El Niño controls Holocene rabbit and hare populations in Baja California

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ABSTRACT

The El Niño/Southern Oscillation (ENSO) is a major source of climatic variation worldwide, with significant impacts on modern human and animal populations. However, few detailed records exist on the long-term effects of ENSO on prehistoric vertebrate populations. Here we examine how lagomorph (rabbit and hare) deposition rate, population age structure and taxonomic composition from Abrigo de los Escorpiones, a well-dated, trans-Holocene vertebrate fauna from northern Baja California, Mexico, vary as a function of the frequency of wet El Niño events and eastern Pacific sea-surface temperatures (SSTs) derived from eastern Pacific geological records. Faunal indices vary significantly in response to El Niño-based precipitation and SST, with substantial moisture-driven variability in the middle and late Holocene. The late Holocene moisture pulse is coincident with previously documented changes in the population dynamics of other vertebrates, including humans. As the frequency and intensity of ENSO is anticipated to vary in the future, these results have important implications for change in future vertebrate populations.

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Introduction

The El Niño/Southern Oscillation (ENSO) is a major source of climatic variation worldwide, including in the eastern Pacific Ocean and the interior of western North America. The El Niño phase of ENSO brings warm sea-surface temperatures (SSTs) to the eastern Pacific and drives especially heavy precipitation, while the La Niña phase is characterized by cooler SSTs and lower regional precipitation (Philander, 1985, 1990; Diaz and Markgraf, 1992). The variation in precipitation associated with ENSO has had a tremendous impact on a wide range of historic marine and terrestrial ecosystems as well as human populations over much of the world (Barber and Chavez, 1983; Meggers, 1994; Holmgren et al., 2001; Stenseth et al., 2002; Fagan, 2007). In recent years, increasing attention has focused on past patterns of ENSO variation, especially in relation to potential impacts on human cultures both in prehistoric and historic times (e.g., Caviedes, 2001; Sandweiss and Quilter, 2008). And while attempts have been made to evaluate the impacts of Holocene ENSO variation on certain marine fisheries and seabird populations (Broughton, 2004; Sandweiss and Quilter, 2008) little work has focused on its effects on past small mammal faunas. Modern studies of the latter suggest, however, that those impacts would have been substantial.

Irruptions of small mammal populations and associated increases in taxonomic diversity have been linked to enhanced precipitation associated with ENSO events in many areas of the world, including South America, Africa, Australia, and North America (Brown, 1973; Brown and Heske, 1990; Jaksic et al., 1997; Ernest et al., 2000; Ostfeld and Keesing, 2000; Holmgren et al., 2001; Jaksic, 2001; Letnic et al., 2005; Farias and Jaksic, 2007; Kelt et al., 2008; Previtali et al., 2009a, 2009b; Thibault et al., 2010; Lightfoot et al., 2011; Meserve et al., 2011). Various complexities in the response rates to enhanced precipitation have been linked to such issues as trophic level, generation time, and specific feeding ecologies. Previtali et al. (2009a, 2009b), for instance, have shown that populations of degu (*Octodon degus*), a long-lived, slow reproducing rodent inhabiting semiarid areas of Chile, track ENSO variation with a lag response—exploding a year after wet El Niño events and crashing with a short delay after a dry La Niña. They also demonstrated an additive effect of consecutive wet years to degu populations. Populations of *Phyllotis darwini*, however, a shorter-lived, fast reproducing mouse reached population maxima immediately after the onset of wet El Niño conditions, without a noticeable lag. Response lags may also reflect the phenology of the specific plant structures utilized by small mammals. Granivorous rodents (e.g., *Dipodomys*) decline in activity levels and abundance during intense El Niño rains in southern California (Orland and Kelt, 2007; Kelt et al., 2008) but increase dramatically several months later as an elevated abundance of seed resources materializes (e.g., Gutiérrez et al., 2000).

Predatory vertebrates also show predictable lags based on the nature of the population response of their dominant prey species, and predation risk can interact with changes in primary productivity to produce significant differences in small mammal population dynamics under similar precipitation regimes (e.g., Jaksic et al., 1997; Jaksic, 2001; Farias and Jaksic, 2007; Thibault et al., 2010).

Despite our increased understanding of short-term ENSO effects on small mammal population dynamics—including an appreciation of the individualistic nature of species response—no detailed records of ENSO

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effects on small mammal populations have been provided on centennial or millennial time scales. Such information may be crucial to predicting long-term dynamics of mammalian communities in the context of future variation in ENSO.

The trans-Holocene mixed anthropogenic and raptor deposited vertebrate fauna from Abrigo de los Escorpiones (Figs. 1 and 2; hereafter, Escorpiones) on the Pacific coast of northern Baja California, Mexico, provides a unique opportunity to provide such information. Although analyses are underway on many aspects of the rich vertebrate record from the site, lagomorphs (pikas, rabbits and hares) have proven to be especially sensitive to change in past moisture regimes in several other settings in western North America—especially the Great Basin (Grayson, 1977, 1983, 1985, 1987, 1998, 2000, 2005, 2006; Grayson et al., 1988; Hockett, 2000; Schmitt et al., 2002)–and we focus on that group here. In addition to providing a relatively high-resolution assessment of the impact of ENSO on Holocene small mammal populations, our analysis provides an unprecedented 10,000 year history of lagomorphs from a North American locality outside of the Great Basin.

Paleoclimates of western North America and Baja California

Antevs's (Antevs, 1948, 1952, 1955) climate model for the Holocene Great Basin provides a starting point from which to explore the paleoclimate of northern Baja California and its influence on lagomorph populations. This extensively tested model proposes a relatively cool and moist early Holocene between 10,000 and 8000 yr ago, a warmer and drier middle Holocene from about 8000 to 4000 yr ago, and a late Holocene after 4000 yr ago with a mesic climate more or less similar to modern times. While over sixty years of paleoenvironmental research shows that many aspects of this characterization are overly simplistic, in broad outline the trends he proposed have held up remarkably well for many areas of western North America (see review in Grayson (2011)). While detailed Holocene paleoclimatic records are not abundant in Baja California, what data there are appear broadly consistent with the Antevs scheme.

Davis (2003) analyzed the lacustrine history from Lake Chapala of northern Baja California and found evidence supporting a cooler, wetter early Holocene, and a warmer, drier middle Holocene. Radiocarbon dating of Lake Chapala's high and low stands demonstrates the basin filled to a high stand around 9000 radiocarbon years before present (^{14}C yr BP), after which the lake persisted until at least 7600 ^{14}C yr BP. By 7450 ^{14}C yr BP however, the lake had dried up and sand dunes formed in the basin as the climate transitioned to generally warmer, drier conditions in the region.

Recent syntheses of vegetation and pollen records from southern California and northern Baja California (e.g., Holmgren et al., 2010, 2011; Barron et al., 2012), suggest this wetter early Holocene was characterized by substantial summer precipitation associated with a more westward position of the North American Monsoon. After 7500 ^{14}C yr BP, however, that system shifted eastward, leaving southern California and northern Baja with hot and dry summer conditions. These data are consistent with Rhode's (2002), analysis of plant remains from an early Holocene woodrat (*Neotoma* sp.) midden from the Sierra San Francisco in central Baja that suggests early Holocene climate was 5–6 °C cooler than modern conditions, with at least twice the precipitation levels of the region today.

A generally cooler and wetter later Holocene is supported by the existing paleoenvironmental data from Baja California as well. Clark and Sankey (1999) and Sankey et al. (2001) report that insect and plant remains from a woodrat midden at Cataviña in northern Baja from 1700 ^{14}C yr BP demonstrate late Holocene climate in Baja California similar to, and perhaps slightly more mesic than, modern.

