (*Urocyon littoralis*). We conducted stable isotope analysis of bone collagen samples from ancient and modern island foxes ($n = 214$) and mainland gray foxes (*Urocyon cinereoargenteus*, $n = 24$). We compare these data to isotope values of ancient humans and dogs, and synthesize 29 Accelerator Mass Spectrometry (AMS) radiocarbon dates that fine-tune the chronology of island foxes. AMS dates confirm that island foxes likely arrived during the early Holocene (>7300 cal BP) on the northern islands in the archipelago and during the middle Holocene (>5500 cal BP) on the southern islands. We found no evidence that island foxes were consistently using anthropogenic resources (e.g., food obtained by scavenging around human habitation sites or direct provisioning by Native Americans), except for a few individuals on San Nicolas Island and possibly on San Clemente and Santa Rosa islands. Decreases in *U. littoralis* carbon and nitrogen isotope values between prehistoric times and the 19th century on San Nicolas Island suggest that changes in human land use from Native American hunter-gatherer occupations to historical ranching had a strong influence on fox diet. Island foxes exhibit considerable dietary variation through time and between islands and have adapted to a wide variety of climatic and cultural changes over the last 7300 years. This generalist foraging strategy suggests that endemic island foxes may be resilient to future changes in resource availability.

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1. Introduction

Humans have had profound effects on past and present wildlife population demography, genetic diversity, and biogeography

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(Boivin et al., 2016; Erlandson et al., 2014; Grayson, 2001; Hofman et al., 2015a; Lorenzen et al., 2011; Rick and Erlandson, 2008; Storey et al., 2013; Zeder, 2015). A growing body of evidence demonstrates that people have also influenced the foraging ecology of ancient and modern wild animals (Auman et al., 2011; Bentzen et al., 2014; Kristan et al., 2004; Merkle et al., 2011; Newsome et al., 2010, 2015; Wiley et al., 2013). The diets of wild animals can be altered through intentional (direct feeding) or unintentional (scavenging of human refuse) provisioning by humans (Auman et al., 2011; Merkle et al., 2011; Newsome et al., 2010) or due to anthropogenic changes to ecosystems and resource availability (e.g., landscape clearing and burning, plant and animal introductions) (Wiley et al., 2013). Human provisioning of animals is an important step in the domestication process (Axelsson et al., 2013; Barton et al., 2009; Hu et al., 2008; Makarewicz and Tuross, 2012; Zeder, 2006; Zeder et al., 2006) and dietary changes have also been identified in captive and ritually sacrificed animals held by prehistoric peoples (Sugiyama et al., 2015; White et al., 2001). Unintentional or intentional human provisioning of wild animals can impact body condition (Heiss et al., 2009) and the ability of an animal to effectively teach their young how to forage for wild food. Data sets that track dietary changes over long-term timescales (centuries, millennia) are therefore valuable for identifying anthropogenic impacts. Stable isotope analysis provides a powerful tool for understanding food-web structure (Tieszen and Boutton, 1989) and, along with other data, can provide insights into past and present human-wildlife interactions (Beard and Johnson, 2000; Guiry, 2012; Newsome et al., 2015, 2010; Wiley et al., 2013).

To examine temporal changes in foraging patterns and explore the utility of stable isotopes in evaluating the impact of potential human provisioning of wildlife, we focus on the chronology and isotope ecology of the island fox (*Urocyon littoralis*), a range-restricted species of management concern. The island fox, closely related to the mainland gray fox (*Urocyon cinereoargenteus*) (Hofman et al., 2015b), is endemic to six of California's eight Channel Islands (Fig. 1). Several Accelerator Mass Spectrometry (AMS) radiocarbon (^{14}C) dates suggest that the island fox may be a relatively recent (early to middle Holocene) arrival to the islands. The oldest published island fox remains on the islands are found in archaeological sites and date to ~7100 years ago (Hofman et al., 2015b; Rick et al., 2009; Vellanoweth, 1998), long after humans first colonized the islands at ~13,000 cal BP (Erlandson et al., 2011). Recent analysis of mitochondrial genomes also supports an early to mid-Holocene introduction (Hofman et al., 2015b). The origin of foxes on the Channel Islands is uncertain, with hypotheses ranging from a human introduction, to a natural rafting event, or to a combination of the two. Most researchers agree, however, that Native Americans introduced island foxes from the northern to the southern island group >5000 years ago (Aguilar et al., 2004; Collins, 1993, 1991a, 1991b; Hofman et al., 2015b; Johnson, 1975; Orr, 1968; Rick et al., 2009; Vellanoweth, 1998; Wayne et al., 1991). Evidence of resource provisioning by humans could lend support to a human introduction and suggest greater interactions between humans and foxes, including possible semi-domestication, which we define as captive wild animals whose breeding may have been influenced by humans.

Here we review and analyze human-fox relationships on California's Channel Islands by examining carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values in bone collagen from paleontological, archaeological, historic, and modern island foxes. To place these data in chronological context, we also synthesize 29 new (n = 21) and previously (n = 8) reported AMS ^{14}C dates measured directly from archaeological and sub-fossil island foxes. Together these data are used to address three interrelated research questions: 1) When and how did foxes arrive on the Channel Islands? 2) Do island fox diets vary through time and between islands? 3) Were island fox diets affected by changes in human occupation and land use patterns?

2. Background and context

2.1. Stable isotopes and the canine surrogacy approach

To investigate changes in the diet of island foxes, we adopt the "Canine Surrogacy Approach" (CSA) that has been used to investigate human provisioning of dogs in the archaeological record as well as human diets (Cannon et al., 1999; Guiry, 2012; Rick et al., 2011; Tankersley and Koster, 2009; West and France, 2015). CSA asserts that dogs can serve as a proxy for human diet because dogs consume similar foods as their human handlers via handouts and scavenging (Guiry, 2012). Although dogs are generally good proxies for humans, animal age needs to be considered when sampling from the archaeological record (Guiry, 2012). Isotope values from dog bone collagen reflect shorter periods of time than values from humans, due to differences in body size and related differences in collagen isotopic incorporation rates (Guiry, 2012; Pearce et al., 2007). Weaning can also affect isotope values as pups and juveniles have higher δ^{15}N values than adult females because mothers produce milk from proteins and lipids sourced from their own tissues (Fuller et al., 2006; Jenkins et al., 2001; Newsome et al., 2006). After accounting for age effects, we can expand the CSA with human or dog isotope data to test for human provisioning of wild animals.

Rick et al. (2011) analyzed a small sample ($n = 3$) of late Holocene island foxes recovered from an archaeological site on Santa Rosa Island (CA-SRI-2) and found that foxes had lower δ^{13}C and δ^{15}N values in comparison to humans and dogs from the same site that had consumed a marine-based diet. Primary production on the California Channel Islands is dominated by plants that use the C_3 photosynthetic pathway, low δ^{13}C and δ^{15}N values in foxes are indicative of a terrestrial-based diet consisting of rodents, insects, and plants, prey items similar to those consumed by modern island foxes (Cypher et al., 2014). While these samples suggest continuity between the diet of late Holocene and modern foxes on Santa Rosa Island, the sample size from Santa Rosa is small and questions remain about whether these samples fully represent variability in island fox diet across space and through time.

Here we expand on these preliminary data and evaluate the hypothesis that humans provisioned island foxes, using a large dataset ($n = 214$) of island foxes spanning 7300 years and seven islands. We define provisioning as the intentional feeding of foxes by humans, including the potential scavenging of anthropogenic foods, because both mechanisms imply human involvement and would yield similar isotope values in foxes. We compare isotope values between humans, dogs, and island foxes to test if humans and island foxes had commensal or mutually beneficial relationships. If humans and foxes had a commensal relationship following the arrival of foxes on the islands, we expect similar isotope values between species, supporting the hypothesis that humans introduced foxes to the Channel Islands.

