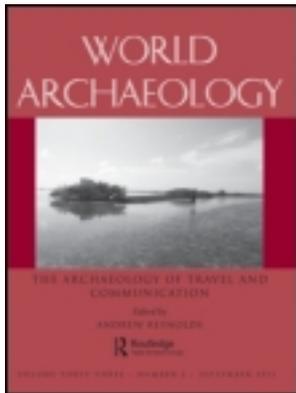


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Flightless ducks, giant mice and pygmy mammoths: Late Quaternary extinctions on California's Channel Islands

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Abstract

Explanations for the extinction of Late Quaternary megafauna are heavily debated, ranging from human overkill to climate change, disease and extraterrestrial impacts. Synthesis and analysis of Late Quaternary animal extinctions on California's Channel Islands suggest that, despite supporting Native American populations for some 13,000 years, few mammal, bird or other species are known to have gone extinct during the prehistoric human era, and most of these coexisted with humans for several millennia. Our analysis provides insight into the nature and variability of Quaternary extinctions on islands and a broader context for understanding ancient extinctions in North America.

Keywords

Megafauna; island ecology; human-environmental interactions; overkill; climate change.

Introduction

In earth's history there have been five mass extinctions – the Ordovician, Devonian, Permian, Triassic and Cretaceous events – characterized by a loss of over 75 per cent of species in a short geological time period (e.g. 2 million years or less: Barnosky et al. 2011). Although not a mass extinction, one of the most heavily debated extinction events is the Late Quaternary extinction of megafauna, when some two-thirds of large terrestrial mammalian genera (>44kg) worldwide went extinct (Barnosky et al. 2004). Explanations for this event include climate change, as the planet went from a glacial to interglacial

period, to human overkill, extraterrestrial impacts and disease (Faith and Surovell 2009; Firestone et al. 2007; Grayson 2001, 2007; Grayson and Meltzer 2002; Haynes 2007; Koch and Barnosky 2006; Martin and Klein 1984). The debate has involved archaeologists, paleontologists, ecologists, geneticists and other researchers who seek an explanation for this most recent major extinction event and a better understanding of the geographic and demographic expansion of our own species. Although debate continues on many of the details and causes, in North America as many as thirty-five mammalian genera may have become extinct in as little as 2000 years between about 12,000 and 10,000 RYBP (Faith and Surovell 2009).

In this paper, we review archaeological and paleontological evidence of Late Quaternary animal extinctions on California's Channel Islands. Researchers have long been interested in the extinction of Channel Island pygmy mammoths (*Mammuthus exilis*), giant island deer mice (*Peromyscus nesodytes*), flightless ducks (*Chendytes lawi*) and other species – ornate shrews (*Sorex ornatus*) and voles (*Microtus miguelyensis*) – but the precise causes and timing of many of these extinctions is debated or unknown. Island species are generally considered to be more susceptible to human-induced extinctions than those on continents and archaeologists have used data from islands to help contextualize broader Late Quaternary extinctions in the Americas and Australia (Steadman and Martin 2003; Wroe et al. 2006). Because the Channel Islands were first occupied by humans around 13,000 cal. BP (~11,000 RYBP), a period of extensive extinctions in North America, our analysis provides insight into the relationships between ancient peoples, prehistoric extinctions, climatic and environmental changes, and similarities and differences between extinctions on islands and continents.

Background

Today, the eight Channel Islands are located between 20 and 98km from the southern California mainland (Fig. 1). During glacial periods of the Quaternary, when sea levels were considerably lower than today, all the islands were still separated from the mainland by a water gap of 7–8km or more. The four northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa) formed a super-island (Santarosae) that began to break up around 11,000 cal. BP (Kennett et al. 2008). The southern islands (San Nicolas, Santa Catalina, Santa Barbara and San Clemente) were larger in size and other offshore islets appeared during glacial periods, but they remained more isolated and dispersed (Porcasi et al. 1999). The islands currently range in size from about 2.6 to 249km² and are characterized by a relatively mild climate, with most precipitation during winter and spring.