Although the specific climatic forcing mechanisms underlying these trends are not fully resolved, Holocene patterns in precipitation in many areas of western North America and especially Baja California may be linked to variation in the ENSO. For example, the prevalence of more mesic conditions during the late Holocene may stem in part from an increased duration and incidence of wet El Niño events.

The timing of the onset of the modern periodicity of ENSO and the nature of its Holocene variation in general has been the subject of growing attention over the past 15 yr (e.g., Moy et al., 2002; Cane,
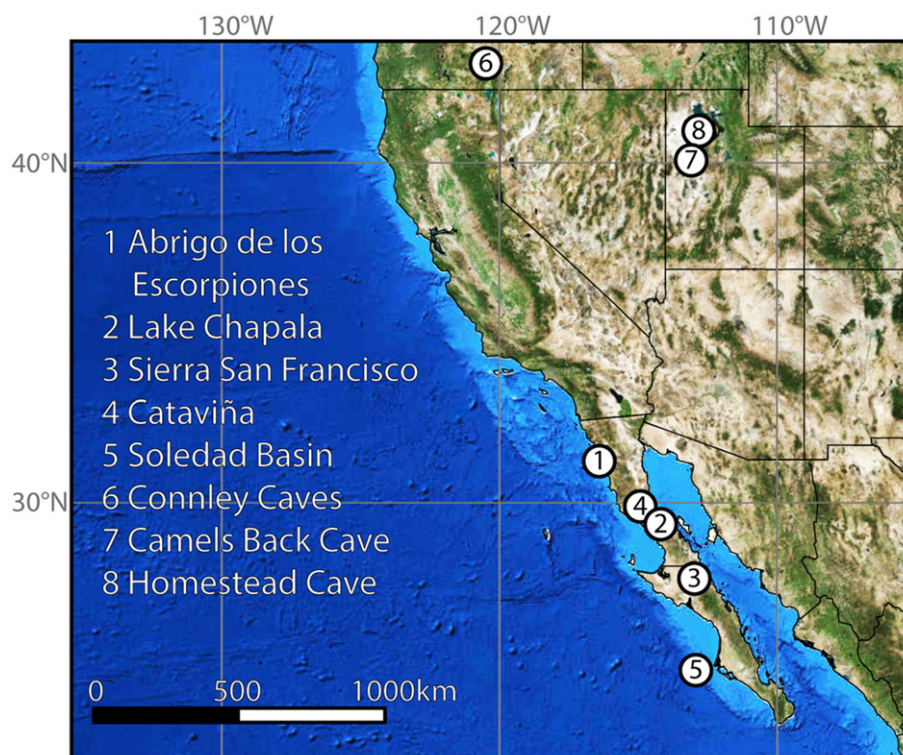

Figure 1. Map of locations of Abrigo de los Escorpiones and sites mentioned in text.
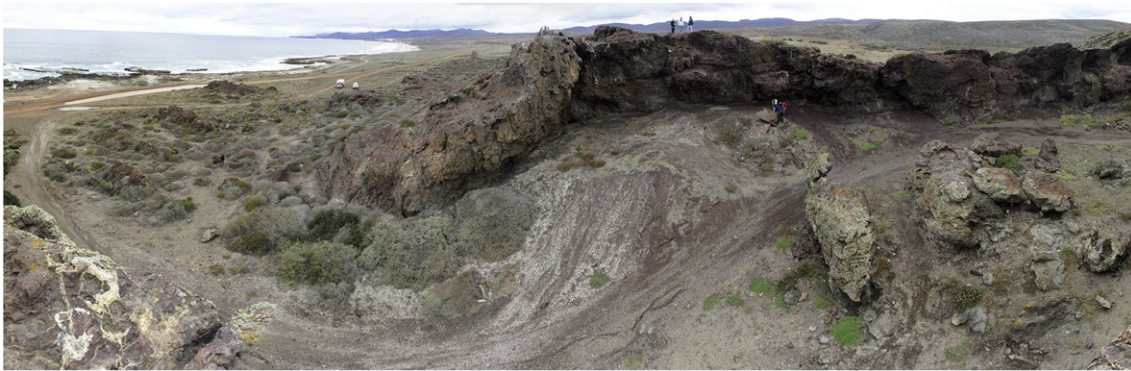
Figure 2. Interior view of Abrigo de los Escorpiones and surrounding landscape. Excavated portion is at center.

2005; Marchitto et al., 2010; Cobb et al., 2013). Most records show an onset of more or less modern ENSO variability at around 5000 calibrated radiocarbon years BP (cal yr BP; e.g., Sandweiss et al., 1996; Rodbell et al., 1999; Sandweiss et al., 2001; Moy et al., 2002), yet some records have been interpreted to show ENSO onset as late as 4000 cal yr BP (Shulmeister and Lees, 1995; Conroy et al., 2008; Donders et al., 2008).

Prior to the onset of the modern ENSO periodicity, conditions characteristic of either El Niño or La Niña may have dominated large blocks of time, up to several thousand years each. Antinao and McDonald (2013) show, for example, that the terminal Pleistocene and early Holocene from 14,600–11,000 cal yr BP was dominated by semi-permanent El Niño-like conditions, while the period from 9000–6000 cal yr BP likely saw persistent La Niña-like conditions. La Niña in Baja California is generally associated with reduced SSTs and regional precipitation. This may account in part for the observed early Holocene mesic conditions and subsequent drying in the region after 8000 cal yr BP.

One of the best resolved trans-Holocene records of ENSO is derived from the sedimentation record of Laguna Pallcacocha in the southern Ecuadorian Andes (Rodbell et al., 1999; Moy et al., 2002). Holocene variation in the thickness of clastic laminae deposited in this freshwater lake basin provides a record of the strength, frequency and duration of prehistoric El Niño high precipitation events. The record demonstrates that El Niño events increased in frequency through the Holocene, reaching its more or less modern periodicity around 5000 cal yr BP, with notable peaks centered at about 5000, 3000 and 1000 cal yr BP. We utilize this record as a proxy for precipitation variation and its influence on the Holocene history of lagomorphs in northern Baja California. Additionally, since ENSO phases are defined with respect to SST anomalies, we utilize an eastern Pacific SST proxy from the Soledad Basin off Baja's western coast (Fig. 1; Marchitto et al., 2010). This record records variation in Magnesium/Calcium ratios in planktonic Foraminifera over the Holocene and shows a strong link between local SSTs and ENSO.

Holocene moisture history and lagomorph faunas in western North America

The broad trends in Holocene climate change summarized above have provided a framework for understanding the history of lagomorph distributions and abundances in many settings across western North America, but the most detailed records are derived from dry cave faunas from the Great Basin. To provide a context for our analyses of the Escorpiones lagomorphs, we summarize key aspects of those patterns here.

In the first detailed assessment, Grayson (1977) evaluated the Holocene abundance of two species of *Lepus*: black-tailed jackrabbit (*Lepus californicus*) and white-tailed jackrabbit (*Lepus townsendii*), from Connley Caves in the northwestern Great Basin (Fig. 1). These two species exhibit distributional and ecological differences: *L. townsendii* has a more northern distribution and tends to occupy higher elevation more grassy habitats with thicker sage. *L. californicus*, by contrast, has a more southerly distribution and prefers lower elevation and more open habitats. Grayson found that *L. californicus* replaced *L. townsendii* after the early Holocene and concluded the change was consistent with the Antevs model of Holocene climate change (but see also Purdue, 1980).