Alternatively, if foxes were scavenging marine carrion, including pinniped carcasses, we also expect they would have higher δ^{13}C and δ^{15}N values similar to those of ancient humans and dogs on the Channel Islands that consumed a marine-based diet (Rick et al., 2011). However, occasional scavenging of marine resources might not be detected by analyzing the isotopic composition of bone collagen. This is because bone collagen has a relatively slow isotopic incorporation rate and represents diet integrated over the last several years prior to death, depending on the size of the animal (Hobson and Clark, 1992; Tieszen et al., 1983). Thus, fox bone

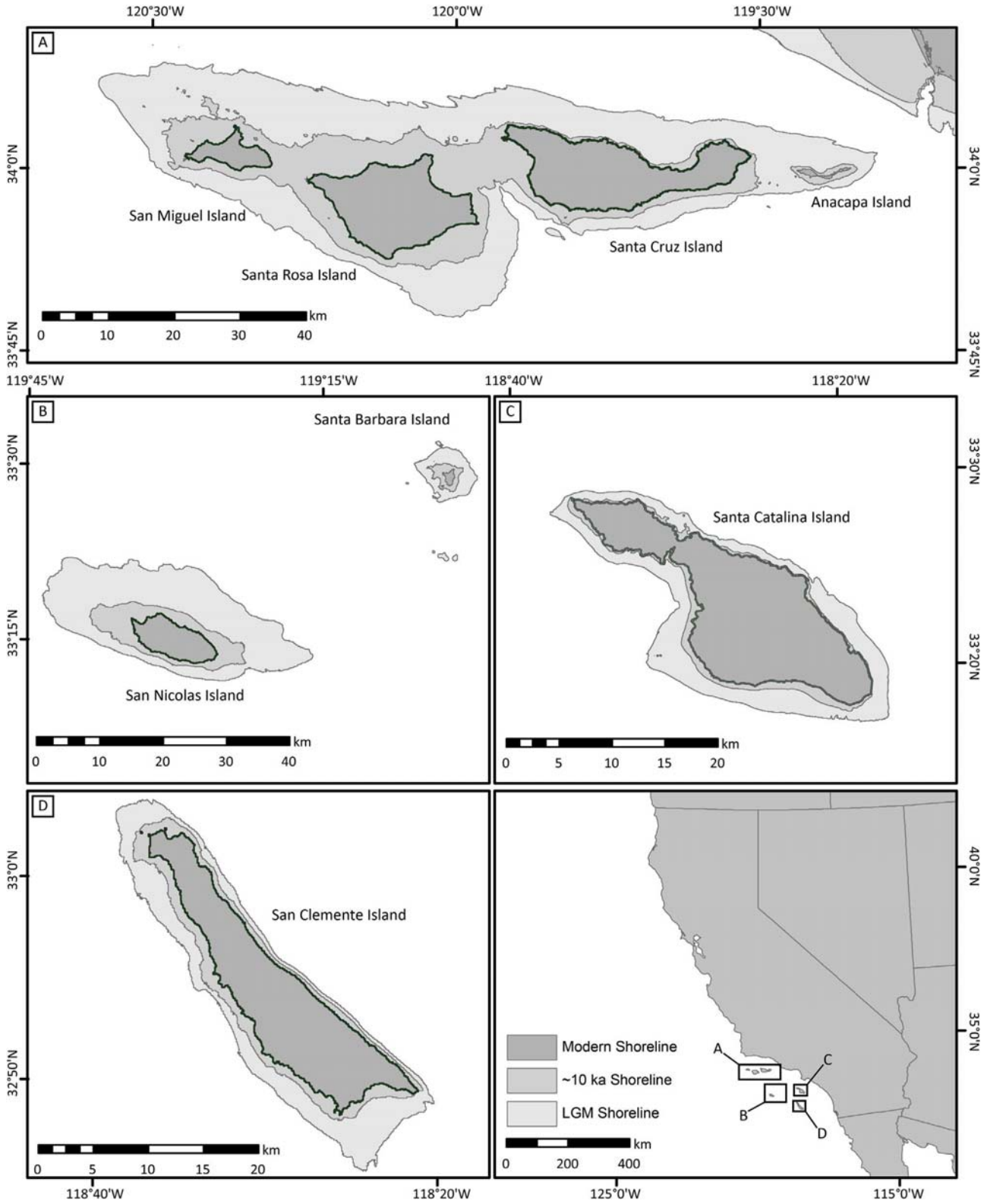


Fig. 1. Map of the California Channel Islands. Island shape and size are modeled at key time points (Last Glacial Maximum (~20,000 BP), 10,000 BP, and present day). Islands with extant island fox populations are outlined in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

collagen that has high $\delta^{13}C$ and $\delta^{15}N$ values is likely the result of the consistent consumption of marine resources, a phenomenon that is rare in modern island fox populations (Cypher et al., 2014). Distinguishing between human resource provisioning and scavenging of marine carrion is difficult; therefore we considered foxes that had isotope values within the standard ellipse area of human populations from the Channel Islands to be evidence of human provisioning.

Island foxes may have been valued by humans for their fur and their role in managing island rodent populations (Rick et al., 2009). Domestic cats did not arrive in North America until European colonization (Wastlhuber, 1991). If pest control were a factor in fox dispersal, we would expect an island fox diet consistent with terrestrial foods. Ultimately, comparisons of stable isotope bone collagen data from modern foxes to archaeological human, fox, and dog remains can help us explore human resource provisioning and long-term trends in island fox diet within the CSA framework.

2.2. The California Channel Islands and island foxes: what do we know?

The California Channel Islands, an eight-island archipelago ~20–100 km off the southern California coast, have never been connected to the mainland during the Quaternary. However, the northern islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) composed a single landmass (Santarosae) in the Pleistocene. Santarosae began to separate into what would become the four northern Channel Islands around 11,000 cal BP, with the islands completely separated by 9000 cal BP (Fig. 1) (Muhs et al., 2014, 2012; Reeder-Myers et al., 2015; Wenner and Johnson, 1980). Although the southern islands were larger in terms of landmass when sea levels were lower, they were not connected to each other or to the mainland (Reeder-Myers et al., 2015).

The paleogeography of the islands has shaped their biodiversity (Johnson, 1983, 1980, 1975; Wenner and Johnson, 1980). Channel Island terrestrial mammal populations are unevenly distributed among islands and less diverse than the mainland, with only six extant endemic mammals (excluding bats): the island fox, western harvest mouse (*Reithrodontomy megalotis*), Catalina ground squirrel (*Otospermophilus beecheyi nesioticus*), the island spotted skunk (*Spilogale gracilis amphiala*), the deer mouse (*Peromyscus maniculatus*), and the ornate shrew (*Sorex ornatus*) (Rick, 2013). Native Americans also introduced dogs to many of the islands during the middle Holocene or earlier (Rick et al., 2008) and a number of non-native and invasive species arrived or were introduced to the islands within the last 200 years after Spanish colonization of California.

From ancient hunter-gatherers to historic ranchers, island landscapes have changed significantly since people first arrived on the islands 13,000 years ago (Rick et al., 2014). During the warmer, drier transition at the terminal Pleistocene, island vegetation shifted from a landscape dominated by temperate forest to shrubland-grasslands. By 11,000 cal BP, coastal sage shrub dominated the landscape. Evidence from pollen and charcoal on Santa Rosa Island suggests that by 6900 years ago grassland and perennial herbs predominated, with evidence of wetland plants suggesting that the region became wetter around 4500 years ago (Anderson et al., 2010; Rick et al., 2014). Fire frequency also increased around 9150 years ago and again 3500 years ago (Anderson et al., 2010) with the latter thought to be from burning by Native Americans. During the ranching era (mid 1800s-late 1900s), introduced livestock transformed the landscape due to vegetation stripping from overgrazing, soil compaction, and increased erosion from trampling of the native grassland, which resulted in vegetation changes and large-scale erosion (Erlandson et al., 2005; Johnson, 1980; Rick et al., 2014). Most of the livestock and introduced game species have recently been removed from the islands and vegetation communities are recovering (Corry and McEachern, 2009; McEachern et al., 2015).

As one of the few terrestrial mammals on the Channel Islands, the island fox is an apex predator and currently of considerable conservation concern, especially on San Nicolas, where populations have extremely low genetic diversity (Funk et al., 2016; Robinson et al., 2016) and population sizes declined by 25% between 2013 and 2014 (Coonan, 2015). In the 1990s, fox numbers dropped rapidly due to the introduction of distemper by domestic dogs on Santa Catalina (Coonan et al., 2010) and by golden eagle predation on the northern Channel Islands (Roemer et al., 2002). Through a captive breeding and re-release program, however, fox populations have recovered dramatically on the northern islands (Coonan et al., 2010, 2014). Contemporary island foxes are opportunistic omnivores with diets that vary both seasonally and spatially across the archipelago (Cypher et al., 2014). Beetles, deer mice (*Peromyscus maniculatus*), lizards, jerusalem crickets (*Stenopalmatus spp.*), terrestrial snails, and a number of native and non-native fruits are currently important resources for island foxes (Cypher et al., 2014). Island foxes also consume birds and scavenge livestock or ungulate carcasses when present (Laughrin, 1977; Cypher et al., 2014). Cypher et al. (2014) also found trace amounts of pinniped remains (<5 occurrences/season) in island fox scat from San Nicolas, San Miguel, San Clemente and Santa Catalina, suggesting some marine dietary input. We predicted that ancient island foxes would also show a high degree of isotopic variation since most fox species, including mainland gray foxes, are opportunistic omnivores (Cunningham et al., 2006; Fritzell, 1988).