Channel Island terrestrial ecosystems have lower species diversity when compared to the adjacent mainland. The extinct and extant endemic mammals on the islands are limited to about ten species, including island fox (*Urocyon littoralis*), spotted skunk (*Spilogale gracilis amphialus*), ornate shrew and deer mouse (*Peromyscus maniculatus*), found on some or all of the islands, and several bats (Table 1). The herpetofauna is slightly more diverse, and includes the island night lizard (*Xantusia riversiana*), southern alligator lizard (*Elgaria multicarinatus*), side-blotched lizard (*Uta stansburiana*), Channel Islands slender salamander (*Batrachoseps pacificus*), Pacific Chorus Frog (*Pseudacris regilla*), island

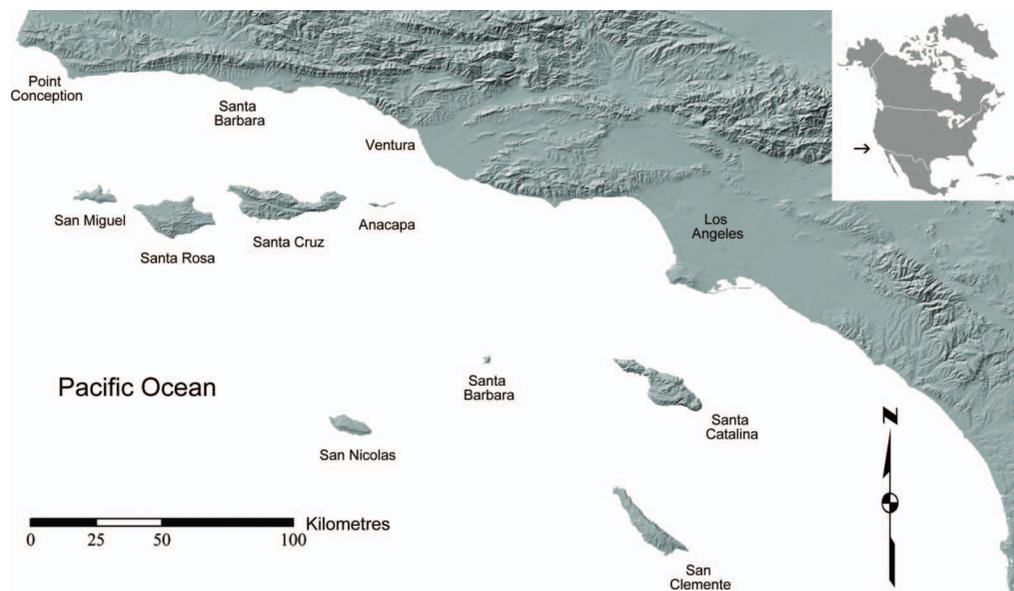


Figure 1 The Channel Islands and southern California coast.

Table 1 Extinct and extant land mammals (except bats and historically introduced species) and their distribution on the California Channel Islands.

Island	Extinct land mammals	Extant land mammals
San Miguel	Giant island deer mouse (<i>P. nesodytes</i>), mammoths (<i>M. columbi</i> and <i>M. exilis</i>), spotted skunk? (<i>S. gracilis</i>), San Miguel Island vole (<i>M. miguelensis</i>), ornate shrew (<i>S. ornatus</i>)	Deer mouse (<i>P. maniculatus</i>), island fox (<i>U. littoralis</i>)
Santa Rosa	Giant island deer mouse, mammoths, ornate shrew	Deer mouse, island fox, spotted skunk
Santa Cruz	Giant island deer mouse, mammoths	Deer mouse, island fox, spotted skunk, harvest mouse (<i>R. megalotis</i>)
Anacapa	Giant island deer mouse, mammoths, Anacapa deer mouse (<i>P. anayapensis</i>)	Deer mouse
San Nicolas	–	Deer mouse, island fox
Santa Barbara	–	Deer mouse, island fox
Santa Catalina	–	Deer mouse, ornate shrew, island fox, harvest mouse, California ground squirrel (<i>Otospermophilus beecheyi</i>)
San Clemente	–	Deer mouse, island fox

Note

Ornate shrews, SMI vole and *P. nesodytes* may have occurred on all northern Channel Islands when they were connected as Santarosae, but they have been identified only on the islands noted above.

gopher snake (*Pituophis catenifer pumilis*), Pacific rattlesnake (*Crotalus oreganus*) and about fourteen additional species found on various islands (Savage 1967; Schoenherr et al. 1999). Despite supporting large populations of sea and land birds, only one extant, endemic bird species, the island scrub-jay (*Aphelocoma insularis*), is known from the Channel Islands (Johnson 1972).

The Channel Islands contain an archaeological record that spans some 13,000 calendar years and has generally good integrity and preservation. Chumash and Tongva (Gabrielino) peoples who occupied the northern and southern Channel Islands, respectively, at the time of European contact were densely populated hunter-gatherer-fishers, whose predecessors occupied the islands for at least 13,000 (northern islands) to 9,000 (southern islands) calendar years (Erlandson et al. 2008). Maritime voyaging and a heavy reliance on coastal resources extend back to the earliest island colonists (Erlandson et al. 2011; Kennett 2005; Rick et al. 2005). With a research tradition extending back over a century, Channel Island archeofaunal samples are available from three sites dated to ~12,200–11,400 cal. BP and several others dated between about 10,000 and 7500 cal. BP on the northern Channel Islands (Erlandson et al. 2011; Rick et al. 2005), one San Clemente Island site dated to *c.* 9000 cal. BP (Raab et al. 2009) and numerous sites dated throughout the Middle and Late Holocene on all but the two smallest islands (Anacapa and Santa Barbara: Rick et al. 2005).

