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The Mescal Cave Fauna (San Bernardino County, California) and testing assumptions of habitat fidelity in the Quaternary fossil record

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ABSTRACT

The late Pleistocene and Holocene vertebrate fossil record for the northern Mojave Desert (southwestern USA) is known primarily from five sites. Until now, only two of these have been radiometrically dated, and temporal placement of the others has been based on stratigraphic or biostratigraphic correlation, leading to circular interpretations of mammal extirpations in the Mojave. Here, I report a revised and complete faunal list for Mescal Cave, along with 22 AMS radiocarbon dates from 5 vertebrate taxa recovered from its deposits. The results reported here demonstrate time-averaging in Mescal Cave encompassing around ~34 ka, a maximum age 14 ka older and minimum age 10 ka younger than previously thought. Furthermore, radiocarbon analyses suggest local extirpation of *Marmota flaviventris* around 3.6 cal ka BP, considerably younger than expected based on regional patterns of warming and aridification in the Mojave. Conversely, radiocarbon dates from another presumably boreal species, *Neotoma cinerea*, are considerably older than expected, suggesting either that climate change at this site did not directly mirror regional patterns, that habitat requirements for these two species are not strictly boreal or cool/mesic as has often been assumed, or that local edaphic conditions and/or competitive interactions override the regional climatic controls on theses species' distribution.

Introduction

The late Pleistocene and Holocene vertebrate fossil record for the northern Mojave Desert (southern physiogeographic Great Basin), southwestern USA, is known primarily from five cave sites: Quien Sabe Cave (UCRRV64-34; Holocene), Kokoweef Cave (SBC1.11.13; glacial), Antelope Cave (SBC1.10.10; glacial), Mitchell Caverns (LACM 3497; Late Wisconsin), and Mescal Cave (SBC1.10.12, UCMP V3864; previously presumed glacial). Of these sites, only specimens from Kokoweef and Antelope Caves have been radiometrically dated prior to this report, while the temporal placement of the others has been based on stratigraphic or biostratigraphic correlation. Here, I report a revised and complete faunal list for Mescal Cave along with 22 AMS radiocarbon dates on 5 vertebrate taxa from Mescal Cave. These results demonstrate high time-averaging in Mescal Cave (~34 ka), a maximum age more than 14 ka older and minimum age 10 ka younger than previously thought, and dates of local extirpation for taxa thought to be indicative of cooler climates, *Marmota flaviventris* and *Neotoma cinerea*. While dated material from *M. flaviventris* is much younger than would be expected based on regional patterns of the timing of warming and aridification in the Mojave, *N. cinerea* disappears from Mescal Cave deposits predictably at the onset of regional aridification (Grayson, 2011).

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End-Pleistocene and Holocene climate

Between 30 and 15 ka, the southern Great Basin was cool and mesic, pluvial lakes covered much of the area, marshes and ponds were abundant, and juniper woodland was the dominant vegetation (Quade, 1986; Mensing, 2001; Grayson, 2011). The shores of Pleistocene Lake Mojave were within approximately 35 km of Mescal Cave, and Lake Mojave fluctuated in extent and depth until about 15.5 ka, when the basin dried completely (Grayson, 2011) (Fig. 1). On a regional scale, Pleistocene lakes across the Great Basin began to shrink around 14 ka (Quade, 1986; Mensing, 2001). From ~11.3–8.3 ka, the environment was still relatively cool and wet, and Lake Mojave returned intermittently; however, desert shrubs became more abundant, piñon and juniper were largely absent, and marshes were less common (Grayson, 2000, 2011; Mensing, 2001). Grayson (2000) documents higher species richness and evenness in the Great Basin during the early Holocene than any time afterward. During the middle Holocene, from around 8–5 ka, aridity increased sharply and climate warmed: again, Lake Mojave completely dried (Grayson, 2011). Extirpations of mesic-adapted or boreal vertebrate species occurred on Great Basin mountain ranges at this time (Brown, 1978; Grayson, 2000). Because the mountain ranges are separated by wide valleys, subsequent recolonization via dispersal is thought to have been rare for most species, though there is evidence that some mammals readily disperse across these arid basins, and the faunas of these ranges have been impacted by both extinction and