Island foxes are morphologically similar, yet considerably smaller (~30%), than mainland gray foxes, raising the possibility that the fox has been on the islands for a significant time to undergo dwarfing. However, rapid morphological change is possible and can occur within time periods of centuries or less (Cuarón et al., 2004; Gompper et al., 2006). All known ancient and modern fox specimens are indicative of small fox size and there is a lack of evidence in the fossil record that island foxes have undergone dramatic morphological change over the past 7000 years (Collins, 1993, 1991a, 1991b). Despite claims of the occurrence of fossil island foxes as old as 40,000 or 16,000 years ago that date to prior to human arrival (Collins, 1991a; Guthrie, 1993; Orr, 1968), direct AMS dating and re-analysis of these specimens demonstrated that foxes appeared on the islands around ~7100 cal BP, about the same time dogs appear in the archaeological record of the Channel Islands (Hofman et al., 2015b; Rick et al., 2009, 2008). There is also no archaeological or paleontological evidence of island fox ancestors on the islands, such as a larger gray fox from mainland California (Collins, 1993, 1991a, 1991b; Rick et al., 2009).

A growing body of evidence suggests that Native Americans may have first introduced foxes from the mainland to the Channel Islands. Rick et al. (2009) suggest that a human translocation is supported by their widespread distribution; their absence in Pleistocene fossil deposits and very early archaeological components on the islands; the significance of foxes in Native American religion and ceremony (including over 51 fox burials –described in Collins, 1991b); use of fox pelts by people; the demographic decline of ground nesting birds in deposits following hypothesized early Holocene fox colonization; and, evidence for rapid morphological change among mammals, including domestic dogs (Collins, 1993, 1991a, 1991b; Rick et al., 2009). While there is little evidence of human consumption of island foxes (Collins, 1991b), island fox bones have been recovered in a variety of archaeological contexts including middens or refuse piles, as well as intentional burials of foxes, some of which are associated with human burials (Collins, 1991a, 1991b; Hofman et al., 2015b; Vellanoweth, 1998; Vellanoweth et al., 2008). Collectively, these data suggest a diverse set of human-fox interactions over time. Nonetheless, significant questions remain about how ancient cultural and landscape change affected island fox populations on the Channel Islands over the millennia.

3. Materials and methods

3.1. Specimens

Paleontological, archaeological, historical, and recent island fox and mainland gray fox bones were obtained from the collections at Santa Barbara Museum of Natural History, National Museum of Natural History, California State University, Los Angeles, California State University, Northridge, and Catalina Island Museum (Table 1 and Table S1). Paleontological and archaeological island fox samples ($n = 67$) come from 25 different archaeological or subfossil localities, or approximately half of the sites where foxes have been identified ($n = 53$). In selecting prehistoric fox samples, we surveyed published and unpublished accounts of island and gray foxes, investigated museum collections, and contacted colleagues to ensure that we had the widest temporal and spatial coverage possible. Our goals were to make sure that we had samples from the potentially oldest foxes on each island and had adequate diachronic coverage. Although intentional fox burials ($n > 51$) have been recovered on the southern and northern islands (see Collins, 1991b), the vast majority of archaeological specimens represent a single bone or small number of bones from unknown or poorly

Table 1
Paleontological and archaeological island fox samples.

Island	Site	Site chronology	Fox date[a]	NISP[b]	MNI[c]	Reference	Isotope[d]
San Miguel Island	SMI-1	7120–3070	7310–7170	2	1	Collins, 1991a; Rick et al., 2009	1
	SMI-87	4830–2360		1	1	Rick et al., 2009	
	SMI-261	12,600-550	980–920; 960-800	13	1	Collins, 1991a; Rick et al., 2009	2
	SMI-470	4410–3940; 460-Historic		1	1	Rick et al., 2009	
	SMI-525	3290–470		1	1	Collins, 1991a; Rick et al., 2009	–
	SMI-603	8500–910		1	1	Rick et al., 2009	1
	SMI-Locality 7C[e]	Pleistocene/Holocene	7160–6910	1	1	Guthrie, 1993; Rick et al., 2009	
	SMI-Locality 10[e]	Pleistocene/Holocene	950–800	6	1	Guthrie, 1993; Rick et al., 2009	
	SMI-Locality 11[e]	Pleistocene/Holocene	300–0	1	1	Guthrie, 1993; Rick et al., 2009	
Santa Rosa Island	SRI-1	9390–1980 cal BP	1290–1180; 480-320	9	6	Collins, 1991a; Rick et al., 2009	2
	SRI-2	2460-Historic	530–480	>16	9	Collins, 1991a & b; Rick et al., 2009	5
	SRI-3	8860–2760	310–0	3	2	Collins, 1991a; Rick et al., 2009	2
	SRI-4	7560–1830	660–550	1	1	Collins, 1991a; Rick et al., 2009	1
	SRI-25	n/a		2	1	Shelley, 2001; Rick et al., 2009	–
	SRI-41	5610–1040	3830–3640	2	1	Collins, 1991a; Rick et al., 2009	1
	SRI-168	Late Holocene		2			1
	SRI-347	n/a		1			–
	SRI-365	n/a		n/a	1	Rick et al., 2009	–
	SRI-670	Late Holocene		2			2
	SRI-XX	Late Holocene	530–340	n/a	n/a		3
	Upper Tecolote[e]	Terminal Pleistocene	1510–1280	3	1	Collins, 1991a; Shelley 2001; Rick et al., 2009	1
Santa Cruz Island	SCRI-1	2670-Historic		2			2
	SCRI-122	Late Holocene		2	2	Collins, 1991a; Rick et al., 2009	–
	SCRI-131	Late Holocene		2	2	Collins, 1991a; Rick et al., 2009	–
	SCRI-147	Late Holocene		>18	5	Collins, 1991a; Rick et al., 2009	–
	SCRI-206	n/a		1	1	Collins, 1991a; Rick et al., 2009	–
	SCRI-236 (SCRI-86)	5320–500		7	6	Collins, 1991a; Rick et al., 2009	–
	SCRI-240	5570–320		5	n/a	Noah, 2005; Rick et al., 2009	–
	SCRI-257	Late Holocene		4			4
	SCRI-306	760–270		n/a	n/a	Arnold, 1987; Rick et al., 2009	–
	SCRI-328/330	910-Historic		9	n/a	Noah, 2005; Rick et al., 2009	–
	SCRI-333 (SCRI-3)	6280–1090	6180–5950; 2750–2510	45	13	Collins, 1991a; Rick et al., 2009	2
	SCRI-474 (SCRI-100)	Late Holocene		>46	11	Collins, 1991a; Rick et al., 2009	–
	SCRI-496	Late Holocene		4			2
Anacapa Island	ANI-2	3250–2710	3210–3010	1		Reeder and Rick 2009; Jew et al., 2015	1
Santa Catalina Island	SCAI-17	5990–4270; 1520-470	5460–5310	3	2	Collins, 1991a; Rick et al., 2009	1
	SCAI-26	720-Historic		22		Porcasi, 2012	–
	SCAI-32	Late Holocene		51		Porcasi, 2014	–
	SCAI-137	Historic		3	1	Collins, 1991a; Rick et al., 2009	–
San Nicolas Island	SNI-7	Late Holocene	2110–1900	n/a	20	Collins, 1991a & b; Rick et al., 2009	13
	SNI-11	7160–330	5070–4790	>5	2	Collins, 1991a; Rick et al., 2009; Shelley 2001	–
	SNI-16	Late Holocene	1870–1730	n/a	n/a		3
	SNI-25	740-Historic	530–490; 500–320	n/a	10	Rick et al., 2009	9
	SNI-51	2870–1720		2	1	Collins, 1991a; Rick et al., 2009	–
	SNI-102	2870–2440		n/a	n/a	Martz, 2005; Rick et al., 2009	–
	SNI-119	n/a		4	1	Collins, 1991a; Rick et al., 2009	–
	SNI-160	1810–800		n/a	n/a	Martz, 2005; Rick et al., 2009	–
	SNI-161	5450–4710		1	1	Vellanoweth, 1998; Rick et al., 2009	–
San Clemente	SCLI-43	12,540-510	2200–2300; 1810–1610	>28	4		1
	SCLI-48	n/a		1	1	Collins, 1991a; Rick et al., 2009	–
	SCLI-1215	5440–310		>2	2	Collins, 1991a; Rick et al., 2009	–
	SCLI-1531	n/a	530–490	3			1
	SCLI-1524	2360- Historic	540–500; 430–150: 300-0	8		Collins, 1991a; Rick et al., 2009	3
						Total	**64**

[a] Calibrated AMS direct dates on fox bone. Uncalibrated AMS dates are available in Table S2.
[b] Minimum number of individuals (MNI) as identified by the cited publications or this study.
[c] Number of identified specimens (NISP) as identified by the cited publications or this study.
[d] Number of samples included in our isotope analyses from each site.
[e] These sites are paleontological contexts.

documented contexts. This makes our efforts to associate these materials with human activity challenging for understanding fox diet and their relationships with humans. We were able to sample a number of the possible fox burials ($n = 25$), although not all burials were available for this study. Island foxes from the late 19th century ($n = 33$) and both island ($n = 114$) and gray foxes ($n = 24$) from the 20th century fill in more recent time gaps.