There are also more than 380 fossil and sub-fossil Late Quaternary localities on the northern Channel Islands that contain pygmy or full-sized mammoths (Agenbroad 2009:15), at least twenty-one open-air and cave deposits on San Miguel and Santa Rosa islands that contain bird, amphibian, reptile and micro-mammal remains (Ainis and Vellanoweth 2012; Guthrie 1980, 2005; Walker 1980) and other fossil deposits in raised beaches and alluvial sequences preserved on marine terraces (Lipps 1964; Lipps et al. 1968). Considerably more Late Quaternary paleontological research has been conducted on the northern Channel Islands than on the southern Channel Islands, and with one notable exception (*C. lawi*) the dataset is currently limited to the northern Channel Islands. Together these archaeological and paleontological data provide a framework for evaluating Late Quaternary extinctions on California's Channel Islands.

A mammoth ending: extinction of *Mammuthus exilis*

In North America, mammoths and mastodons are the only Pleistocene megafauna that have well-documented kill sites with evidence of human hunting (Grayson and Meltzer 2002). An enduring research question on the Channel Islands has focused on the relationship between humans and pygmy mammoths. The pendulum has swung widely over the years, often paralleling trends in continental megafaunal extinction debates, between human overkill, climate change and, more recently, an extraterrestrial impact as the driving force of extinction (Agenbroad 2002, 2009; Agenbroad et al. 2005; Berger and Orr 1966; Cushing et al. 1986; Erlandson et al. 2004; Kennett et al. 2008; Orr 1968; Orr and Berger 1966).

Beginning perhaps 200,000 years ago, Columbian mammoths swam to the northern Channel Islands, underwent a roughly 30 per cent size reduction (shrinking to just under a 2m average shoulder height) and gave rise to island pygmy mammoths (Agenbroad 2009:

16). Although Columbian mammoths may have periodically re-colonized the islands, pygmy mammoths constituted at least 90 per cent of the terminal Pleistocene island proboscidean population (Agenbroad 2009).

Some twentieth-century researchers believed the northern Channel Islands were colonized by humans at least 40,000 years ago and associations between artifacts, 'fire features' and mammoth remains pointed towards a human-induced extinction (Berger and Orr 1966; Orr 1968; Orr and Berger 1966). The Americas are now thought to have been colonized during the last ~15,000 years and careful scrutiny of some of these questionable associations suggests that most or all of the fire areas or 'mammoth roasting pits' were natural burn features or the result of groundwater processes (Cushing et al. 1986; Wendorf 1982). There is currently no direct evidence that Paleoindians hunted Columbian or pygmy mammoths on the Channel Islands.

Recent Accelerator Mass Spectrometry (AMS) radiocarbon dating has offered new insight into the possible contemporaneity of pygmy mammoths and humans. AMS dating of charcoal associated with bone collagen from a Santa Rosa Island mammoth vertebra yielded dates between ~13,000 and 12,900 cal. BP, considered to be the terminal age for pygmy mammoths (Agenbroad et al. 2005; Kennett et al. 2008). A re-analysis of the stratigraphic sequence at the Arlington Springs site on Santa Rosa Island and direct dating of human remains recovered from this site by Orr (1968) has set the initial human presence on the islands between 13,000 and 12,900 cal. BP (Erlandson et al. 2011; Johnson et al. 2002). This apparent overlap led Agenbroad et al. (2005) to speculate that humans may have been responsible for the extinction of Channel Island mammoths.

No clear resolution currently exists on the cause or causes of island mammoth extinction. The land area of the northern Channel Islands shrank by nearly 80 per cent between 18,000 and 7,000 years ago as rising sea levels broke Santarosae into four separate landmasses (Kennett et al. 2008). Postglacial warming drastically altered island catchments, vegetation communities and freshwater sources (Erlandson et al. 2004: 56–7), which would have exerted stress on large herbivores. Although radiocarbon dating suggests that pygmy mammoths and humans may have overlapped on the islands, human population densities may have been fairly low and faunal remains associated with archaeological sites dated between 12,200 and 11,500 cal. BP on the Channel Islands contain the remains of shellfish, marine fishes, marine mammals, seabirds and waterfowl with no terrestrial mammals except small rodents (Erlandson et al. 2011). Finally, a controversial new hypothesis suggests that wild fires and massive biomass burning triggered by a comet or other extraterrestrial impact over North America may have been responsible for the demise of pygmy mammoths and other New World megafauna (Firestone et al. 2007; Kennett et al. 2008), but others have raised significant questions about the viability of this model (Pinter et al. 2011). More questions than answers remain and continued research will be the only way to resolve these debates. An important avenue for future research is assessing the abundance of mammoth remains through time, but such studies are currently not possible with the available published data. The apparent synchronicity of the last proboscideans and first people on the islands is suggestive of a human influence, but until direct associations between human artifacts and island mammoths are found we are left to conclude that climate change and ecological disturbance were the primary driving forces of this extinction.