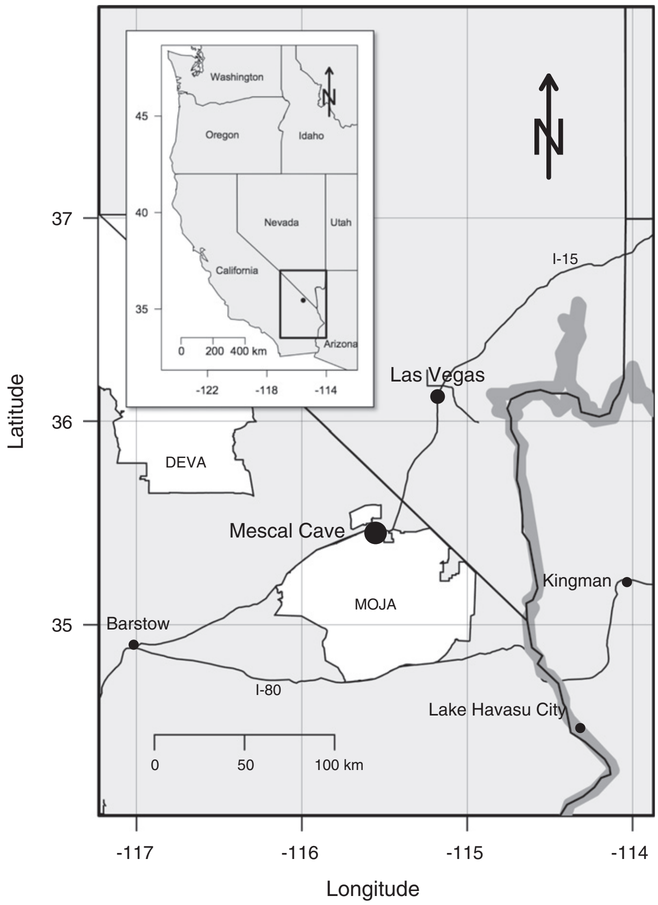

Figure 1. Map showing location of Mescal Cave; regional map of the western United States is inset. MOJA: Mojave National Preserve; DEVA: Death Valley National Park.

colonization (Lomolino et al., 1989; Floyd, 2004; Floyd et al., 2005; Rickart et al., 2008).

The Great Basin reached a thermal maximum around 6.8 ka and temperatures cooled somewhat afterward, allowing timberline to move downslope. Although precipitation did not recover to pre-middle Holocene levels, some lakes and springs returned and some species apparently extirpated during the middle Holocene recolonized (Grayson, 2000). In the Mojave, higher water tables and soils high in organic material did not return until about 2.3 ka (Grayson, 2011).

Overall, the northern Mojave experienced more drying and warming than other parts of the Great Basin during the Holocene (Kueppers et al., 2005). Currently, this region receives the lowest rainfall amounts (~100 mm average annual rainfall) and has the highest evaporation rates in the Great Basin (~2100 mm average annual evaporation) (Grayson, 2011), and, by as early as 2080, is projected to experience a ~3–5°C increase in annual temperature and as much as 35% less spring precipitation (USGCRP, 2009). Each of the past biotic and abiotic changes in the Mojave may have had a pronounced, but as yet poorly-understood, impact on the fauna. Understanding these impacts is important in light of the currently changing climate, in order to identify whether the responses of biota presently are paralleling those of past climate changes, and what might be expected in the near future. This requires a more detailed record of faunal change in this area with accompanying radiometric dates, a key focus of this paper.