Stringent precautions were taken to ensure that any potential for contamination was reduced during fox bone sampling. Specimens were handled with gloves, and all equipment and table surfaces were cleaned with bleach in between each sample. To obtain samples for stable isotope analysis and AMS ^{14}C dating, a small (ca. 100–400 mg) fragment of bone was removed using a clean razor blade, tweezers, or a new Dremel rotary cutting wheel. When crania were present, bone was sampled from nasal turbinates or the internal tentorium plate near the base of the cranium. In some cases, only long bone fragments were available and were cut with a Dremel rotary tool. For archaeological specimens, we sampled different excavation units and, when possible, the same element and side to minimize the possibility of sampling the same individual.

3.2. AMS radiocarbon dating

Eight AMS radiocarbon dates on island fox bones have been reported previously (Hofman et al., 2015b; Rick et al., 2009; Shelley, 2001). To expand on these data, AMS radiocarbon dates were obtained for 21 additional island fox bones with the aim of documenting the antiquity of island foxes and the chronological age of individual specimens with limited context. Samples were chosen to potentially represent some of the oldest island fox remains or sites with long occupational histories and complex stratigraphy. These include specimens from SCAI-17, SRI-1, SRI-3, and SRI-5, SCRI-333, and SMI-1 and SMI-261, that have trans-Holocene or early Holocene deposits and fox remains that came from the surface or unknown contexts (Table 1).

Bone fragments of 19 foxes were sent to the Oxford Radiocarbon Accelerator Unit (ORAU) at the University of Oxford (Ramsey et al., 2007a, 2007b). A juvenile dog from a site on San Clemente (SCLI-1524) with 11 canid ritual burials (including 6 foxes) was also dated at ORAU to determine whether foxes and dogs were interred simultaneously. Two fox samples (SRI-XX and SNI-7) were sent to Beta Analytic. All bones were pretreated using ultrafiltration techniques (except SRI-XX, which did not have enough sample for ultrafiltration), collagen was extracted, and analyzed for ^{14}C dating. All dates were calibrated using OxCal v. 4.2 (Ramsey, 2013, 2009). As some foxes may have consumed high amounts of marine resources, which would require a marine reservoir correction (ΔR), δ^{13}C values were measured in each specimen independently from the radiocarbon analysis. None of the specimens required a ΔR correction. A previously reported date for a fox from SNI-11 without a δ^{13}C value was corrected ($\Delta R = 261 \pm 21$; Jazwa et al., 2012) due to evidence of marine diet in archaeological foxes on San Nicolas Island. All dates were calibrated using the Intcal13 dataset, except for the fox from SNI-11, which used the Marine13 calibration dataset (Reimer et al., 2013).

3.3. Stable isotope analysis

For carbon (δ^{13}C) and nitrogen (δ^{15}N) analysis, dog ($n = 1$), gray fox ($n = 24$), and island fox ($n = 202$) bone fragments were demineralized in 0.5 N hydrochloric acid (HCl) for ~12–15 h at 5 °C. The resulting material was soaked in a 2:1 chloroform/methanol solvent solution for ~72 h to remove lipids and then lyophilized. Freeze-dried sub-samples (~0.5 mg) of bone collagen were sealed in tin boats and δ^{13}C and δ^{15}N values were measured using a Costech elemental analyzer coupled to a Thermo-Finnigan Delta Plus isotope ratio mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, WY). Stable isotope results are expressed as delta (δ) values: δ^{13}C or δ^{15}N = 1000* [(R_{sample}/$R_{standard}$)−1], where R_{sample} and $R_{standard}$ are the ^{13}C/^{12}C or ^{15}N/^{14}N ratios of the sample and standard, respectively. δ values are expressed as parts per thousand or per mil (‰). The internationally accepted standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for δ^{13}C and atmospheric N_2 for δ^{15}N. Fox samples from the 1860s to the present were corrected for the Suess effect following equations in Francey et al. (1999) and Wiley et al. (2013). Historic museum samples without a collection year were corrected by 0.5‰. Previously reported stable isotope data were compiled for the temporal and spatial comparison to human ($n = 349$), dog ($n = 19$), and island fox ($n = 12$) isotope values (Goldberg, 1993; Rick et al., 2011; Smith, 2013).

To explore the utility of the CSA in detecting human provisioning of island foxes, bone collagen δ^{13}C or δ^{15}N data were used to calculate standard ellipse areas of humans, dogs, and foxes from archaeological, historic, and recent contexts using the Stable Isotope Bayesian Ellipses in R (Jackson et al., 2011; Parnell and Jackson, 2011), a tool in the R package Stable Isotope Analysis in R (SIAR, Jackson and Parnell, 2010; Parnell et al., 2010). If an individual fox fell within the human or dog ellipse, it was labeled as potentially provisioned. In some cases, we combined data for human and dogs to test whether a shared group included any fox data points. To compare foxes between time points and islands we conducted an analysis of variance as implemented in R v3.2.3 (R Core Team, 2015).

4. Results

4.1. Island fox chronology

AMS ^{14}C dates from 19 island foxes in this study complement previously published data (Hofman et al., 2015b; Rick et al., 2009; Shelley, 2001), giving a total of 29 directly-dated island fox bones (Table 1). Despite targeting potentially terminal Pleistocene, early Holocene (~11,700–7000 cal BP), and middle Holocene (~7000–3500 cal BP) contexts, our AMS ^{14}C dating results support a largely late Holocene (3500–200 cal BP) record of island foxes on all the islands (Fig. 2, Table S2). We identified considerable variation between inferred archaeological site chronologies from published AMS dates and the AMS date of the island foxes recovered in some sites. In a few cases (SRI-1, SRI-3, and SRI-4), fox AMS dates are considerably younger than the known chronology of the site (Table 1). The earliest evidence of the island fox comes from an archaeological site (SMI-1) overlooking Cuyler Harbor on San Miguel and dates to 7310–7170 cal BP, which is comparable in age to a previously reported date from a SMI subfossil locality of V-7C (Rick et al., 2009). Early dates from Santa Cruz come from the middle/late Holocene site of SCRI-333 and date to 6180–5960 cal BP. On the southern islands, the oldest fox date comes from Catalina (SCAI-17) and dates to 5460–5310 cal BP. On San Nicolas, the oldest fox dates to 5070–4790 cal BP (SNI-11) and is contemporaneous with a fox auditory bulla from SNI-161 that has not been directly dated but has good associated ^{14}C dates (Vellanoweth, 1998); without the marine correction this fox from SNI-11 could be as old as 5860–5590 cal BP. The earliest directly dated fox on San Clemente dates to 2300–2200 cal BP.

We report the first documented record of an island fox on Anacapa Island. Island foxes are not currently present on Anacapa or known from previous archaeological or paleontological research. Five island fox bones (broken proximal left femur, matching broken