A tale of two mice: *Peromyscus nesodytes* and *P. maniculatus*

When introduced to islands with naïve fauna, rodents have a transformative effect on island ecosystems and organisms (Grayson 2001). Rat predation on birds' eggs, nestlings and adult birds, for instance, is a notable contributor to bird extinctions throughout the Pacific Islands (Steadman 2006: 405–6). Mice were also introduced prehistorically to islands and continental landmasses by humans in Greenland and the Mediterranean (Grayson 2001).

On the Channel Islands, two species of deer mice are common in sub-fossil and archaeological assemblages, *Peromyscus nesodytes* and *P. maniculatus* (Guthrie 1993; Walker 1980; White 1966; Wilson 1936). A third form, *P. anyapahensis*, is not as well documented, but may be ancestral to *P. nesodytes* (White 1966), a giant deer mouse that was present on the northern Channel Islands during the Late Pleistocene, prior to human arrival around 13,000 cal. BP (Guthrie 1993; Rick 2012). *Peromyscus nesodytes* is about 35 per cent larger than the extant island deer mouse (*P. maniculatus*) and has been identified in both San Miguel and Santa Rosa archaeological and fossil localities, but probably was on the four northern islands when they were connected as Santarosae. *Peromyscus maniculatus* is the only land mammal (other than humans) currently found on all eight of the Channel Islands and in archaeological sites on all but the two smallest islands (Rick 2012).

P. maniculatus may have been introduced prehistorically by humans incidentally as stowaways in Native American canoes (Rick 2012; Walker 1980). *Peromyscus maniculatus* and *P. nesodytes* coexisted with one another until some point in the Late Holocene when *P. nesodytes* went extinct (Walker 1980). Well-dated assemblages with large, diachronic samples of both *P. maniculatus* and *P. nesodytes* are currently available only from Daisy Cave and Cave of the Chimneys (CA-SMI-603) on San Miguel Island. Stratigraphic mixing of Walker's (1980) assemblage from Daisy Cave precludes these data from being used to understand changes in *P. nesodytes* and *P. maniculatus* abundance through time. Analysis of a more recent sample from Daisy Cave without stratigraphic mixing issues supports the pre-human colonization of *P. nesodytes* and Early Holocene colonization of *P. maniculatus*, but seemed to indicate that *P. nesodytes* may have gone extinct during the Middle Holocene (Guthrie 1993). High-resolution data from Cave of the Chimneys, however, indicate that *P. nesodytes* is present throughout the 7500 year sequence, with at least a small population persisting to about 1000 cal. BP (Ainis and Vellanoweth 2012). No data for *P. maniculatus* remains are yet available from Cave of the Chimneys. The abundance of *P. nesodytes* in the Cave of the Chimneys assemblage varies through time, with some 28 per cent of the total assemblage (NISP/m³) dated to 8500–7500 cal. BP, about 18 per cent around 4400 cal. BP, declining to 2–5 per cent in the next two strata, then peaking at 43 per cent between 3800 and 2200 cal. BP and finally dropping to about 4 per cent by 1000 cal. BP (Ainis and Vellanoweth 2012). Ainis and Vellanoweth (2012) argue that these changes in abundance could result from differing sample sizes, changing human use of the cave or changes in the use of the cave by birds of prey (*Tyto alba*, barn owl) that may have deposited the mouse remains.

Collectively, these data suggest that the extinction of *P. nesodytes* may have been influenced by inter-specific competition following the appearance of *P. maniculatus*, with the larger size of *P. nesodytes* perhaps making them more susceptible to predation by barn

owls, island foxes and perhaps other predators (Guthrie 1993, 1998; Rick 2012). The earliest known island foxes appear in the Channel Island sub-fossil and archaeological record at ~7000 cal. BP, and would have been a prime predator on island deer mice as they are today. Because *P. nesodytes* may have been isolated for millennia on the islands, the addition of a new terrestrial predator could have affected the population.