Perhaps the most well-documented trends involve the dramatic terminal Pleistocene through middle Holocene range changes and declining abundances of the most mesic of the western lagomorphs: American pika (*Ochotona princeps*) and pygmy rabbit (*Brachylagus idahoensis*). American pikas are restricted today to higher elevation settings in habitats with talus slopes near mountain meadows with abundant herbaceous forbs. Pygmy rabbits require tall dense stands of big sagebrush (*Artemisia tridentata*) that occur in generally cooler and wetter lower and middle elevation environments. Both taxa decline in abundance relative to other small mammals from the late Pleistocene through the early Holocene in many western faunas (Butler, 1972; Grayson, 1977, 1983, 1985, 1998, 2000, 2006; Harris, 1985; Lyman, 1991; Hockett, 2000; Schmitt et al., 2002). In addition, their overall geographic distributions have shifted upwards in both elevation (most clearly in pikas (Grayson, 2006)) and latitude as a result of increasing temperature and declining precipitation over this period of time resulting in their disappearance within local faunal sequences.

Other climatically driven patterns have involved changing relative abundances of the two most widespread lagomorph genera in the west: *Sylvilagus* and *Lepus*. *Sylvilagus* is more abundant in habitats with thicker vegetative cover, whereas *Lepus* (especially *L. californicus*) is more abundant in more open, xeric habitats (e.g., Bayham, 1982; Bayham and Hatch, 1985; Schmitt et al., 2002). Two Bonneville Basin dry cave deposits have provided the longest and most detailed Holocene records of the relative abundances of these taxa: Camels Back Cave and Homestead Cave.

From the trans-Holocene deposits of Camels Back Cave in western Utah, Schmitt et al. (2002) document a dramatic decline in the abundance of *Sylvilagus* (both *Sylvilagus nuttallii* and *Sylvilagus audubonii*) relative to *L. californicus* across the early Holocene sequence of deposits, with *Lepus* continuing to dominate both middle and late Holocene strata. The trend is interpreted to reflect the early and middle Holocene deterioration of more mesic sagebrush communities and the expansion of more open desert habitats.

Homestead Cave is located approximately 100 km to the north of Camels Back Cave, and has provided the best-dated, largest, and highest resolution late Quaternary record of small mammals, including lagomorphs, in North America (Fig. 1; Grayson, 2000, 2006; Madsen et al., 2001). Homestead Cave sits directly adjacent to Great Salt Lake and receives "lake-effect" enhancement of precipitation from Pacific storms and, as is the case today, the region has apparently always been wetter and cooler than Camels Back Cave located in Great Salt Lake Desert (Schmitt et al., 2002). Accordingly, Holocene trends in lagomorphs are somewhat distinct between the two sites. Most notably, *Sylvilagus* dominates the terminal Pleistocene and early Holocene lagomorph fauna—as at Camels Back Cave—but declines relative to *Lepus* during the middle

Holocene. However, unlike the Camels Back Cave record, *Sylvilagus* rebounds during the late Holocene. The abundance histories of several other mesic-oriented small mammals from Homestead Cave (e.g., western harvest mice [*Reithrodontomys megalotis*], Ord's kangaroo rat [*Dipodomys ordii*], and Great Basin pocket mouse [*Perognathus parvus*]) show these smooth middle Holocene "troughs," apparently reflecting hotter and drier climate at the time compared to both the early and late Holocene (Grayson, 2000, 2006; Madsen et al., 2001). Given the broad climatic trends outlined above and the dramatic variation in ENSO based precipitation, we seek to answer the following question: Did the lagomorph population of northern Baja California follow the Great Basin trend of a shift toward more xeric taxa during the middle Holocene, or did ENSO play a more dominant role in shaping the lagomorph community?

Escorpiones and the lagomorphs of northern Baja California

Escorpiones is a large volcanic rockshelter located in northwestern Baja California, Mexico, near the town of Eréndira on the Pacific coast (Figs. 1, 2). The site contains a large stratified shell midden mixed with raptor deposits and was excavated from 2000–2004 (Gruhn and Bryan, 2009). Excavation revealed a long history of human occupation and raptor deposition of faunal materials—31 radiocarbon assays, all on charcoal, span the entire Holocene. This work recovered a massive faunal assemblage representing a wide array of marine and terrestrial taxa, including a large collection of lagomorph specimens.

Three lagomorph species were identified in the Escorpiones fauna: brush rabbit (*Sylvilagus bachmani*), desert cottontail (*S. audubonii*), and black-tailed jackrabbit (*L. californicus*). The historic ranges of no other lagomorph species approach this area of Baja (Huey, 1964; Hall, 1981). Of the three identified taxa, *S. bachmani* has the most mesic orientation due to diet and habitat and preferences. This rabbit feeds primarily on grasses and forbs within or near dense, brushy vegetative cover (Orr, 1940; Shields, 1960; Chapman, 1974). *S. audubonii* has a similar diet but prefers more open vegetation and can tolerate more xeric conditions than can *S. bachmani* (Chapman and Willner, 1978). *L. californicus* is the most xeric-oriented of the three taxa, and thrives in more sparsely vegetated environments (Orr, 1940; Davis, 1975; Best, 1996). Insofar as periods of high precipitation associated with El Niño dramatically increase primary productivity and vegetative cover in this part of the world (Polis et al., 1997), we can anticipate four response patterns in these northern Baja lagomorphs to be reflected in the Escorpiones fauna:

1. Absolute lagomorph abundance should correlate positively with El Niño frequency and SST. During periods of elevated precipitation we anticipate an overall increase in the density of lagomorphs on the landscape, regardless of changes in species relative abundance. Other things equal, we expect higher absolute deposition rates (total Number of Identified Specimens, NISP) of lagomorph materials at Escorpiones during such conditions.
2. The relative abundance of *Sylvilagus* should be positively correlated with El Niño frequency and SST. Higher regional precipitation should be associated with increases in the proportional abundance of the more mesic *Sylvilagus* relative to *Lepus*, as documented in several Great Basin faunas cited above. The *Sylvilagus* Index (SI = *Sylvilagus* NISP ÷ [*Sylvilagus* + *L. californicus*] NISP) should thus co-vary positively with El Niño frequency.
3. The relative abundance of *S. bachmani* should be positively correlated with El Niño frequency and SST. We expect the population of *S. bachmani*, the most mesic of the three species, to increase relative to the other two taxa during periods of higher precipitation. We use a Brush Rabbit Index (BRI = Σ *S. bachmani* NISP ÷ Σ [*S. bachmani* + *S. audubonii* + *L. californicus*] NISP) below to measure the relative abundance of this rabbit over time.
4. The proportion of un-fused elements in the assemblage should be

positively correlated with El Niño frequency and SST. Small mammal populations tend to be skewed toward younger age classes during periods of population growth (e.g., Tkadlec and Zejda, 1998). More frequent bouts of increased precipitation and vegetation growth should have resulted in repeated (but relatively short-term) boom phases in lagomorph population size at Escorpiones. The starvation phase of a boom–bust cycle is relatively short (Keith et al., 1984), causing dramatic declines in population size, more rapid than the population growth during a boom. In other words, booms last longer than busts, and so the population age structure should be characteristic of a boom for a longer period of time. The absolute population size during booms will also be larger, such that more individuals will be deposited during boom phases than during busts. An increase in the frequency of boom–bust cycles caused by resource pulses such as temporary increases in precipitation and associated primary productivity should thus manifest itself in a faunal assemblage as a decrease in the average age at death of individuals deposited. We measure the average age at death in each excavation level as the proportion of un-fused skeletal elements using a Fusion Index (FI = Σ unfused NISP ÷ Σ [unfused + fused] NISP; lower values indicate more juveniles, higher values indicate more adults).