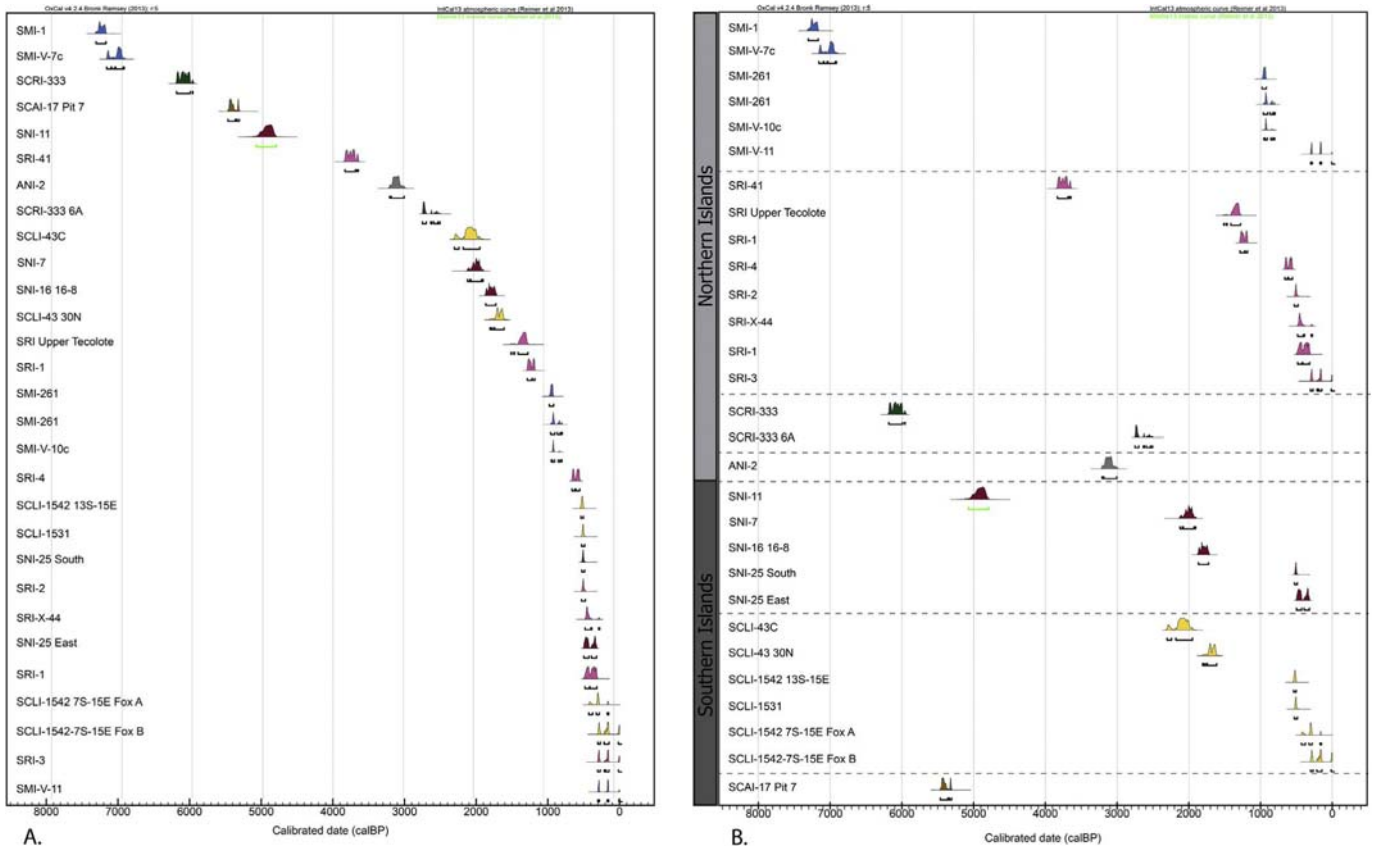


Fig. 2. AMS radiocarbon dates of island foxes. Dates are colored by island and dates with marine calibrations are highlighted in green. Radiocarbon dates are organized by date (Fig. 2A) and by island (Fig. 2B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distal left femur, metarsal, rib, proximal tibia), perhaps representing a single individual, were recovered from ANI-2, a shell midden on East Anacapa occupied between about 3250 and 2710 cal BP (see Jew et al., 2015; Reeder and Rick, 2009). This island fox bone was directly dated to 3210–3010 cal BP and fits well within the site chronology.

4.2. Island fox stable isotopes and diet

We compared island fox, dog, and human isotope values to test the hypothesis that humans provisioned island fox populations (Fig. 3) by quantifying isotope niche width with calculations of standard ellipse area (SEA), sample size corrected standard ellipse area (SEAc), and the overlap between the SEAc of two groups (Table 2, Fig. S1). Isotope niche width varies considerably between islands and species. Ancient human diet varied ($\delta^{13}C$: −19.9‰ to −8.7‰, $\delta^{15}N$: 4.4‰–23.0‰; Goldberg, 1993) on Santa Rosa, Santa Cruz, San Nicolas, San Clemente, and especially on the mainland where larger isotopic variation suggests a more mixed diet of terrestrial and marine resources; SEAc was 6.5‰^{2} and 4.9‰^{2} on the mainland and islands respectively. On the islands, isotope data confirmed that ancient peoples consumed a large proportion of marine resources supplemented by plants (see Gill, 2014). Ancient dogs from San Clemente, San Nicolas and Santa Rosa clustered closely with humans but only on San Nicolas did the standard ellipses for dogs overlap with humans (Table 2). Isotope values of most island foxes differed from those of humans and dogs, although we documented variation between islands, time points (Figs. 3 and 4) and SEAc estimates (Table 2). Island foxes on San Nicolas and San Clemente had the most variation in diet (SEAc of 14.0‰^{2} and 12.8‰^{2}, respectively) and provided the strongest evidence that foxes were consuming marine resources (Figs. 3 and 5). Several San Nicolas, Santa Rosa, and San Clemente fox samples show overlapping isotope values with those of humans (Fig. 3); however, there was no overlap in SEAc between foxes and humans and/or dogs.

Fox $\delta^{13}C$ and $\delta^{15}N$ values differ significantly between islands ($\delta^{13}C$: $F_{(7,232)} = 8.97$, $P < 0.001$ and $\delta^{15}N$: $F_{(7,232)} = 24.39$, $P < 0.001$, $n = 240$) and time period on Santa Cruz ($\delta^{13}C$: $F_{(3,24)} = 6.88$, $P < 0.01$ and $\delta^{15}N$: $F_{(3,24)} = 4.059$, $P < 0.05$, $n = 28$) and San Nicolas ($\delta^{13}C$: $F_{(2,50)} = 12.87$ $P < 0.001$ and $\delta^{15}N$: $F_{(2,50)} = 26.32$, $P < 0.001$, $n = 53$) and just in $\delta^{13}C$ on Santa Catalina ($F_{(2,18)} = 5.561$, $P < 0.05$, $n = 21$), San Clemente ($F_{(2,27)} = 7.119$, $P < 0.01$, $n = 30$), and San Miguel ($F_{(5,30)} = 5.65$, $P < 0.001$, $n = 35$). On the northern islands, small temporal differences in $\delta^{15}N$ values were observed on San Miguel where late and middle Holocene foxes had higher $\delta^{15}N$ values in comparison to earlier and later time periods (Fig. 4). On Santa Cruz and Santa Rosa, there is little difference in isotope values between time periods, although 19th century samples from Santa Rosa showed more variability in $\delta^{13}C$ and $\delta^{15}N$ values.

The southern islands showed a dramatically different pattern. On San Clemente, archaeological, historic, and recent foxes have much higher $\delta^{15}N$ values than the northern islands. Late Holocene samples in particular show a unique isotope pattern, with relatively high mean (±SD) $\delta^{13}C$ (−19.0 ± 1.2‰) and $\delta^{15}N$ (14.9 ± 2.1‰) values. Late Holocene foxes on San Nicolas had higher mean $\delta^{13}C$ (−16.0 ± 1.9‰) values relative to late Holocene San Clemente foxes, but had similar $\delta^{15}N$ values. Historic Santa Catalina foxes from the

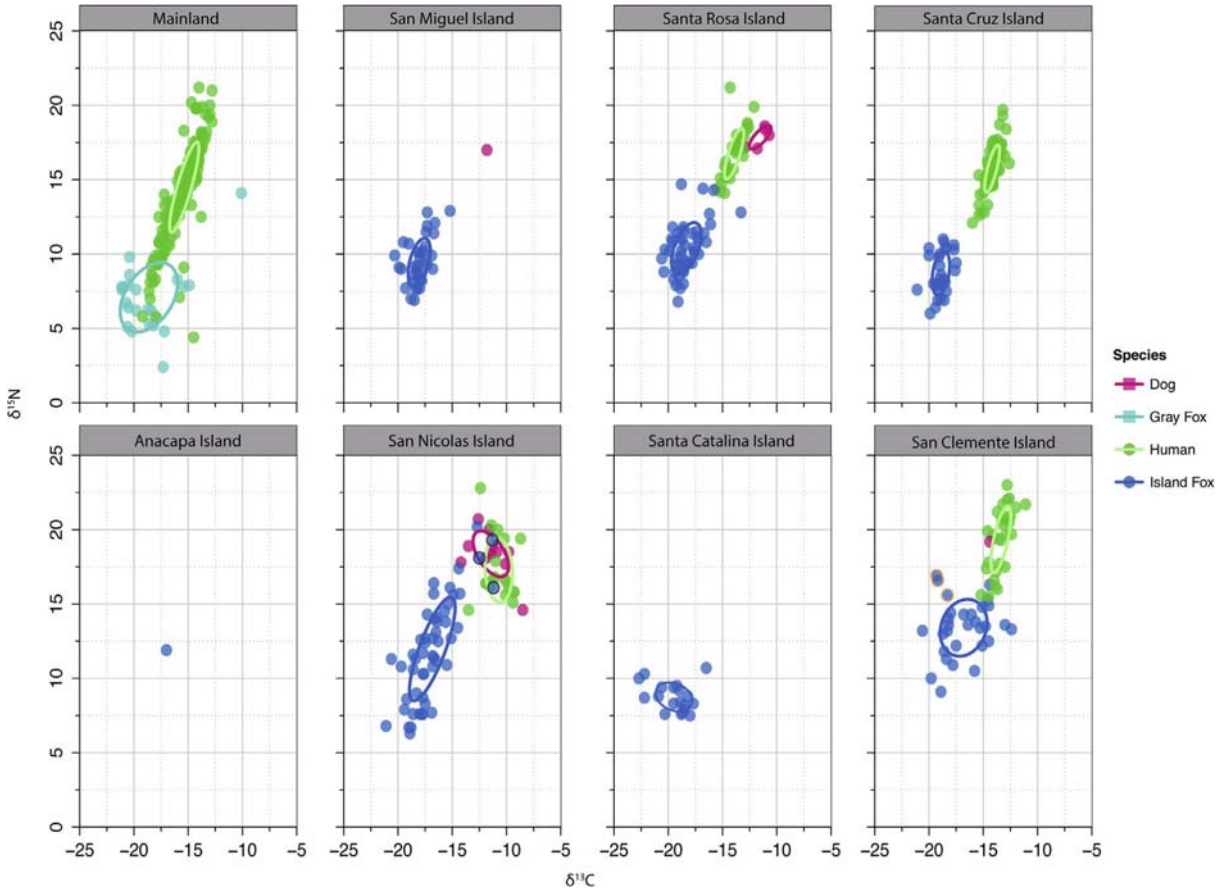


Fig. 3. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope bivariate plot of archaeological humans, archaeological, historic and modern island foxes and modern mainland gray foxes. Standard ellipse areas (SEA) are shown for each species and island foxes within the human ellipse are outlined in black and juveniles with weaning signatures are outlined in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Standard ellipse area for humans, dogs, island foxes, and gray foxes.