Walker (1980: 716) and Ainis and Vellanoweth (2012) speculated that *P. nesodytes* may have persisted into the historic period and was driven to extinction by widespread nineteenth-century landscape clearance, vegetation stripping and habitat changes from overgrazing and severe drought, but it is unclear why these landscape changes did not also cause the extinction of *P. maniculatus*. Although it remains possible that *P. nesodytes* persisted into the historic era, no *P. nesodytes* bones have yet been reported from deposits younger than 1000 cal. BP and none were documented by late nineteenth-century museum collectors. If historic landscape changes caused the extinction of *P. nesodytes* this may have happened relatively soon after severe drought and overgrazing events commenced in the mid-1800s (Johnson 1980). Because only twenty-five *P. nesodytes* bones have been identified in the 1000 cal. BP stratum at Cave of the Chimneys compared to 547 in the previous stratum dated to 3800–2200 cal. BP, it is also possible that *P. nesodytes* was already in decline about eight centuries prior to historic landscape changes and had already gone extinct by the nineteenth century. Although further study is needed, especially from well-dated assemblages with both species of mice, the extinction of *P. nesodytes* is one of the few Channel Island mammalian extinctions that may have been caused by the introduction of another rodent species and/or canids by people, or possibly by historical vegetation stripping and erosion.

A slow death: Holocene extinction of the flightless duck, *C. lawi*

Many flightless land birds were driven to extinction on Pacific islands by prehistoric humans, often through a combination of direct predation and indirect causes such as landscape clearance and burning, and the introduction of rats or other animals that prey on birds or bird eggs (Steadman 2006). *Chendytes lawi* was a flightless duck that had occupied the Channel Islands and mainland coast by at least 40,000 years ago (Guthrie 1993; Howard 1955, 1964; Miller 1925). Jones et al. (2008) provided an updated synthesis and analysis of the extinction of *C. lawi* on the mainland and Channel Islands, including a series of direct AMS radiocarbon dates on *C. lawi* bones from archaeological sites. Although Pleistocene age *C. lawi* remains have been found as far north as Oregon, the highest concentration of *C. lawi* bones occurs on the Channel Islands (Jones et al. 2008: 4106). There are 106 bones found in four northern Channel Island archaeological sites, including seventeen from CA-SCRI-109 on Santa Cruz Island, fifty-five from Daisy Cave and forty-three from CA-SMI-1 on San Miguel Island and one from CA-SRI-512 on Santa Rosa Island (Erlandson et al. 2011; Rick et al. 2008a). There are 1523 bones found in nine San Miguel Island fossil localities that are mostly Late Pleistocene, but could also have some Holocene-age materials (Guthrie 1993). There are additional fossil specimens from west Anacapa (Howard 1964) and other specimens from San Nicolas Island fossil deposits and possibly archaeological sites that may include a different species, *C. milleri*

(Howard 1955). Eggshell fragments, presumably from ground-breeding colonies of *C. lawi*, have been found on San Miguel Island, dated to the close of the Pleistocene (Guthrie 1993: 408).

Researchers have long speculated that *C. lawi* was driven to extinction by ancient human hunting (Grayson 2001; Guthrie 1993; Jones et al. 2008; Martin and Klein 1984). These birds undoubtedly were susceptible to human hunting, but burning, butchering or other evidence of processing of *C. lawi* bones has been documented for only one burned bone from CA-SRI-512, a terminal Pleistocene archaeological site on Santa Rosa Island (Erlandson et al. 2011; Rick et al. 2008a). Moreover, at Daisy Cave and CA-SMI-1, where some fifty-five and forty-three *C. lawi* bones have been reported, they make up about 3 per cent and 24 per cent, respectively, of avian assemblages dominated by cormorants, auklets and other sea birds (Guthrie 1980). A potential influence on the decline of *C. lawi* is from predation by dogs and island foxes, neither of which is found in archaeological or sub-fossil sites until the Holocene, but which may have preyed on *C. lawi* and contributed to their extinction (Rick et al. 2008b, 2009).