Study site

Mescal Cave (University of California Museum of Paleontology (UCMP) Locality #V3864) (N 35°27′0.45″ latitude and W 115°32′60″ longitude) is a limestone cave located in the Mescal Range, approximately 1550 m in elevation, at the northern edge of the Mojave Desert. This site was excavated in 1938 by a University of California Museum of Paleontology party led by R.A. Stirton, and it contains material that was evidently accumulated by woodrats (*Neotoma*). The cave is comprised of two chambers, approximately 6.4 m wide and extending into the rock about 14 m in total, but fossils were recovered only from the outer chamber, nearest the cave entrance. Stirton's crew initially dug a 46-cm-deep trench but continued excavations laterally in several directions; no stratigraphic information was recorded. They hauled the un-sifted material out of the cave, dumped it, then "sifted and picked out the bones" (Stirton, 1938). Although, according to the field notes, the sediment contained abundant plant macrofossils and scat (primarily from *Neotoma*), these materials never entered the UCMP collection and may not have been saved during excavation. Furthermore, Stirton writes that "not all of the tiny bone scraps were saved" (Stirton, 1938), which may explain the paucity of small teeth in this collection. The site also contained archeological evidence, most notably a "large pine bowl" (Stirton, 1938), though the current location and disposition of this bowl is unknown. Stirton estimated the age of the site to be younger than Pleistocene based on the overall faunal composition and stratigraphy; however, Jefferson (1991) suggests a date between 20 and 10 ka, based again on faunal composition and geographic context.

Methods

I examined over 3300 skeletal specimens from Mescal Cave; these specimens are reposited at the UCMP and records are publically available through the UCMP database (http://ucmpdb.berkeley.edu/). Measurement methods follow von den Driesch (1976) and were taken with Fowler Sylvac Ultra-Cal IV 6″/150 mm digital calipers, accurate to 0.01 mm. Statistical analyses were performed in R, version 2.14 (R Core Team, 2013).

Taxonomic identification

Skeletal specimens from Mescal Cave were identified by direct comparison to modern skeletal specimens of known species identity in the UCMP element collection and Museum of Vertebrate Zoology (MVZ). When direct comparison was not possible (i.e., relevant comparative material was not available in the UCMP or MVZ), fossil specimens were identified using published descriptions and illustrations (see Supplemental Data 1) (Fig. 2).

Radiocarbon dating

Given the potential for stratigraphic mixing in the site, 22 specimens representing 4 taxa (see Table 1) were radiocarbon dated using Accelerator Mass Spectrometry (AMS) dating techniques at the Center for Accelerator Mass Spectrometry (CAMS), Lawrence Livermore National Labs (Livermore, California, USA). The taxa selected for dating included two morphologically distinct *Neotoma* (*N. cinerea* and *N.* spp.) and two size classes of leporid. Because Mescal Cave was excavated without stratigraphic control, dating specimens of known taxonomic identity was the only way to identify if there were turnover within these taxonomic groups through time. Woodrats and leporids were the most abundant taxa in these deposits and so were particularly valuable for establishing a chronology (Table 3).

Specimen preparation follows the modified longin method described by Brown et al. (1988) for collagen extraction, and methods outlined in Vogel et al. (1987) for converting CO_2 into graphite for AMS analysis. Results include a matrix-specific background correction and an estimate of the $\delta^{13}C$ value of the material, and are reported as a conventional radiocarbon years before present (Stuiver and Polcah, 1977). To obtain calendar years BP, I used OxCal Online, version 4.2 (Bronk Ramsey, 2009), implementing the IntCal 13 calibration curve (Reimer et al., 2013).

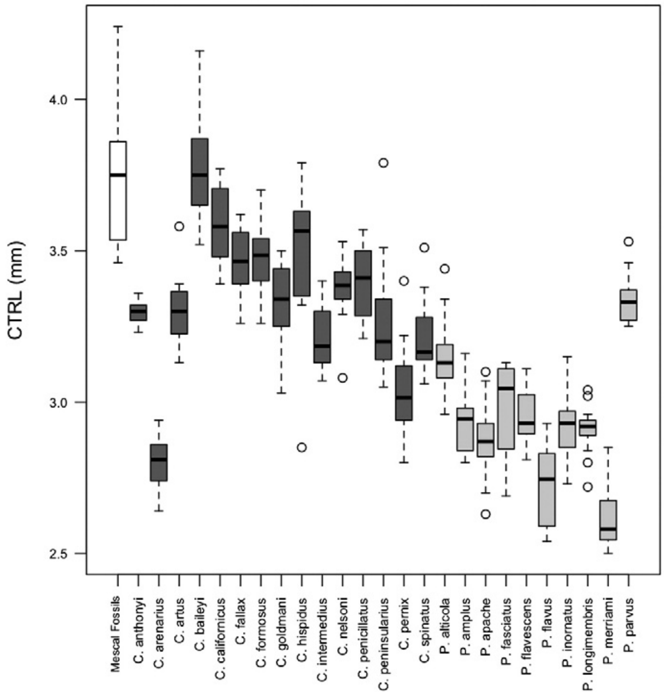

Figure 2. Boxplot of complete lower tooth row (CTRL) measurements for modern and fossil Perognathinae. Dark gray = *Chaetodipus*; light gray = *Perognathus*; white = fossil specimens from Mescal Cave. Bars extend to the most extreme data point, but not more than 1.5 × the interquartile range. Open circles represent outliers.