Dating, stratigraphy and temporal-analytic units

The materials analyzed in this study consist of the lagomorph remains recovered with 1/8 in (0.32 cm) screens from two of the sixteen 2 m × 2 m excavation units (D3 and D4) from Escorpiones (Gruhn and Bryan, 2009). These units were chosen for analysis here because they are the best dated (dates from these two units make up 15 of the 31 radiocarbon dates from the site) and seem relatively undisturbed based on the radiocarbon chronology. Depth is significantly correlated with radiocarbon age in both units (for D3, $r = 0.91$, $p < 0.01$; for D4, $r = 0.93$, $p < 0.01$) and so depth, in general, is a good estimate of age in these deposits.

Unit D4 was excavated to 500 cm below the present ground surface (BPGS) and had associated radiocarbon dates ranging from 1350 ± 30 (Beta-311418) to 8870 ± 60 (Beta-173865) ^{14}C years BP. Unit D3 was excavated to 800 cm BPGS, with similar radiocarbon dates (Table 1). Both excavation units were excavated by 5-or 10-cm arbitrary vertical spits.

Four major stratigraphic units were encountered during the excavation (Fig. 3; see Gruhn and Bryan (2009) for a more thorough discussion of the stratigraphy). The bulk of the shell midden material was contained in the upper three strata. The upper shell midden stratum consisted of a brown silty sediment matrix with multiple thick lenses of sediment and shell from rock mussel, abalone and small gastropods, and with abundant bird and small mammal bones. The middle shell midden zone consisted of a more compact brown ashy silt sediment matrix and shell midden material, with a lower number of faunal remains. The lower shell midden zone consisted of brown loamy silt sediment with abundant rock rubble and with abundant faunal remains. The three shell midden strata have abundant lithic artifacts indicating repeated intermittent human presence at the site after 9 ka, while the presence of faunal remains within and between the many shell midden lenses suggests raptor activity at the site was relatively constant over time, resulting in a steady input of faunal remains to the site. The lowest stratum consisted of a largely homogenized (based on the radiocarbon dates) rubble layer, largely sterile of human artifacts but with abundant faunal remains.

The stratigraphy at the site slopes down from an apex below the rim of the rockshelter both away from and into the rockshelter (Fig. 3). This suggests materials in the three shell midden layers accumulated below the rim of the overhanging shelter and in the cave behind it gradually, as raptors eating their prey above the overhanging wall of the shelter and other predators including people occupying the shelter deposited materials. No cut marks were found on any lagomorph bones, and

Table 1
Radiocarbon dates from Abrigo de los Escorpiones units D3 and D4.

Unit	Depth	^{14}C yr BP	Cal yr BP	Probability	Lab ID
D3	115	1680 ± 30	1529–1628	0.85	Beta-311419
			1655–1659	0.01	
			1666–1692	0.09	
D3	210	3130 ± 40	3242–3413	0.88	Beta-157354
			3420–33445	0.07	
D3	301	4460 ± 90	4865–5311	0.95	Beta-157355
D3	410	8470 ± 40	9442–9533	0.95	Beta-311421
D3	470	8560 ± 100	9319–9355	0.02	Beta-157356
			9400–9823	0.92	
			9846–9868	0.01	
			9873–9886	0.01	
D3	670	8650 ± 40	9538–9686	0.95	Beta-311422
D4	50	1610 ± 90	1334–1707	0.95	Beta-144831
D4	70	1350 ± 30	1186–1204	0.07	Beta-311418
			1239–1311	0.83	
D4	200	6340 ± 100	7007–7132	0.12	Beta-146369
			7141–7433	0.83	
D4	270	6960 ± 30	7697–7855	0.92	Beta-311420
			7905–7916	0.02	
D4	340	8040 ± 70	8649–8677	0.02	Beta-144833
			8683–8688	0.01	
			8693–9094	0.90	
			9101–9121	0.02	
D4	430	8790 ± 40	9269–9648	0.01	Beta-144834
			9653–9938	0.88	
			9995–10004	0.01	
			10064–10119	0.05	
D4	460	8240 ± 160	8774–9531	0.95	Beta-146370
D4	465	8870 ± 60	9742–10181	0.95	Beta-173865
D4	510	8540 ± 110	9291–9799	0.93	Beta-146372
			9801–9819	0.01	
			9847–9867	0.01	
			9875–9886	0.01	

very few show burning or any other signs of a human hand in their deposition and so it is likely that the majority of them were deposited by raptors.

Despite the stratigraphy at the site being largely undisturbed as noted above, the radiocarbon chronology does show some problematic features. Dates below 470 cm BPGS in unit D3, and below 465 cm BPGS in unit D4 show several reversals, suggesting the lower midden zone and the rubble zone below may have undergone turbative homogenization. Because the radiocarbon chronology is problematic for these lower deposits in both units, only specimens recovered from above 470 cm BPGS in unit D3 and above 465 cm in unit D4 are analyzed and reported here. These depths correspond with dates (using the age–depth model described below) of 10,315 and 10,050 cal yr BP, respectively.

Several analytic steps were required in order to temporally align the Escorpiones lagomorph fauna with the El Niño and SST records. The El Niño record was presented as the frequency of wet El Niño events per 100 yr (Moy et al., 2002), and we chose to use the 100-year analytic unit to make our data and the SST data comparable. To provide chronological control for our lagomorph dataset, first, age–depth models based on the 15 radiocarbon dates for these units (Table 1) were used to assign date ranges to each 5- or 10-centimeter excavation level from the two units. Due to the sloping stratigraphy at the site, specimens from identical depths but in different horizontal excavation units may not have been deposited closely in time. Therefore two separate age models were created, one for each unit, so that specimens could be grouped for analysis by age. The two age models were created using smooth spline interpolation in the R software package Clam 2.2 (Blaauw, 2010; Fig. 4). Calibration in the age models use the IntCal13 calibration curve (Reimer et al., 2013). Based on the date ranges for each 10 cm level, lagomorph specimens from each level were assigned to their closest 100-year time interval. This resulted in some 100-year intervals without associated bone data. For example, if level 20–30 cm had associated date ranges from 270 to 440 cal yr BP, the bones from that level
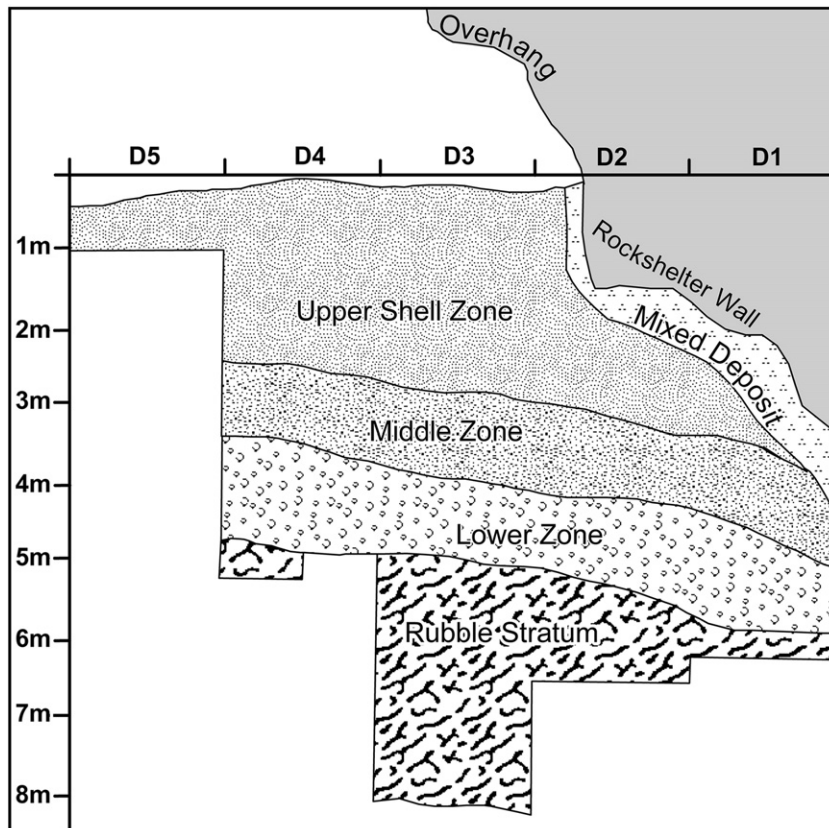