If humans did cause the extinction of *C. lawi* through direct or indirect means, it was a protracted process that took some 8000 years (Jones et al. 2008). While the radiocarbon sequence demonstrates that *C. lawi* persisted until the Late Holocene on the mainland coast, questions linger about how long *C. lawi* persisted on the Channel Islands and how rapidly they declined in abundance through time. Similar to pygmy mammoths and island deer mice, one of the challenges with the available Channel Islands *C. lawi* dataset is that few well-dated assemblages are available for analysis. The best sequences for *C. lawi* come from Daisy Cave and CA-SMI-1, two sites that are stratified, but have large avian assemblages excavated in the 1960s in arbitrary levels (Guthrie 1980). *Chendytes lawi* persisted until at least 6300–5300 cal. BP at CA-SCRI-109 (Glassow et al. 2008). Six bones in the upper 30cm of control pits 681, 754 and 824 at CA-SMI-1 (Guthrie 1978: 101, 1980) might be Late Holocene in age since a single date of *c.* 3300 cal. BP was obtained from control pit 420 at a depth of ~40cm (Erlandson 1991). Four bones in the upper 30–45cm at Daisy Cave in grid E-3 and D-5 (Guthrie 1978: 99, 1980) may also date to the Late Holocene (Erlandson et al. 1996; Jones et al. 2008). Because both Daisy Cave and CA-SMI-1 contain multiple components that were excavated in arbitrary 6-inch levels, direct ¹⁴C dating is needed to determine whether *C. lawi* persisted on the Channel Islands as late as it did on the mainland. While these radiocarbon data help inform the timing of the extinction, NISP and other data used to calculate abundance for *C. lawi* are relatively small or available in large quantities from a limited number of sites, making it difficult to investigate changes in *C. lawi* abundance through time.

Regardless of the precise age of extinction, humans and *C. lawi* coexisted for several millennia on the Channel Islands and adjacent mainland, a pattern that contrasts with the rapid rates posited for many Late Quaternary mammalian extinctions (see Faith and Surovell 2009). Jones et al. (2008) attribute this slow rate to the Late Holocene refinement of watercraft needed to take *C. lawi* at offshore rocks and the diversity of human subsistence economies. Sea-level rise and coastal erosion during the Late Pleistocene and Holocene also inundated a number of offshore islets and may have further restricted *C. lawi* habitat through the Middle and Late Holocene, perhaps making them more vulnerable to human and canid predation. Although the precise mechanism is unknown, the extinction of

C. lawi contrasts with the rapid nature of flightless bird extinctions caused by human activities on other prehistoric islands, such as the tropical Pacific (see Steadman 2006).

Other extinctions and range contractions

A few additional vertebrate species appear to have once been present on the Channel Islands, but are now extinct or extirpated. Insufficient specimens from these species have been identified, and questions remain about how widespread they were when they went extinct or what caused the extinction. The San Miguel Island vole (*M. miguelensis*) is known from just two specimens, but may have persisted on the northern Channel Islands until at least the terminal Pleistocene. Guthrie (1980) also reported the remains of vampire bats (*Desmodus stocki*) at Daisy Cave and rattlesnake (*Crotalus* sp.) remains from a few fossil deposits on San Miguel Island. Rattlesnakes currently occur on Santa Catalina Island. Guthrie (1998: 190) argued that both vampire bats and rattlesnakes on the northern islands likely went extinct prior to human arrival, but further dating of these specimens could help refine their chronology. *Fratercula dowi*, an extinct puffin, also lived on San Miguel and San Nicolas islands from about 120,000 to 12,000 RYBP, but little is known about why it went extinct (Guthrie et al. 2002). The same is true for an extinct owl (*Asio priscus*), caracara (*Caracara prelutosa*) and gannet (*Morus reyanus*) identified by Howard (see Guthrie 1998; Orr 1968: 42–5).

Perhaps the best example of a range contraction on the California Channel Islands is the ornate shrew (*Sorex ornatus willetti*), which still lives on Santa Catalina Island. The Santa Catalina Island shrew was originally described as a species, but later was relegated to subspecific status under *S. ornatus* (von Bloeker 1967). A phylogeographic study using mtDNA of *S. ornatus* placed the Catalina Island shrew in a clade with other mainland southern California ornate shrews. However, the Santa Catalina population was found to be one of the most divergent in that clade and was not closely related to the nearest mainland populations (Maldonado et al. 2001). To date, no shrews have been recorded in recent biological surveys of the northern Channel Islands, although some have suggested that more intense surveys on these islands may reveal that shrews still occur there (von Bloeker 1967; Walker 1980; Williams 1986). Ornate shrews have been found prehistorically on San Miguel and Santa Rosa, and presumably existed on all of the northern Channel Islands that once were part of Santarosae (Guthrie 1998; Walker 1980). They date throughout the Holocene and perhaps terminal Pleistocene at Daisy Cave. Guthrie (1998: 188) suggested that the ornate shrew may have been extirpated from the northern Channel Islands during the historic period, but further research is needed to help clarify the timing and the process of extirpation of northern Channel Island shrew populations.