Results

Specimens identified from Mescal Cave represent a minimum of 20 genera (Table 2), including members of Rodentia (rodents), Lagomorpha (rabbits, hares, pikas), Procyonidae (raccoons), Canidae (wolves, coyotes, foxes), Felidae (cats), and Bovidae (sheep, etc.). A total of 2281 individual specimens were identified at least to family (minimum number of individuals = 310).

All 22 bone samples selected for AMS ^{14}C dating yielded sufficient collagen. See Table 1 for dates and associated data.

Table 1
Radiocarbon dating results.

CAMS #	UCMP #	^{14}C yr BP	Cal yr BP	Species
154748	196747	50 ± 30	31–257	Leporid A
154751	196750	14,780 ± 210	17,453–18,572	Leporid A
154750	196749	26,820 ± 1040	29,593–34,111	Leporid A
154747	196746	2510 ± 35	2366–2745	Leporid B.
154754	291751	2540 ± 40	2488–2751	Leporid B
154763	291752	10,940 ± 120	12,616–13,097	Leporid B
154749	196751	11,460 ± 130	13,099–13,635	Leporid B
154753	291750	11,790 ± 140	13,346–13,929	Leporid B
154752	196748	15,430 ± 230	17,453–18,572	Leporid B
160638	196334	4910 ± 35	3641–3766	*Marmota flaviventris*
160636	196329	9260 ± 50	8326–8621	*Marmota flaviventris*
160646	77156	11,080 ± 60	10,789–11,176	*Marmota flaviventris*
160637	222641	13,450 ± 80	14,139–14,944	*Marmota flaviventris*
160639	196337	14,400 ± 100	151,198–15,938	*Marmota flaviventris*
154757	196722	10,660 ± 120	12,151–12,859	*Neotoma cinerea*
154758	196721	12,750 ± 160	14,226–16,094	*Neotoma cinerea*
154756	196741	15,700 ± 240	18,567–19,409	*Neotoma cinerea*
154755	196706	25,330 ± 860	28,461–31,447	*Neotoma cinerea*
154762	196753	180 ± 35	−4–301	*Neotoma* sp.
154760	196757	5260 ± 170	5657–6386	*Neotoma* sp.
154761	196760	8200 ± 80	9002–9408	*Neotoma* sp.
154759	196768	13,940 ± 190	16,711–17,566	*Neotoma* sp.

Table 2
Minimum number of individuals (MNI) and number of identified specimens (NISP) for all taxa. c.f. designations are included in these counts.

Taxon	MNI	NISP
Rodentia		
Sciuridae		
Ammospermophilus sp.	1	1
Marmota flaviventris total	7	41
Otospermophilus sp.	2	2
Sciurus sp.	1	1
Spermophilus sensu lato sp.	2	6
Geomyidae		
Thomomys sp.	5	26
Heteromyidae		
Chaetodipus sp. total	7	28
Dipodomys sp.	6	18
Cricetidae		
Arvicolinae	10	39
Baiomys sp.	6	10
Lemmiscus curtatus	7	18
Microtus sp.	2	3
Neotoma cinerea total	30	289
Neotoma sp.	91	745
Neotominae	18	50
Lagomorpha		
Ochotona sp.	6	24
Leporidae A (small)	72	636
Leporidae B (large)	21	300
Procyonidae		
Bassariscus astutus	2	5
Canidae		
Canis sp.	2	10
Urocyon cinereoargenteus total	1	3
Felidae		
Lynx rufus	1	1
Mephitidae		
Spilogale cf. *gracilis* total	4	8
Bovidae		
Ovis canadensis total	6	17