Locality	Group	SEAb[a]	SEAc[b]	SEAc overlap[c]
Mainland	Gray Fox	16.9	17.7	0.0
	Human	6.5	6.5	
San Miguel	Island Fox	4.3	4.4	
Santa Rosa	Dog	1.2	1.7	0.0
	Human	2.9	3.0	
	Island Fox	6.3	6.4	
Santa Cruz	Human	3.4	3.5	0.0
	Island Fox	2.2	2.2	
San Nicolas	Dog	6.0	6.6	4.0 (Dog-Human)
	Human	8.1	8.6	
	Island Fox	13.7	14.0	0.0
	Human/Dog	8.1	8.3	0.0
	Island Fox	13.7	14.0	
	1900s	9.1	9.5	0.0
	Late Holocene	6.9	7.3	
Santa Catalina	Island Fox	4.7	5.0	
San Clemente	Human	4.5	4.7	0.0
	Island Fox	12.3	12.8	

[a] Bayesian Standard Ellipse Area in ‰^{2}.
[b] Standard Ellipse Area corrected for small sample sizes.
[c] The overlap between two SEAc ellipses.

1900s had slightly higher $\delta^{13}C$ values than the 1800s but similar $\delta^{15}N$ values. The best evidence for a temporal change in diet came from San Nicolas, where late Holocene foxes had significantly higher $\delta^{15}N$ values and virtually no isotopic overlap with those from the 20th century (Figs. 4 and 5).

5. Discussion

5.1. Island fox origins, antiquity, and chronology

We identified and dated all island fox remains ($n = 29$) from potentially early archaeological sites and none were older than 7310 cal BP, supporting the pattern found by Rick et al. (2009). This study includes the largest sample available to date and supports the hypothesis that island foxes arrived during the early Holocene. Extensive survey, excavation, and analysis of the late Pleistocene and early Holocene archaeological contexts of the northern Channel Islands (Erlandson et al., 1996, 2011; Rick et al., 2013), as well as paleontological localities have yielded no other fox remains. Rick et al. (2009) noted that many of the Channel Islands fossil localities were thought to be ancient bald eagle nests (Guthrie, 1993) that likely would have contained remnant prey fox remains if they were available on the islands. While historic and modern bald eagle nests occasionally contain island fox remains (Erlandson et al., 2007; Newsome et al., 2010; 2015), foxes have not been recovered from Pleistocene fossil contexts. The oldest date of ~7300 years also fits well with genetic estimates of island and gray fox divergence (Hofman et al., 2015b). Analysis of mitochondrial genomes calibrated with a slightly younger date (7160–6910 cal BP), suggested that island foxes diverged from their mainland progenitor ~9200–7100 cal BP (Hofman et al., 2015b). This is well after humans first arrived on the Channel Islands (~13,000 cal BP), although it is still not clear whether foxes originally arrived on the northern islands through a natural or human-assisted dispersal.

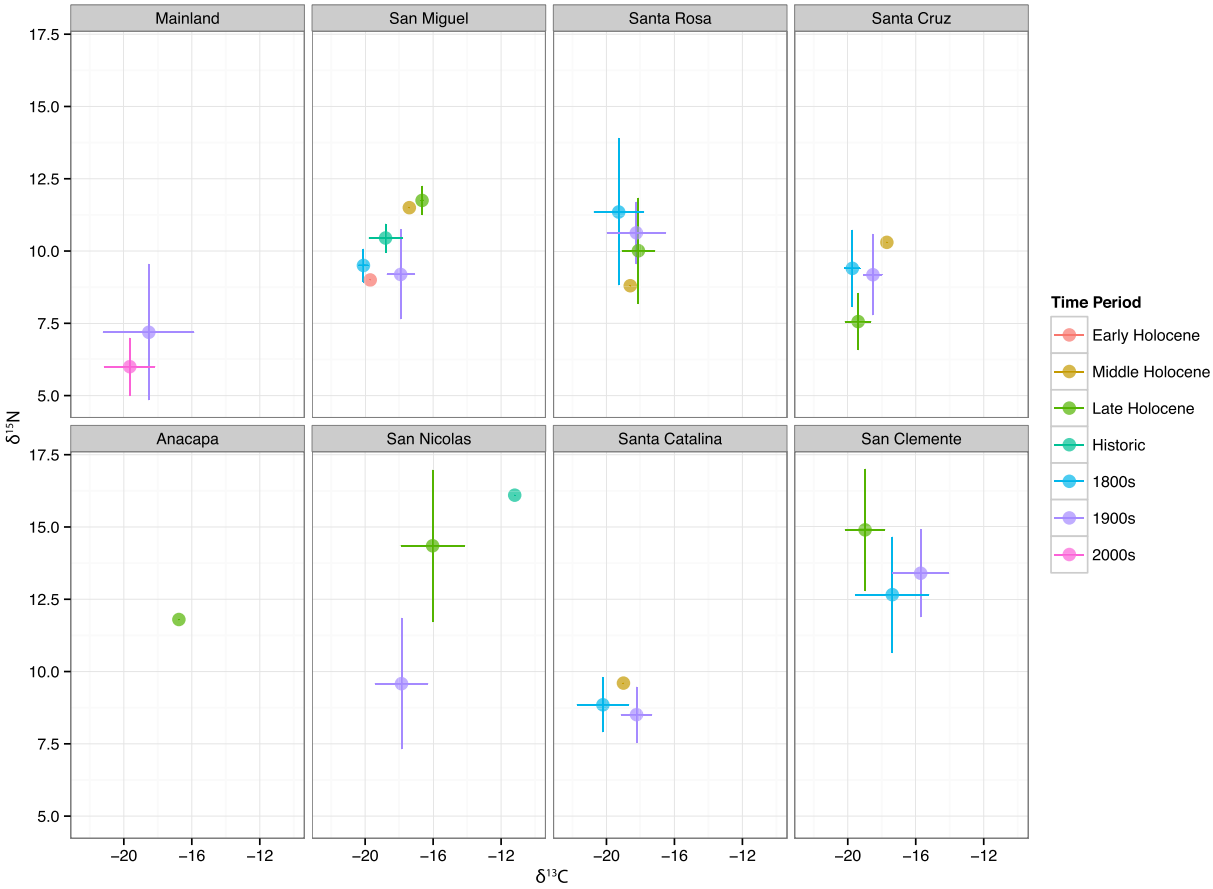


Fig. 4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope bivariate plot of island and gray foxes by time period.

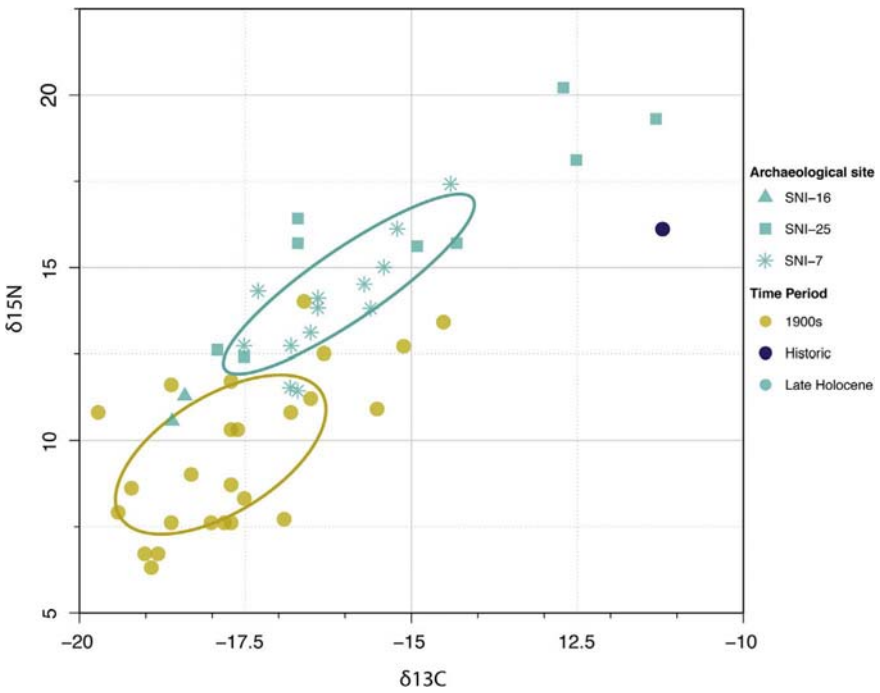


Fig. 5. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope bivariate plot of San Nicolas Island foxes by time period. Island foxes in the late Holocene show evidence of more marine resource use than foxes in the 1900s.