Three other Channel Island animals also experienced range contractions during the Pleistocene and/or Holocene. The island scrub-jay, found today only on Santa Cruz Island (Johnson 1972), appears to have been more widespread prehistorically, with a single bone found in a Santa Rosa Island fossil locality (Collins 2009), suggesting scrub-jays may have once been present throughout Santarosae. Based on a historical account and two bones found in Daisy Cave, spotted skunks, known today only from Santa Rosa and Santa Cruz islands, may once have been present on San Miguel Island (Walker 1980). However, the

historical account is speculative, and at least one of the fossil bones appears to be morphologically similar to mainland skunks (Rick 2012; Walker 1980). Gopher snakes currently occur on Santa Rosa and Santa Cruz islands, but a few gopher snake remains from San Miguel Island fossil localities suggest that they also underwent a range contraction (Guthrie 1993).

Discussion

Evidence from the fossil and archeological records of pygmy mammoths, flightless ducks, giant island deer mice and other species demonstrates that several Channel Island animals went extinct or were extirpated during the Late Pleistocene and Holocene. For many of these animals (i.e. rattlesnakes, voles, caracara and vampire bats) so little is known about their abundance, distribution and evolutionary history that the cause of the extinction or implications for Channel Island ecology are unknown and may be unrelated to human activities. The extinction of two animals (*P. nesodytes* and *C. lawi*) that can possibly be attributed to prehistoric humans during the Holocene and perhaps a third (*M. exilis*) during the Terminal Pleistocene represents less than 10 per cent of the known terrestrial vertebrate fauna from the islands. When looking at individual islands, however, patterns of extinction vary considerably. For instance, on the southern Channel Islands, other than *C. lawi* on San Nicolas Island, there are no other documented Late Quaternary vertebrate extinctions. Most of the known extinctions occurred on the northern Channel Islands, in part because more research has been conducted on the northern islands and fewer mammals and other species colonized the more distant and isolated southern islands, with the exception of Santa Catalina Island.

The timing and nature of Late Quaternary extinctions on the Channel Islands share some similarities and differences with the well-documented extinctions on the nearby mainland. Late Quaternary extinctions around the world resulted in a disproportionate loss of large mammals, especially in the Americas and Australia (Martin and Klein 1984; Koch and Barnosky 2006). Some thirty-five genera of large-bodied mammals disappeared from the Americas, including mammoths, mastodons, giant sloths, saber tooth cats and dire wolves (Faith and Surovell 2009; Grayson 2001). Consistent with this trend, the only terrestrial megafauna ever known to occupy the Channel Islands prior to human arrival, mammoths, went extinct at the end of the Pleistocene. Although Orr (1968) and more recently Agenbroad et al. (2005) speculated that humans may have caused the pygmy mammoth extinction, no butchered or processed mammoth bones, secure associations of human tools with mammoth remains or other direct evidence of human hunting of mammoths have been documented. Current evidence suggests that if humans and mammoths coexisted on the Channel Islands they likely overlapped only briefly when the human population was small and pygmy mammoth populations were already in decline. The Holocene extinctions of *C. lawi* and *P. nesodytes* both stand in contrast to many Late Quaternary extinctions documented on other islands and continents. Although humans probably played a role in the extinction of *C. lawi* and *P. nesodytes* through direct or indirect means, both extinctions took several millennia rather than the 2000 years posited for most megafauna extinctions (see Faith and Surovell 2009).

Extinction on islands is often related to the translocation of new animals by humans, such as rats on Pacific Islands (Grayson 2001; Steadman 2006). Translocation of island foxes, deer and harvest mice, dogs and perhaps other species from the mainland or between islands is an important component of the Holocene history of the Channel Islands (Collins 1991; Johnson 1983; Rick 2012; Rick et al. 2008b, 2009; Vellanoweth 1998; Walker 1980). The translocations of island foxes from the northern to southern islands starting by 5000 cal. BP, and perhaps of a founding fox population to the northern islands sometime prior to 7000 cal. BP, represents a major ecological change as foxes are now the apex terrestrial mammalian predator on the Channel Islands, preying on deer mice, birds and other fauna (Rick et al. 2009; Vellanoweth 1998). Similarly, dogs were first introduced sometime prior to 6000–7000 years ago and may also have influenced island ecology (Rick et al. 2008b). Questions remain about how big a role humans and the animals they introduced to the islands played in Channel Island extinctions, with current data suggesting a combination of natural (e.g. bats, rattlesnakes), probably human induced (e.g. *C. lawi* and *P. nesodytes*) and unknown or perhaps a combination of natural and human influences (*M. exilis*).