Discussion

Of the 24 taxa reported here, the most abundant groups are *Neotoma*, consistent with Mescal Cave having been used by woodrats. Leporids (*Lepus* and possibly *Sylvilagus*) are also extremely abundant in this site. Large bird bones, likely from owls and raptors, suggest use of this site by avian predators, while the pine bowl reported by Stirton indicates human influence as well. Many of the bones recovered from Mescal Cave are acid etched, characteristic of bones that have been partially digested by raptors or mammalian carnivores. Taxa found in the deposits that are no longer present in the Mescal Range include: *Ochotona princeps* (pika), *Baiomys* sp. (pygmy mouse), *Lemmiscus curtatus* (sagebrush vole), *M. flaviventris* (yellow-bellied marmot), and *N. cinerea* (bushy-tailed woodrat) (Reid, 2006; IUCN, 2014; VertNet database, 2014).

Stirton concluded that all the bones recovered at Mescal Cave were deposited around the same period of time, and that the site was relatively young, "certainly not Pleistocene" (Stirton, 1938). In contrast, Jefferson (1991) estimated Mescal Cave to be Rancholabrean. These casual age estimates have confused interpretation of Mescal Cave, but generally the site has been considered fairly young, and probably Holocene, and so it has been interpreted as an example of unusually late extirpation in several mesic, high-elevation taxa. The radiocarbon dates reported here indicate that, although some of the Mescal Cave material is older than previously thought, this site also contains an exceptionally young record of *M. flaviventris* at this relatively low elevation and latitude. In contrast, with respect to extirpation of *N. cinerea*, this site is in

Table 3
Welch two-sample t test results comparing lower tooth row measurements of Mescal Cave fossil *Thomomys* (mean CLTR = 7.93 mm; standard error = 0.04 mm) and modern species of *Thomomys*. CLTR = complete lower tooth row length.

Species	Mean CLTR (mm)	Standard error (mm)	t statistic	P value
T. bulbivorous (n = 14)	11.56	0.16	−21.07	3.05×10^{-12}
T. townsendii (39)	10.09	0.07	−26.27	1.00×10^{-15}
T. umbrinus (20)	7.75	0.12	−1.70	0.11
T. bottae (20)	8.00	0.11	−0.29	0.76

concordance with predictions of regional patterns of range shifts observed elsewhere in the western U.S.

Yellow-bellied marmots prefer montane and alpine meadows associated with talus and rock outcrop (Floyd, 2004). Within the arid Great Basin, they tend to favor cooler and more mesic habitats (Reid, 2006 Grayson, 2011;). *M. flaviventris* declined in abundance in the Great Basin at the end of the Pleistocene, contracting their range northward and higher in elevation (Grayson, 2011). Until now, the youngest precisely dated fossil specimens of *M. flaviventris* found south of their current distribution—an individual from Dry Cave, New Mexico—is 14,720–14,220 cal yr BP, but few of the southern extralimital specimens have been dated precisely (Grayson, 2011). Nevertheless, their extirpation from these lower latitudes—including the Mojave—has been thought to have occurred by the middle Holocene (Grayson, 2011). In terms of their modern range, Floyd (2004) found that *M. flaviventris* occurs as low as 1560 m (approximately the elevation of Mescal Cave) on one Great Basin mountain range—the Desatoya Mountains in Churchill County, Nevada—but this range is considerably higher in latitude than Mescal Cave (approximately 520 km north), and over 80% of the individuals Floyd (2004) studied occurred above 2100 m. Vegetation associated with *M. flaviventris* burrows included oceanspray, elderberry, wild rose, and chokecherry: species generally found in higher-elevation, mesic environments in the Great Basin today (Floyd, 2004).

Although three of the five radiocarbon dates for marmots in Mescal Cave are Pleistocene, several are younger than expected, particularly considering that Mescal Cave is at the southern extent of the Great Basin and therefore more likely to have lost cool, mesic species earlier than the rest of the region. These younger specimens are dated to 8330–8620 cal yr BP and 3641–3770 cal yr BP, suggesting that *M. flaviventris* was present at this low elevation in Mescal Cave around 4.5 ka later than in other parts of the southern Great Basin. According to Grayson (2011), water returned to Lake Mojave around 5 ka, marking a change from the precipitation trends of the Middle Holocene; however, the lake basin dried again shortly thereafter and modern plant communities were established around 4.8 ka in the Mojave. Nevertheless, if marmots were able to persist near Mescal Cave through the middle Holocene (Clark Mountain, less than 10 km north is a plausible refuge), it is conceivable that they could have briefly recovered in the Mescal Range and surrounding areas before increased drought and aridity drove them out permanently.