Our oldest island fox remains come from San Miguel Island (Fig. 2A) and support the hypothesis that foxes first arrived on the northern islands and were subsequently introduced to the southern islands. The two early dates from San Miguel predate any dates from the southern islands by ~1500–2000 years. Foxes may have dispersed naturally to the northern islands during the human era, or been introduced by Native Americans (Hofman et al., 2015b). Depending on when foxes arrived on the northern islands, changes in sea level could have affected their natural dispersal between islands. As noted earlier, the northern islands coalesced into a super-island, Santarosae (see Fig. 1), that began to separate into its current configuration of four separate islands around 11,000 cal BP and was completely separated by 9000 cal BP (Muhs et al., 2014; Reeder-Myers et al., 2015). Our earliest AMS dates suggest that foxes arrived well after the islands had separated. However, molecular clock divergence estimates based on the analysis of whole mitogenomes suggest that island and mainland fox populations diverged ~9200 years ago (95% HPD: 13,300–6100) (Hofman et al., 2015b), around the time the northern islands were completing their separation into distinct land masses. If foxes arrived after the islands separated, then the most parsimonious explanation for their distribution would be a human-assisted translocation by ancient peoples between the northern islands.

The first evidence of foxes on the southern islands comes from remains found on Santa Catalina and San Nicolas that date to 5460–5310 cal BP and 5070–4790 cal BP, respectively. Genetic estimates suggest that southern island lineages diverged from northern lineages ~7100 (95% HPD: 9000–5200) years ago shortly after foxes arrived on the northern islands (Hofman et al., 2015b). Colonization by rafting on floating vegetation or debris to the three southern islands that are further from the mainland than the northern islands is unlikely. Our results based on both AMS dates and molecular clock divergence estimates (Hofman et al., 2015b) support a more likely scenario that ancient peoples transported foxes on their vessels to the southern islands after their initial arrival on the northern islands. If this is true, it lends anecdotal support to the hypothesis that humans first transported foxes to the northern islands.

While investigating the contexts of all recorded island fox material, we documented considerable variation between previously reported site chronologies and AMS dates on island fox bones recovered from the same site. For example, 15 AMS dates from SRI-3 suggest a trans-Holocene occupation from 8860 to 2760 cal BP, but the island fox remains from the site were directly radiocarbon dated to ~300 years ago. A similar discrepancy between known site chronologies and direct AMS island fox dates was also identified at SRI-1 and SRI-4 (Table 1). Rick et al. (2009) analyzed island foxes from subfossil localities previously reported to be > 40,000 (beyond the limits of radiocarbon dating) and 16,000 years old and documented the same problem as all fox remains from these subfossil localities were dated to the Holocene and even historic times (Rick et al., 2009; Shelley, 2001). Much of the problem likely stems from the fact that these subfossils and archaeological specimens noted above were obtained from the surface of a site or from an unknown locality rather than in good stratigraphic context. In one case, fox remains recovered by Orr (1968) at a subfossil locality on Santa Rosa Island were argued to be at least 16,000 years old. These data were used to support a pre-human colonization of the northern Channel Islands by foxes (Collins, 1991a; Orr, 1968) and were used to calibrate many of the initial genetic studies of island foxes (Aguilar et al., 2004; Gilbert et al., 1990; Wayne et al., 1991). However, direct AMS dating of this bone indicated that it was only 1510–1280 years old and likely from a fox bone intruded into Pleistocene deposits or whose stratigraphic association was misidentified (Rick et al., 2009; Shelley, 2001). These findings underscore the importance of direct AMS ^{14}C dating of island foxes and other animal bone samples when interpreting species chronology, biogeography, and dispersal.

5.2. Ancient Island fox diets

5.2.1. Early and middle holocene

We explored changes in island fox diet spanning 7300 years and seven islands, including Anacapa, where foxes had not been previously reported. We hypothesized that if humans introduced foxes to the northern islands, early fox remains might have isotope values similar to humans or dogs, which in this context would indicate consumption of marine resources with high δ^{13}C and δ^{15}N values relative to terrestrial foods. However, there is no overlap between the SEAc of human/dogs and foxes on any of the islands (Table 2). The earliest fox from San Miguel does not have a marine isotope signature suggestive of anthropogenic resource consumption or provisioning, but instead has isotope values indicative of a terrestrial diet in comparison to foxes from later time periods (Fig. 3). On Santa Cruz, a middle Holocene (6180–5950 cal BP) fox has higher δ^{13}C and δ^{15}N values relative to chronologically younger foxes, but there is no definitive evidence of provisioning on Santa Cruz. On the southern islands, the earliest fox on Catalina has isotope values that are slightly higher than those from later periods, however, comparable human data are not available from this island so it is difficult to make an assessment of anthropogenic resource consumption or provisioning. Unfortunately, the earliest fox from San Nicolas (SNI-11, 5070–4790 cal BP) was not available for isotopic analysis. Together our results based on these few data points do not support the scenario that early and middle Holocene foxes were scavenging anthropogenic resources or that ancient peoples were provisioning them. However, just because we did not detect direct human provisioning in these samples, does not preclude an association with humans or an ancient human introduction.

Although fox furs may have been important to Native Islanders, another reason why humans would translocate foxes to the Channel Islands was for pest management—to manage deer mouse populations on islands with few natural predators that contained human settlements rich in refuse (Collins, 1991a; Rick et al., 2009, 2005; Vellanoweth, 1998). If pest control was a factor influencing translocation of foxes, and mice were a large component of their diet, we would not expect to find isotopic signatures of human provisioning. Interference competition with dogs also may have forced many foxes to focus on deer mice and other wild foods rather than human refuse. Even if ancient peoples were not provisioning foxes directly, midden refuse could have attracted mice, which were likely a dietary staple for foxes (Cypher et al., 2014). However, distinguishing between intentional or accidental pest management is difficult in the archaeological record.

5.2.2. Late Holocene

In the late Holocene (3500–200 cal BP), we observed high δ^{13}C and δ^{15}N values in island foxes from San Nicolas Island that overlapped with isotope values of humans, suggesting that foxes consumed significant amounts of marine resources. However we did not find any overlap in the niche width estimates using standard ellipses between human and fox populations. On Santa Rosa, a fox initially associated with the Pleistocene Upper Tecolote member, but dated to much later (1510–1280 cal BP), has isotope values similar to some humans, although not within the SEAc for humans as a group (Fig. 3). Human population sizes on some of the islands increased during the late Holocene as people settled in large sedentary villages (Kennett, 2005). Higher population densities producing more refuse could provide a valuable resource for island foxes living near a village. Nevertheless, it is difficult to distinguish

between scavenging from human refuse and intentional human provisioning, yet either way, humans may have influenced fox diet.

Late Holocene foxes from San Nicolas have considerable isotopic variation with $\delta^{13}C$ and $\delta^{15}N$ values varying by 7.3‰ and 9.7‰ respectively. Late Holocene foxes from SNI-7, where the presence of nearly 20 island fox skulls in a single site may suggest production of fox capes or blankets (see Collins, 1991b), have relatively high $\delta^{13}C$ and $\delta^{15}N$ values, but lie just below the standard ellipse for human and dogs (Figs. 3 and 5). However, we detected three foxes with isotope values suggestive of human provisioning with marine resources at the Tule Creek Village site (SNI-25). The east locus of SNI-25 has artifacts and features associated with ceremonial events, including shell effigies, feasting pits, and animal burials (Smith, 2013). Three disarticulated foxes from the east locus have higher mean (±SD) $\delta^{13}C$ (−12.2 ± 1.4‰) and $\delta^{15}N$ (19.2 ± 2.1‰) values when compared to three foxes from the south locus with mean $\delta^{13}C$ and $\delta^{15}N$ values of −15.6 ± 3.2‰ and 14.6 ± 3.3‰ respectively (Smith, 2013). The higher isotope values in foxes from the east locus could mean that the animals interred there were provisioned and kept for ceremonial purposes. At Teotihuacan in Mexico, some felids (*Panthera onca* and *Puma concolor*) intended for sacrifice were first held for several months in captivity, which allowed enough time for bone collagen $\delta^{13}C$ values to reflect consumption of maize, while other individuals were sacrificed before dietary maize was integrated into this tissue (Sugiyama et al., 2015). These differences may be equivalent to the variability in isotope values from foxes found at a single archaeological site, raising the possibility that some animals were provisioned while others were not, and suggesting that differing cultural practices on the northern and southern islands may have influenced the diet of some late Holocene island foxes.