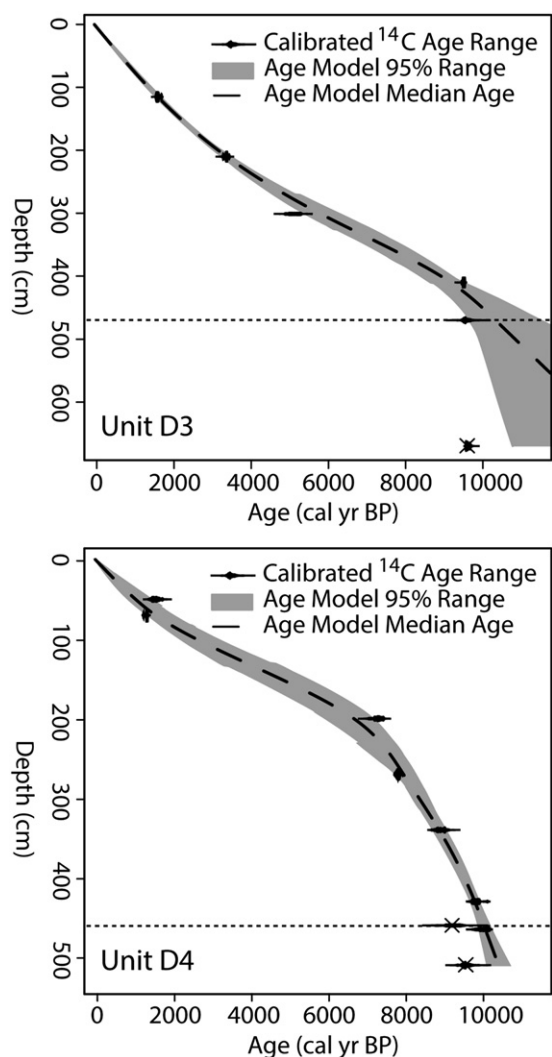**Figure 3.** Stratigraphy at Abrigo de los Escorpiones, re-drawn from Gruhn and Bryan (2009).

Figure 4. Age–depth models used for chronological control. Specimens recovered from depths below dashed lines were not included in this study.

in lagomorph remains from Escorpiones over a similar time frame. That is to say, while we do expect that individual El Niño events would have resulted in impacts to the lagomorph population near Escorpiones on a time scale of one or two years, the nature of the records we use and the chronology employed here only afford a centennial-scale analysis. In any case, such issues, at worst, may inhibit our ability to detect relationships between past ENSO and lagomorph populations, should they have existed.

Taxonomic identifications

The most accurate methods for taxonomic identification of lagomorph skeletal remains are based on cranial features or discrete traits of dental morphology such as crenulation patterns (Findley et al., 1975; Dalquest, 1979; Dalquest et al., 1989; Grayson, 2000). However, the lagomorph cranial materials from Escorpiones are largely edentulous–despite generally excellent bone preservation–thus precluding the use of such features for taxonomic identification. We therefore used a metric technique using cranial measurements, as this approach has proven successful with lagomorph materials in previous studies (Findley et al., 1975; Grayson, 1977, 1983; Neusius and Flint, 1985).

The metric identification technique used in this study makes use of thirteen cranial measurements (Fig. 5 and Table 2) derived from the premaxillae, maxillae and mandibles from 80 museum specimens of the three lagomorph species that occur in northern Baja California: *S. bachmani* (N = 30), *S. audubonii* (N = 30) and *L. californicus* (N = 20). The means and ranges of the measurements for these three taxa are well-separated even though within each species the samples included individuals collected across a broad geographic coverage (Table 3). This suggests that interspecific clinal variation will not likely affect the results of our identifications based on them (see Purdue, 1980). Several of the measurements are also partially redundant—for example the length of the maxillary dental arcade and the length of the maxillary dental arcade minus PM1 and M3 (Fig. 5, measurements A and B, respectively). These redundant measurements were recorded to increase the sample size of lagomorph specimens from the Escorpiones assemblage so as to include broken specimens from which the larger measurement could not be derived. ANOVA suggests each measurement should be useful to some degree in species identification for these three taxa, since all measurements are significantly correlated with taxon at the $\alpha < .001$ level. We used Discriminant Function Analysis (DFA) to predict species with our cranial measurements. Using the leave-one-out classification method and entering variables step-wise, the cross-validated success rates of DFA identification for museum specimens were 92.5% percent for maxillae, 96.3% for mandibles and 96.3% for premaxillae using all available measurements for each specimen. All post-cranial elements not identified with the discriminant function method were identified to either the family or genus level using the reference collection from the Natural History Museum of Utah.

Small mammals in parts of North America have been shown to have undergone varying degrees of body size change in response to changing climate. Woodrats (*Neotoma* spp.) for example, tend toward decreasing body size in warming climates following Bergmann's Rule (Smith et al., 1995, 1998; Smith and Betancourt, 1998, 2003). While this could influence our identifications using this metric approach, it would only affect indices derived from species-level identifications and only one of the four indices we use here is derived from such data (i.e., the Brush Rabbit Index).

Results

The number of identified lagomorph specimens, taxonomic abundance and bone fusion indices are provided in 100-year time intervals for Escorpiones in Supplementary Table 1. A total of 3463 specimens were identified from this sample and form the basis of the four independent indices above. As is typical for archeological and
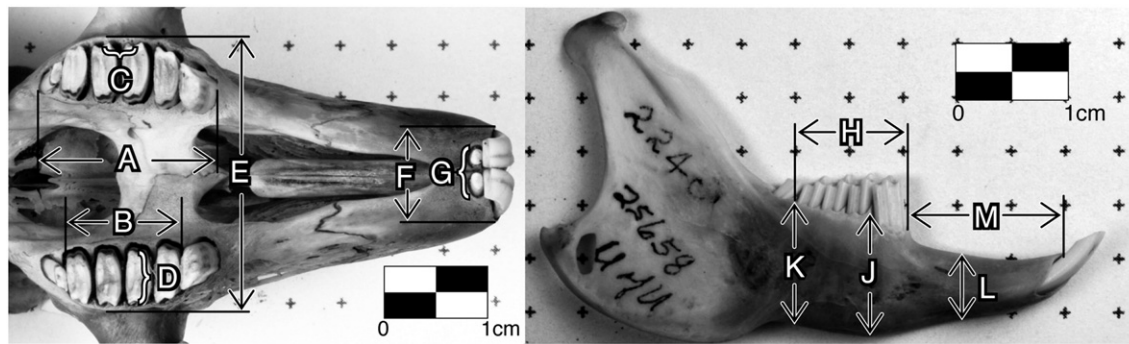
would be assigned to the 200–299 interval rather than 400–499, even though some specimens would likely have been deposited within the latter period. To account for this imprecision, for that introduced from error terms included in our age–depth models themselves and for that introduced in the age–depth models used for the paleoenvironmental proxies against which we compare our lagomorph data, we used a 500-year moving average approach to calculate our lagomorph indices for each 100-year time interval. For example, the 500-year moving average for total lagomorph NISP for the 400–499 cal yr BP interval is calculated as the average of the 5 raw values for this measure between 200 and 699 cal yr BP. We stress here that our results are robust to a range of moving average window sizes—results are similar using 300- or 700-year windows.