Floyd (2004) suggests that a combination of rocky outcrops and suitable vegetation is required to sustain populations of *M. flaviventris*—Mescal Cave is in an approximately north-facing, narrow drainage which potentially could have retained montane vegetation later into Holocene aridification than surrounding areas. Additionally, marmots can apparently disperse up to 15 km (Van Vuren and Armitage, 1994); near Mescal Cave, this dispersal range includes the boreal environments of the Clark Mountains (~2400 m). In a study of marmot genetic relatedness, Floyd et al. (2005) found a strong correlation between genetic and geographic distance, indicating that this species does in fact disperse across the xeric basins that separate suitable montane habitats. In the Rocky Mountains, *M. flaviventris* populations undergo local extinction and recolonization cycles, some populations experiencing temporary extirpation more often than others (Floyd, 2004). A source-sink population dynamic in the northern Mojave during the Holocene is a likely explanation for the young specimens of *M. flaviventris* at Mescal Cave. Nevertheless, the radiocarbon dates reported here suggest that Mescal Cave and surrounds finally became inhospitable for even a sink population of marmots after around 3.6 ka.

Like marmots, bushy-tailed woodrats were, until recently, generally considered montane, and thought to be found in higher-elevation, cool, mesic environments (Grayson et al., 1996). However, *N. cinerea* is found at low elevations (below 1465 m) in the Bonneville Basin, in environments that have classic xeric vegetation and no permanent water sources (Grayson 1996). These not-uncommon xeric, low-elevation populations demonstrate either that, like *M. flaviventris*, *N. cinerea* can disperse across xeric lowlands, or that they are able to persist in xeric regions not typically thought to be suitable habitat (Grayson, 1996; Grayson and Madsen, 2000). However, the youngest radiocarbon date for bushy-tailed woodrats at Mescal Cave is 12,860–12,150 cal yr BP. Across the Great Basin, this species began to decline at the Pleistocene–Holocene transition, declining most steeply around 8.3 ka and contracting their range to higher elevations and latitudes (Grayson, 2011). Given that *M. flaviventris* was able to persist well past 8 ka—perhaps due to micro-refugia or to source-sink population dynamics—it is curious that *N. cinerea* did not also survive beyond this time, though more radiocarbon dates could reveal *N. cinerea* at later times. A smaller and morphologically distinct species of *Neotoma* (likely *Neotoma lepida* or *Neotoma albigula*), on the other hand, dates from 9410 cal yr BP to the present, with one specimen dated at 17,570–16,710 cal yr BP, suggesting that these species coexisted before *N. cinerea* disappeared (Fig. 3, Supplemental 3).

Yet another potential explanation for the difference in environmental response between *M. flaviventris* and *N. cinerea* is competitive exclusion. *M. flaviventris* has no congeners in the Mojave ecosystem, and there are no species sharing the same general ecological role. However, there was species turnover at Mescal Cave within *Neotoma*: *N. cinerea* was replaced by a smaller-bodied congener that was likely more tolerant of warmer, drier conditions. In other systems where species of *Neotoma* coexist, competition over food resources and nesting locations leads to specialization and dominance of one species of *Neotoma* of another (Cameron, 1971; Cameron and Rainey, 1972; Dial, 1988); in the long term, these dynamics could lead to competitive exclusion and species replacement.