On the southern islands, the *Chinigchinich* religion, which according to ethnohistoric accounts involved animal sacrifices (Jackson and Castillo, 1996; Raab and Cassidy, 2009), may have played a role in observed island fox dietary patterns. On San Clemente, island foxes were recovered from a ceremonial site (SCLI-1524) possibly associated with the *Chinigchinich* religion. Excavations within the interior of a circular midden berm surrounding a potential *wamkish*, or an open area ceremonial site, yielded five dog burials and six fox burials (five juvenile) (Hale and Salls, 2000). We dated three juvenile foxes and one juvenile dog from these burials and the calibrated dates span three non-overlapping time periods (730–670 cal BP (dog), 540–500 cal BP (fox), and 430–0 cal BP (double fox burial). These data suggest that people may have buried juvenile canids at this site for several centuries. The youngest fox burial might be associated with the historically described *Chinigchinich* religion while the earlier dog and fox burials are consistent with late prehistoric animal sacrifice documented in other southern Channel Island sites (see Bartelle et al., 2010; Vellanoweth et al., 2008).

Isotope data from these burials are somewhat ambiguous, and may relate to the age of the foxes recovered from this context. In mammals, juveniles typically have higher $\delta^{15}N$ values than adult females (mothers), as mothers catabolize their own tissue to produce milk for their offspring (Fuller et al., 2006; Newsome et al., 2006); the effects of nursing on $\delta^{13}C$ values is unknown in foxes. The young age of these individuals does not allow us to conclude that there was anthropogenic resource consumption or human provisioning, but suggests that ancient people either had immediately removed these juveniles from their mothers or had the mother on hand to feed her offspring. We can also use age at death to identify the seasonality of this ritual. Although foxes give birth in late April and early May on the northern islands, with mothers lactating for ~7–9 weeks and pups emerging from the den in the early summer (Moore and Collins, 1995), parturition seems earlier on the southern islands. Powers (2009) found that foxes had litters from early to mid-March on San Nicolas Island, while Resnick and Andelt (2012) reported that parturition occurred as early as mid-February on San Clemente Island. The juvenile foxes from SCLI-1524 are less than two months of age based on dental eruption (Hale and Salls, 2000). Therefore, this ritual can be dated to late spring or early summer depending on parturition date, but possibly when fox pups are emerging from their dens and learning to forage with their parents. These ritual activities on San Clemente, in addition to possible human provisioning in several San Nicolas foxes, indicate that late Holocene people had considerable interaction with island fox populations.

5.2.3. Historic and recent times

Isotope values of archaeological and late Holocene foxes differ considerably from those collected from 19th and 20th century populations on several of the islands (Fig. 4). Historic ranching dramatically transformed island landscapes in the 19th century. On San Nicolas, where there is no overlap in $\delta^{13}C$ and $\delta^{15}N$ SEAc estimates between the late Holocene and the 19th century foxes, ranching and the introduction of non-native grasses may have affected island fox diet. The most comprehensive study of modern island fox diet to date indicates that as much as 45% of San Nicolas fox diets may include non-native resources (Cypher et al., 2014). On San Clemente, four foxes with higher $\delta^{13}C$ and $\delta^{15}N$ values (similar to humans) date to the late 19th and 20th century (1897; 1977; 1982; 1982). San Clemente has been owned and managed by the United States Navy since 1934 and foxes may have been provisioned by sailors stationed on the island. There are also anecdotal accounts that historic ranchers kept island foxes as pets and moved foxes from Santa Catalina to San Clemente (Collins, 1991a; Johnson, 1975). During the course of the twentieth century, human land use shifted from ranching to conservation-oriented management, likely contributing to the minor shifts we see in island fox $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4).

5.3. Long-term trends and signatures of marine resource use: human provisioning, scavenging in middens or on the coast

Human isotope values on the Channel Islands have relatively high mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of −13.5 ± 1.4 and 16.9 ± 2.2 respectively, and enrichment in fox bone collagen isotope values to these levels would necessitate the consumption of considerable marine resources. The high $\delta^{13}C$ and $\delta^{15}N$ values in some foxes could be a result of scavenging anthropogenic resources or human provisioning, but they might also be generated through scavenging of marine mammal carrion or other marine resources. We found little evidence of considerable marine resource use by recent fox populations from San Miguel and San Nicolas, which have large pinniped rookeries that produce numerous carcasses. However, as island foxes are territorial and males are intolerant of intruders, only a small proportion of the foxes on these islands – those with home ranges that include beaches that contain large amounts of marine resources (e.g., pinniped rookeries) – would be likely to use marine resources. Further research is required to determine if marine mammal scavenging is responsible for these isotopic patterns, including data on how the habitat composition of fox home ranges affects diet variation, as well as comparisons of ancient samples to isotopic values in bone collagen of modern foxes known to scavenge marine carrion.

Long-term patterns in island fox stable isotope values are most consistent on Santa Catalina and Santa Cruz (Fig. 4). Interestingly, in a pairwise analysis of food group contributions in modern island fox scat, Horn's similarity index (0.59) shows that these islands are also similar today (Cypher et al., 2014). Regardless of time period,

foxes from San Clemente have higher $\delta^{13}C$ and $\delta^{15}N$ relative to the other islands (Fig. 4). Two scenarios could explain this pattern. First, variability in climate and habitats between San Clemente and the other islands could affect resource availability and prey choice, or change the baseline $\delta^{13}C$ and $\delta^{15}N$ composition of primary producers that would in turn label primary consumers that island foxes eat. Second, from the late Holocene through the present, people may have provisioned foxes or foxes scavenged anthropogenic and/or marine resources. For San Clemente we do not have data for foxes prior to ~2300–2200 cal BP, or before the human population increase that likely coincided with the development of *Chinigchinich* religious practices. A trend of decreasing $\delta^{13}C$ and $\delta^{15}N$ values through time is evident on San Nicolas (Fig. 5) between the late Holocene and the 1900s. This island provides the best evidence for potential scavenging of Native American refuse or direct human provisioning of foxes, as well as indicating that foxes were eating less marine resources in the wake of early 19th century removal of Native Americans from the island.

6. Conclusions

In this study, we analyzed new and previously reported stable isotope values and AMS radiocarbon dates to explore the antiquity of the island fox and the evolution of its diet from its known history of occupation from 7300 years ago to the present. A suite of 29 AMS radiocarbon dates suggests that the oldest known island fox remains come from San Miguel Island as early as ~7300 cal BP. We have not necessarily identified the earliest fox on the islands, but these data support previous genetic research and radiocarbon dating that indicate an early to middle Holocene arrival of foxes to the Channel Islands (Hofman et al., 2015b; Rick et al., 2009).

We used the Canine Surrogacy Approach to evaluate hypotheses about temporal and spatial variation in island fox diet and human-fox interactions. In general, our data suggest that island fox diets differ substantially from humans and dogs, and that island foxes are not good surrogates for ancient human or dog diets. Beyond the Channel Islands, West and France (2015) also found differences in the isotope signatures of dogs and red foxes (*Vulpes vulpes*) on Kodiak Island, Alaska, where dogs had evidence for marine resource consumption and foxes had mixed terrestrial and marine signatures. We also detected minimal evidence of anthropogenic (marine-based) resource use by foxes, or human resource provisioning of foxes on the Channel Islands. Exceptions to this pattern might have occurred in the late Holocene on San Nicolas, Santa Rosa, and San Clemente, where a few foxes had isotope values that overlapped with those of humans.

These data, however, do support a number of unique human-fox interactions, including ritual sacrifice and potential provisioning. Ancient peoples appear to have ritually sacrificed juvenile foxes on San Clemente in the late Holocene (Hale and Salls, 2000). On San Nicolas there is evidence of potential resource provisioning of adult foxes, including some from ceremonial or ritual contexts. Although our isotope data do not suggest significant human-fox provisioning on the other islands, more than 50 fox burials and other human-associated fox remains show a ritual interaction between humans and foxes.

With a dataset spanning 7300 years and a range of human land use practices, we are able to identify some long-term trends in fox diet. As expected, island foxes exhibited substantial dietary variation through time and across space spanning several trophic levels. Despite the dramatic changes that have altered the environmental and cultural landscapes of the Channel Islands during the Holocene (i.e., Native American, ranching, conservation, military use, and tourism), stable isotope analysis demonstrates the generalist foraging behavior of the omnivorous island fox. It remains to be seen how island fox populations will be impacted by future climatic and cultural changes, but the species' generalist/omnivorous foraging behavior may make it resilient to future environmental changes that influence resource availability on the Channel Islands.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2016.06.010.

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