The last Island Chumash residents were removed from the northern Channel Islands by about AD 1820, bringing to an end some thirteen millennia of Native American occupation and ushering in dramatic cultural and ecological change. The Historic period witnessed the establishment of numerous ranching, military and other operations located on some or all of the islands (Schoenherr et al. 1999). In less than two centuries, island ecosystems were rapidly altered, including the extirpation of several island sub-species. These extirpations resulted from direct hunting of marine mammals during the fur and oil trade, DDT pollution and the introduction of invasive species. These include the extirpation of sea otters (*Enhydra lutris*), which, except for a relocated population on San Nicolas, are extremely rare on the islands today, and bald eagles (*Haliaeetus leucocephalus*) which were only recently re-introduced to the islands. Although most of the island pinnipeds (seals and sea lions) were driven to near extinction during the nineteenth century fur and oil trade, Elephant seals (*Mirounga angustirostris*), California sea lions (*Zalophus californianus*) and northern fur seals (*Callorhinus ursinus*) have recovered dramatically under federal and state protection. Collins (2009) provides anecdotal evidence that island scrub-jays were present on Santa Rosa in the nineteenth century, and thus could have been extirpated by the massive de-vegetation of the island caused by livestock overgrazing. There have also been several near extinctions, including the case of the island fox on several of the Channel Islands beginning in the late 1990s (Coonan et al. 2010). Resulting from a combination of invasive species dynamics between feral pigs and golden eagles and canine diseases, island foxes were taken into a captive breeding program on San Miguel, Santa Rosa, Santa Cruz and Santa Catalina islands (Coonan et al. 2010). The program has been a success and fox populations are recovering. Nevertheless, historical changes on the islands nearly drove this species to extinction even though it had weathered major climatic changes and strong interactions with Native Americans for over 7000 years. The historical introduction of black rats (*Rattus rattus*) to Anacapa, San Miguel, San Clemente and Santa Catalina also had negative impacts on marine birds, invertebrates, island deer mice and other organisms, triggering an eradication campaign on Anacapa by the National Park Service (Howald et al. 2010; Schoenherr et al. 1999).

The apparent differences in extinction rates between ancient and modern times may be the result of variation in the chronological resolution available for paleontological,

archaeological, historical and ecological records. They may also result from globalized economies, population growth and technological enhancements that characterize the modern industrialized world, which make the extinctions and ecological devastation of the last 200 years seem dramatically different from many millennia of occupation by sophisticated hunter-gatherer-fisher peoples.

Conclusions

The causes of the Late Quaternary megafauna extinction continue to be debated by archaeologists, paleobiologists, ecologists and other scholars. Islands have played an important role in this debate (Burney and Flannery 2005; Steadman 2006; Steadman and Martin 2003; Steadman et al. 2005; Turvey et al. 2007; Wroe et al. 2006). Critiquing Burney and Flannery's (2005) assertion that human overkill was the primary cause of North American and Australian megafauna extinctions, Wroe et al. (2006) argued that the exception to a lack of human overkill is found on islands where avian extinctions from human activities are widespread. The bounded nature of islands makes them more susceptible to human impacts and activities than the generally larger and more diverse nature of animals on continents. Current data from Pacific and Caribbean islands and the California Channel Islands suggest that ancient extinctions on islands and the role of humans in those extinctions were highly variable. While some islands in the Pacific witnessed rapid and widespread impacts and extinction in a century or less, others took several millennia or more depending on the size, structure and biodiversity of the island and the nature of its human occupation (Steadman and Martin 2003). Recent analysis of mammalian extinctions on Puerto Rico suggests that many of these extinctions may have been protracted and cannot be firmly attributed to prehistoric peoples (Turvey et al. 2007). On other Caribbean Islands, the Holocene extinction of sloths and some birds may be more closely tied to humans (Fitzpatrick and Keegan 2007; Steadman et al. 2005).

On the Channel Islands, clear human-induced extinctions are relatively rare throughout Native American occupation and often appear to have taken several millennia. This may result from a combination of the lack of large terrestrial herbivores suitable as food resources that could have been overhunted, the dearth of naïve birds because of other terrestrial predators (foxes, mice and skunks), close proximity to the mainland and the fact that Channel Islanders were hunter-gatherer-fishers focused largely on a suite of marine resources from a range of trophic levels (see Erlandson et al. 2009). The Channel Island case study adds to the growing body of data from around the world demonstrating that, similar to the continents, human-environmental impacts and extinctions on islands are variable and may have diverse causes (e.g. human activities, climatic change or a combination). Maritime hunter-gatherers on the Channel Islands were capable of living on islands for over 10,000 years without causing anywhere near the rapid decimation posited under a North American human overkill or 'Blitzkrieg' model, where thirty-five genera were extinct in 1000–2000 years. As we currently live in perhaps the world's sixth mass extinction caused largely by modern industrial human activities (Barnosky et al. 2011), the Channel Islands example shows us the variability and uncertainty that characterize Late

Pleistocene and Holocene extinctions on islands and the challenges involved in trying to implicate rapid human overkill as the primary cause.

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