While the chronological control established here is relatively fine-grained for trans-Holocene faunal assemblages in North America, some discussion is warranted with respect to El Niño event duration, lagomorph generation times and radiocarbon age error terms. Lagomorph generation times can be as short as several months, while the error terms for the radiocarbon dates used here average 50 yr. There is therefore no way to assign any particular faunal remains to any particular ENSO event. We have overcome this weakness by using the moving average approach outlined above. We are not comparing lagomorph bones to ENSO events on a 1:1 basis; rather, we argue that the frequency of ENSO events on a centennial scale should be evident

Figure 5. Cranial measurements used for taxonomic identification. Letters refer to measurements described in Table 2.

paleontological lagomorph faunas, the collection is dominated by specimens identifiable to the genus level including *Sylvilagus* spp. (NISP = 2228), and *Lepus* spp. (NISP = 335), and an additional 294 specimens were identifiable to the order level. However, cranial measurements were used to identify 491, 79, and 36 specimens of *S. bachmani*, *S. audubonii*, and *L. californicus*, respectively.

To evaluate the effect that El Niño and SST have had on lagomorph populations over the Holocene in this setting, data on the frequency of wet El Niño events per 100 yr over the Holocene (Rodbell et al., 1999; Moy et al., 2002) and SST in the Soledad Basin (Marchitto et al., 2010) were arrayed against our lagomorph NISP, *Sylvilagus* Index, Brush Rabbit Index and Fusion Index values in Figures 6 and 7. Table 4 presents the correlations between the frequency of El Niño events, SST and the Escorpiones lagomorph data over the Holocene. Although we emphasize that all but one of these relationships are statistically significant at the $\alpha = 0.01$ level (SST: Brush Rabbit Index, $r_s = 0.228$, $p = 0.025$), effect size is a further means of evaluating the strength of such relationships in zooarchaeological data (Wolverton et al., 2014). In this context, we observe that 3 of the 4 comparisons with El Niño frequency produced effect sizes considered to be moderate to strong (Fusion Index: El Niño, $r_s = 0.688$; NISP: El Niño, $r_s = 0.601$; Brush Rabbit Index: El Niño, $r_s = 0.498$).

Discussion

As compared to the Holocene histories of lagomorphs in other parts of western North America—especially the Great Basin where the records are the most detailed—the Escorpiones lagomorph fauna exhibits both notable differences as well as interesting similarities. For example, local extirpations of mesic taxa did not occur in northern Baja with Holocene climate change as occurred in the case of American pika and pygmy rabbits in areas of the Great Basin. And although certain periods

Table 2

Measurements used for taxonomic identification. Labels (A-M) correspond to measurements depicted in Figure 5.

Maxilla
A   Dental arcade length (first premolar to third molar)
B   Dental arcade length (second premolar to second molar)
C   Distance between mesial central alveolar spines, third premolar to first molar
D   Third premolar alveolus width
E   Maxillary breadth

Premaxilla
F   Incisor one alveoli (pair) width
G   Incisor two alveoli (pair) width

Mandible
H   Dental arcade length (first premolar to second molar)
I   Width of second premolar alveolus (P4)
J   Mandible height at first/second premolar margin (mesial)
K   Mandible height at first/second molar margin (mesial)
L   Mandible height at mental foramen
M   Diastema

within the middle Holocene (e.g., 6500–5500 cal yr BP) were characterized by declines in overall lagomorph population densities and mesic-taxa relative abundances, reflecting arid conditions, these indices were generally high across much of this period. Indeed, a prominent peak in moisture is suggested by our indices between about 5500 and 4000 cal yr BP. This peak coincides with the onset of modern ENSO periodicity (Shulmeister and Lees, 1995; Sandweiss et al., 1996; Rodbell et al., 1999; Sandweiss et al., 2001; Moy et al., 2002; Donders et al., 2008; Conroy et al., 2008) and may mark the point at which the lagomorph population of northern Baja California became strongly controlled by ENSO. For example, the correlation between El Niño frequency and total lagomorph NISP for the past 5500 cal yr BP is much more strong ($r_s = 0.623$, $p < 0.001$) than for the period from 5500–10,300 cal yr BP ($r_s = 0.105$, $p = 0.476$). Certainly, the smooth middle Holocene troughs in the abundance of mesic taxa registered in many small mammal faunas including *Sylvilagus* populations in the eastern Great Basin (Grayson, 1977, 1983, 1985, 1987, 1998, 2000, 2005, 2006; Grayson et al., 1988; Hockett, 2000; Schmitt et al., 2002) are not evident in the Escorpiones lagomorph fauna. This is not surprising, of course, given not only the distinct ecological context and taxonomic composition of this setting but the temperature ameliorating influence of the Pacific Ocean located currently just 100 m west of the site.

More similar to patterns deduced from Great Basin lagomorph faunas and many other regional vertebrate records is a dramatic increase in moisture during the late Holocene that is reflected in each of our lagomorph indices. More specifically, the lagomorph and El Niño records here suggest several spikes that occur between about 3200 and 700 cal yr BP. Moisture pulses within this period have been reflected in a wide range of other vertebrate records in several Great Basin faunas (Madsen et al., 2001; Broughton, 2004; Schmitt and Lupo, 2005; Byers and Smith, 2007; Broughton et al., 2008). Most notably, this trend has been linked to higher artiodactyl densities and corresponding increases in the human hunting of those animals. Holocene variation in artiodactyl population densities has been reconstructed from archeological faunas but also from a unique fecal pellet record from Homestead Cave where the density of pellets per liter of sediment has been used as a proxy for regional artiodactyl populations (Byers and Broughton, 2004; Broughton et al., 2008; but see also Grayson, 2011). We observe here that the Ecuadorian El Niño record shows a significant positive correlation ($r_s = 0.563$, $p = 0.023$) with the Homestead fecal pellet record.

It is also noteworthy that the most prominent late Holocene spike in El Niño frequency that is centered around 1000 cal yr BP (Fig. 6) overlays temporally with the peak in site frequency of the agriculturally-based Fremont complex in the eastern Great Basin—a time period also marked by a high stand of Great Salt Lake referred to as the Fremont Beach (Massimino and Metcalfe, 1999; Simms, 2008; Louderback et al., 2010). Our analysis thus suggests a specific climatic mechanism to account for some of the more mesic late Holocene conditions—originally proposed in detail by Antevs–that appear to have influenced not only lagomorph populations, but those of other small mammals, artiodactyls, and humans alike.

Table 3
Descriptive statistics of measurements (in mm) used in taxonomic identification from museum specimens. Row labels (A-M) correspond to measurements described in Table 2.

