Quaternary Research 71 (2009) 93–98

Contents lists available at ScienceDirect

Quaternary Research

journal homepage: www.elsevier.com/locate/yqres

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

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ARTICLE INFO

Article history:
Received 16 February
Available online 18 January 2009

Keywords:
Island fox
Urocyon littoralis
Animal translocation
AMS ^{14}C dating
Island ecology
California Channel Islands

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 researchers 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 km^2. Currently between 20–98 km offshore, the islands have not been connected to the mainland during the

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0033-5894/$ – see front matter. Published by University of Washington.
doi:10.1016/j.yqres.2008.12.003

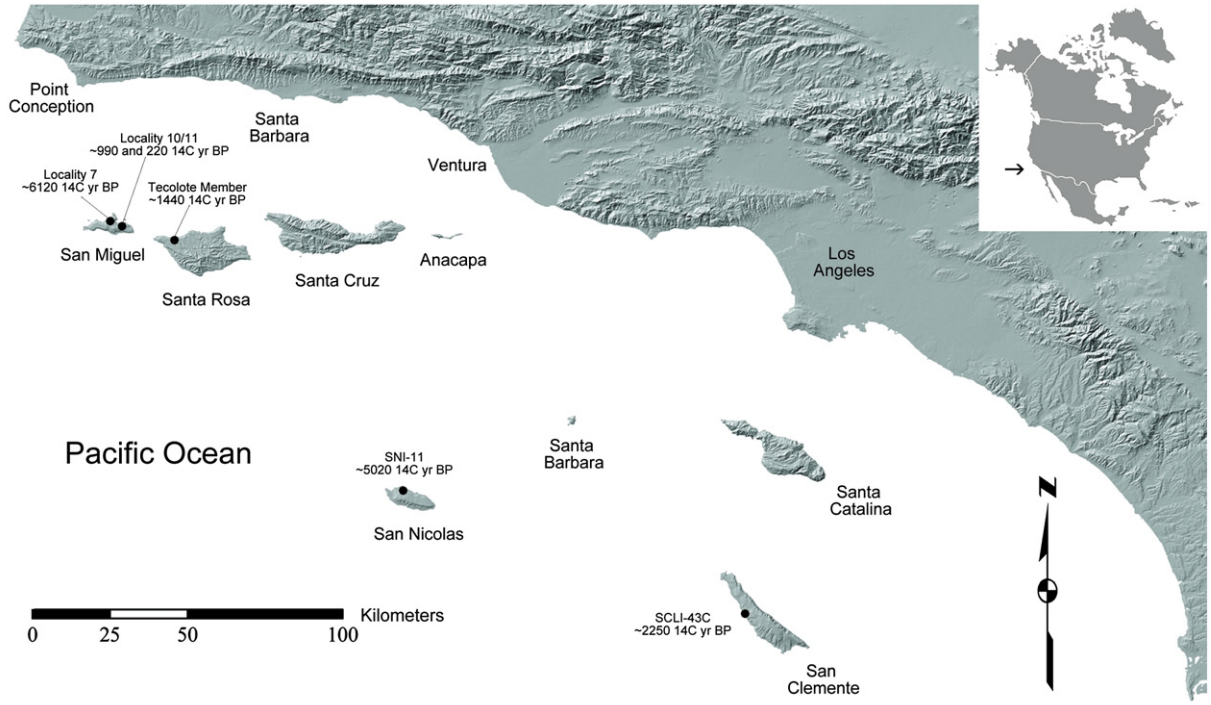

Figure 1. Southern California and the Channel Islands showing the location of directly dated fox specimens and approximate ages (^{14}C yr BP). Tecolote Member, SNI-11, and SCLI-43C are archaeological specimens dated by Shelley (2001).

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).

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

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