The faunal composition of Mescal Cave is broadly similar to other late Quaternary Mojave vertebrate fossil localities like Mitchell Caverns and Kokoweef, Antelope, and Quien Sabe Caves. This is to be expected: with the exception of Mitchell Caverns, these sites are located in the same system of closely-connected peaks—the Mescal Range, Ivanpah Mountains, and Mineral Hills. Reynolds et al. (1991a) report a single radiocarbon date for Kokoweef Cave at 9980–9680 cal yr BP on charcoal from one of the middle excavation levels. Kokoweef samples many more taxa than Mescal Cave, including land snails, a wide variety of birds and reptiles, several species of bat, and fresh water fish. Kokoweef contains *M. flaviventris* in sediments both above and below the dated layer, but maximum and minimum ages for this site are unknown (Goodwin and Reynolds, 1989; Reynolds et al., 1991a). Kokoweef and Antelope Caves contain the extralimital species *Ochotona princeps* (also found in Mescal Cave) and *Otospermophilus variegatus*, and extinct species of large mammals like *Hemiauchenia* and *Camelops* (Reynolds et al., 1991a,b). Kokoweef Cave contains the extinct bird species *Meleagris* sp. c.f. *Meleagris crassipes* and *Gymnogyps* sp. c.f. *Gymnogyps*

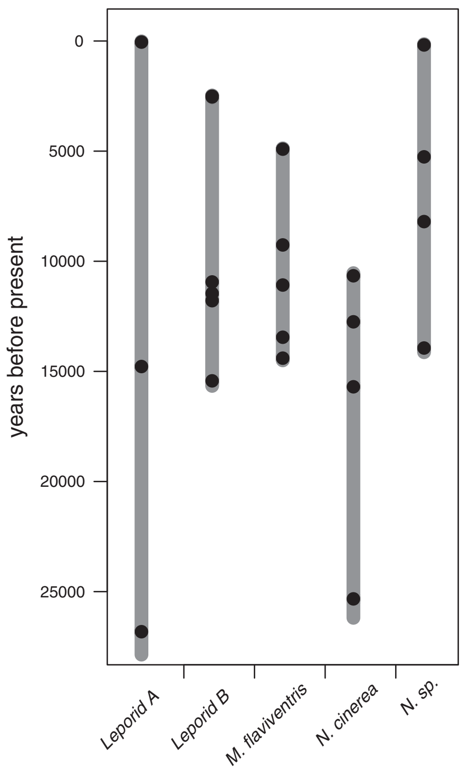

Figure 3. Radiocarbon dating results. Black dots represent the mean date for each sample; the gray bar indicates the durations, including the error on the oldest and youngest dates.

amplus (Reynolds et al., 1991b). Antelope, Kokoweef, and Quien Sabe Caves all sample bats, shrews (*Sorex* and *Notiosorex*), and *Peromyscus*, none of which are found in Mescal Cave (Goodwin and Reynolds, 1989; Reynolds et al., 1991a,b). This is likely because Mescal Cave sediments were not screened with a sufficiently fine mesh, so elements from especially small taxa may have been lost during the excavation process.

Conclusions

New radiocarbon dates and taxonomic identification of vertebrate fossil from a rich fossil accumulation at Mescal Cave, California, indicate the deposits span from at least 34 ka through the present. There is considerable stratigraphic mixing, necessitating many more radiocarbon dates before the deposits become maximally useful in untangling a complex chronology, but even with the 22 new dates reported in this study, useful information emerges, notably persistence of *M. flaviventris* in the area later than previously known, despite disappearance of another putative mesic-environment indicator, *N. cinerea*, near the Pleistocene–Holocene boundary.

Most of the mammals found in Mescal Cave are still present in the Great Basin today, and many are still present in the immediate vicinity. Yellow-bellied marmots and bushy-tailed woodrats are both present in older sediments at this site, corroborating what is known from other studies of the Great Basin Pleistocene: that it was generally cooler and more mesic than today. However, the persistence of yellow-bellied marmots at Mescal Cave into the late Holocene is an important reminder that past mammal distributions can be at odds with expectations based on generalized correlations between modern geographic range and climate, and instead can reflect local edaphic conditions. The discordance in apparent response to climate change of *M. flaviventris* (persistence much later than expected) and *N. cinerea* (disappearance near the Pleistocene–Holocene boundary, though persisting elsewhere in xeric settings) also underscores that mammal species tend to respond to climate change individualistically (Lyons, 2003; Moritz et al., 2008; Rapacciuolo et al., 2014), and that within a species different populations across their geographic range may respond differently to environmental changes and environmental gradients (Rapacciuolo et al., 2014). Microrefugia and local climatic pockets have a major influence on persistence of a species in a particular site, and these small-scale habitat patches are often difficult to detect in the fossil record (Gavin et al., 2014). Interspecific competition may also play a crucial role in whether a species is able to persist at a site. As a result of these many causes of uncertainly, age estimates based solely on which mammals are present in a fossil deposit should be made with extreme care.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2015.02.005.