	Sylvilagus bachmani[a]				*Sylvilagus audubonii*[b]				*Lepus californicus*[b]			
	Mean	SD	Range	n	Mean	SD	Range	n	Mean	SD	Range	n
Maxilla												
A	10.85	0.65	8.83–11.71	30	12.15	0.46	11.34–13.21	30	15.49	1.09	12.53–17.77	20
B	7.68	0.51	6.08–8.44	30	8.22	0.35	7.54–8.97	30	10.75	0.65	8.8–11.79	20
C	1.81	0.14	1.43–1.99	30	1.95	0.14	1.65–2.24	30	2.59	0.22	2.0–2.92	20
D	3.40	0.27	2.73–3.81	30	4.21	0.31	3.48–4.63	30	5.30	0.33	4.36–5.69	20
E	15.28	0.76	12.96–16.3	30	17.13	0.59	16.02–18.19	30	22.38	1.32	18.62–24.91	20
Premaxilla												
F	4.96	0.29	4.34–5.52	30	5.89	0.24	5.43–6.37	30	8.00	0.58	6.29–8.77	20
G	2.76	0.30	1.7–3.17	30	3.21	0.23	2.6–3.57	30	4.18	0.34	3.4–4.75	20
Mandible												
H	9.17	0.65	7.35–10.53	30	10.12	0.42	8.97–10.8	30	12.93	0.91	10.57–14.82	20
I	2.44	0.18	1.9–2.83	30	2.80	0.15	2.48–3.02	30	3.60	0.17	3.3–3.86	20
J	8.48	0.97	5.57–10.95	30	10.78	0.51	9.76–11.82	30	14.01	1.09	11.86–16.29	20
K	8.88	0.91	6.47–11.29	30	10.86	0.52	10.02–11.94	30	13.35	1.13	11.14–15.87	20
L	5.42	0.46	4.33–6.81	30	6.41	0.32	5.78–7.01	30	8.63	0.75	7.49–10.13	20
M	11.92	1.07	8.84–14.0	30	13.84	0.75	12.09–15.07	30	19.60	1.52	16.0–22.66	20

[a] *S. bachmani* specimens are from the Museum of Vertebrate Zoology, University of California, Berkeley.
[b] *S. audubonii* and *L. californicus* specimens are from the Natural History Museum of Utah, University of Utah.

This record also reveals interesting relationships between the ranges of our lagomorph indices and ENSO frequency. For the Brush Rabbit Index, *Sylvilagus* Index and Fusion Index (Figs. 7B, C, D), periods with low ENSO frequency tend to have the widest ranges, including many 100-year intervals with high values of these mesic indices. Periods with relatively more frequent El Niño events, however, tend to have only high Brush Rabbit Index and *Sylvilagus* Index values indicating mesic conditions. A slightly different relationship can be seen between El Niño frequency and NISP (Fig. 7A). Low El Niño frequency tends to

be associated with lower NISP while high El Niño frequency tends to be associated with high NISP. The widest range in NISP is found when El Niño is only moderately frequent, from 3–8 events per century.

That the widest range of variation in the relative abundance of the more mesic rabbits at the site (Brush Rabbit Index and *Sylvilagus* Index) is found when ENSO is infrequent may suggest that during more marginal times, these taxa are more demographically unstable and subject to more frequent turnover in the species that is dominant in the community at any given point in time. Alternatively, the greater
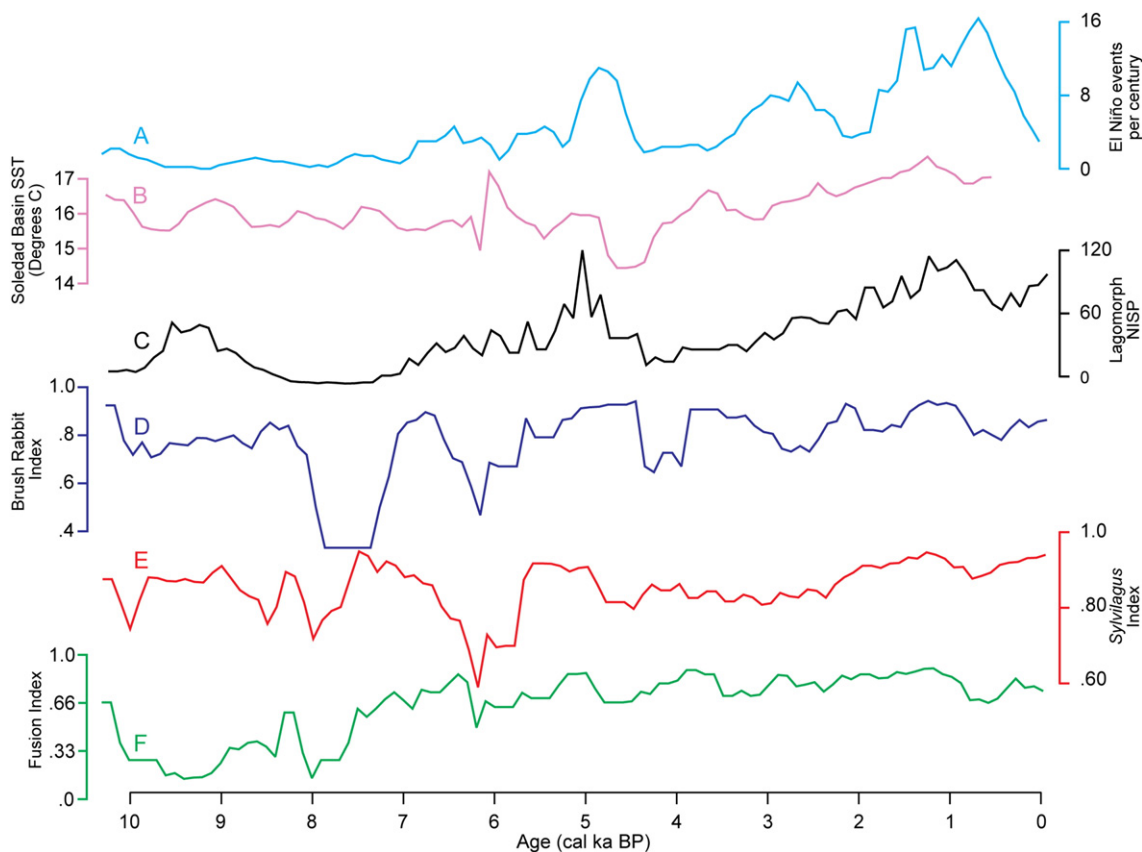

Figure 6. Smoothed (500-year running mean) Holocene El Niño frequency (Moy et al., 2002), Soledad basin SST (Marchitto et al., 2010), and Abrigo de los Escorpiones lagomorph taxonomic abundance and age data.
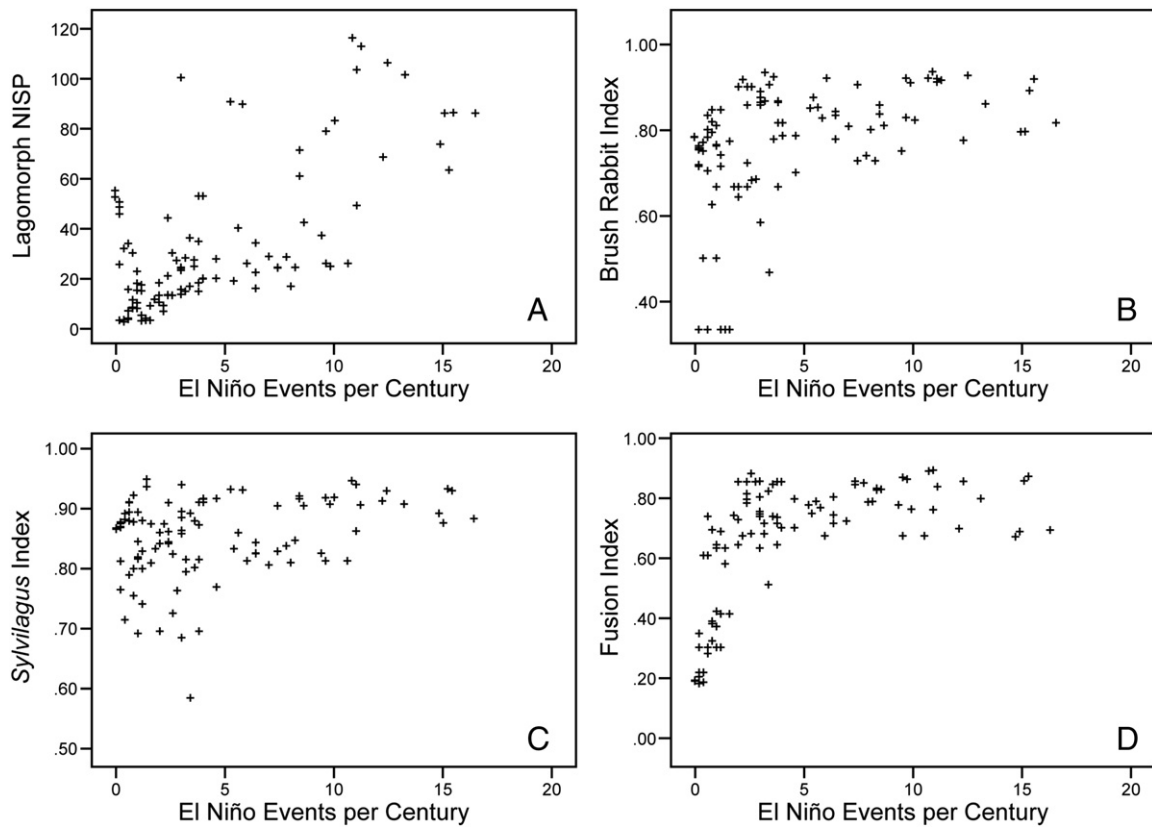
Figure 7. Scatterplots of the relationships between Holocene El Niño frequency and A. Lagomorph NISP, B. Brush Rabbit Index values, C. *Sylvilagus* Index values and D. Fusion Index values at Abrigo de los Escorpiones.

variation in the values of the proportional indices at low ENSO frequencies may be in part due to smaller sample sizes exacerbating the effect of stochastic variation in the relative abundances of different taxa. We are unaware of such a phenomenon being registered in modern analyses of small mammal faunas in relation to ENSO and, although its meaning is not fully clear, it underscores the potential insight that can be gained by examining these relationships on millennial timescales. Further work with other small mammals from the site, including the rich *Neotoma* and *Thomomys* fauna, may help clarify our understanding of this novel patterning.

We have argued above that changes in total lagomorph NISP over time were driven largely by the frequency of El Niño events, but changes in the guild of predators which deposited the remains over time may also have influenced the deposition of bones at the site. For example, if substantial temporal variation occurred in the frequency that raptors perched and fed on the rim of the rockshelter, we would expect variation in lagomorph deposition rates across the period of site occupation. However, this potential problem is alleviated by the weight of evidence approach we have taken here. If changes in NISP we observed over time were the result of changes in use of the site by raptors, they should be

more or less independent from the taxonomic abundance indices and from patterns in the Fusion Index. That NISP, BRI, *Sylvilagus* Index and Fusion Index all vary in concert with one another suggests that it is not changes in the predator population or predator use of the site which is driving the trends but changes in the lagomorph population of this part of Baja California that we are detecting.

Today, Baja California is home to a menagerie of endemic small mammals and other vertebrates with many currently listed as sensitive or endangered. Indeed, the region is represented, collectively, by 11 endemic subspecies of *S. bachmani*, *S. audubonii*, and *L. californicus* as well as black jackrabbit (*Lepus insularis*), the near-threatened endemic hare species (IUCN, 2014). Although a series of reserves have been established to maintain regional biodiversity, the fragmented nature of many populations increases the possibility of stochastic extirpations or extinctions. Exacerbating these concerns, global climate change could substantially alter the current patterns of temperature and precipitation that influence the dynamics of small mammal populations. Although variation certainly exists in forecasted climate patterns, many models call for warmer temperatures, elevated winter precipitation, more extreme weather events, and more frequent ENSO events (Timmerman et al., 1999; Latif and Keenlyside, 2008; Dominguez et al., 2012; Wang et al., 2013; IPCC, 2014). Clearly, understanding the long-term effects of such climatic factors as ENSO will be critical to identifying taxa that will be most adversely affected. Our 10,000-yr record of ENSO effects on Baja California lagomorphs may thus provide invaluable information to conservation biologists tasked with managing these taxa today and in the future.

In this vein, a key takeaway message from this study concerns the difference in the climatic responses of the taxa involved here in Baja California versus those in the Great Basin. While Holocene variation in ENSO appears to have had a strong effect on Baja lagomorphs, mesic oriented taxa persisted through the middle Holocene in this setting while they were depressed or extirpated altogether in the Great Basin. Most

Table 4
Spearman's rank order correlation coefficients (r_s) between El Niño frequency, Soledad Basin SST and Abrigo de los Escorpiones lagomorph data.

		A	B	C	D	E	F
A. El Niño frequency	r_s	1.00	.390**	.601**	.498**	.269**	.688**
B. Soledad Basin SST	r_s		1.00	.430**	.228*	.317**	.422**
C. Lagomorph NISP	r_s			1.00	.422**	.462**	.391**
D. Brush Rabbit Index	r_s				1.00	.304**	.488**
E. *Sylvilagus* Index	r_s					1.00	.308**
F. Fusion Index	r_s						1.00

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

importantly, this geographic pattern in the impacts of Holocene climate change on western lagomorphs may have implications for targeting conservation efforts for a wide range of threatened taxa that are characterized by broad geographic ranges that extend from coastal settings into the interior. Namely, threatened mesic-oriented taxa will be more vulnerable as distance increases from both the temperature ameliorating effect of the Pacific Ocean and the reach of ENSO-based precipitation. Although the ecological and climatic variables differ, analogous conclusions have been reached in considerations of the fate of the American pika that are thriving today in the Sierra Nevada but are struggling on many ranges of the central Great Basin (Beever et al., 2010; Millar and Westfall, 2010; Erb et al., 2011; Wilkening et al., 2011). Our study may thus contribute to the growing understanding of the variables that enable threatened taxa to persist despite the myriad threats they may face in an uncertain climatic future.

Conclusion

The short time scales covered by our instrumental records of ENSO constrain our ability to model the variable affects of this phenomenon on marine and terrestrial ecosystems and the vertebrate faunas that comprise them. Indeed, the most detailed quantitative data on ENSO impacts on marine and terrestrial vertebrate faunas include only the last several major ENSO events (e.g., AD 1982–83, 1987–88, and 1997–98). A clearer understanding of the influence of ENSO on terrestrial and marine vertebrate faunas, that may be crucial to predicting the long-term future dynamics of vertebrate communities, would thus clearly benefit from fine-grained, millennial-scale ENSO-vertebrate response records extending back to the terminal Pleistocene. Our work with the lagomorph fauna from Escorpiones provides such a record and represents the first high-resolution trans-Holocene El Niño response record documented for any group of terrestrial vertebrates. Importantly, this record shows that aspects of the northern Baja California lagomorph fauna that are precipitation dependent (i.e., –overall population size, age structure, and relative abundance of mesic taxa) –varied sensitively over the last 10,000 yr in response to El Niño based precipitation. Further work with other aspects of the rich Escorpiones vertebrate fauna will allow us to gauge the variability of trans-Holocene ENSO impacts on a wide range of terrestrial and marine vertebrates.

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Acknowledgments

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