References

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.
Brown, J.H., 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs 2, 209–227.
Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified longin method. Radiocarbon 30, 171–177.
Cameron, G.N., 1971. Niche overlap and competition in woodrats. Journal of Mammalogy 52, 288–296.
Cameron, G.N., Rainey, D.G., 1972. Habitat utilization by *Neotoma lepida* in the Mohave Desert. Journal of Mammalogy 53, 251–266.
Dial, K.P., 1988. Three sympatric species of *Neotoma*: dietary specialization and coexistence. Oecologia 76, 531–537.
Floyd, C.H., 2004. Marmot distribution and habitat associations in the Great Basin. American Naturalist 64, 471–481.
Floyd, C.H., Van Vuren, D.H., May, B., 2005. Marmots on Great Basin mountain tops: using genetics to test a biogeographic paradigm. Ecology 86, 2145–2153.
Gavin, D.G., et al., 2014. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. New Phytologist 1, 37–54.
Goodwin, H.T., Reynolds, R.E., 1989. Late Quaternary Sciuridae from Kokoweef Cave, San Bernardino County, California. Bulletin of the Southern California Academy of Sciences 88, 21–32.
Grayson, D.K., 2000. Mammalian response to the Middle Holocene climatic change in the Great Basin of the western United States. Journal of Biogeography 27, 181–192.
Grayson, D.K., 2011. The Great Basin: a Natural Prehistory. University of California Press, Berkeley.
Grayson, D.K., Madsen, D.B., 2000. Biogeographic implication of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. Journal of Mammalogy 81, 1100–1105.
Grayson, D.K., Livington, S.D., Rickart, E., Shaver III, M.W., 1996. Biogeographic significance of low-elevation records for *Neotoma cinerea* from the Northern Bonneville Basin, Utah. Great Basin Naturalist 56, 191–196.
Jefferson, G.T., 1991. Rancholabrean age vertebrates from the Southeastern Mojave Desert, California. In: Reynolds, R.E. (Ed.), Crossing the borders: quaternary studies in eastern California and southwestern Nevada. Redlands, California, Mojave Desert Quaternry Research Center, San Bernardino County Museum Association Special Publication, pp. 27–40.
Kueppers, L.M., Snyder, M.A., Sloan, L.C., Zavaleta, E.S., Fulfrost, B., 2005. Modeled regional climate change and California endemic oak ranges. PNAS 102, 16281–16286.
Lomolino, M.V., Brown, J.H., Davie, R., 1989. Island biogeography of montane forest mammal in the American Southwest. Ecology 70, 180–194.
Lyons, K.A., 2003. A quantitative assessment of the range shifts of Pleistocene mammals. Journal of Mammalogy 84, 385–402.

Mensing, S.A., 2001. Late-Glacial and Early Holocene vegetation and climate change near Owens Lake, Eastern California. Quaternary Research 55, 57–65.
Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., Beissinger, S.R., 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322, 261–264.
Quade, J., 1986. Late Quaternary environmental changes in the Upper Las Vegas Valley, Nevada. Quaternary Research 26, 340–357.
R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL http://www.R-project.org/).
Rapacciuolo, G., et al., 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20, 2841–2855.
Reid, F.A., 2006. Peterson Guide to Mammals of North America. 4th ed. Houghton Mifflin Harcourt, New York.
Reimer, P.J., et al., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. Radiocarbon 55, 1859–1887.
Reynolds, R.E., Reynolds, R.L., Bell, C.J., Czaplewski, N.J., Goodwin, H.T., Mead, J.I., Roth, B., 1991a. The Kokoweef Cave faunal assemblage. In: Reynolds, R.E. (Ed.), Crossing the Borders: Quaternary Studies in Eastern California and Southwestern Nevada. San Bernardino County Museum Association, Redlands, pp. 97–103.
Reynolds, R.E., Reynolds, R.L., Bell, C.J., Pitzer, B., 1991b. Vertebrate remains from Antelope Vcave, Mescal Range, San Bernardion County, California. In: Reynolds, R.E. (Ed.), Crossing the Borders: Quaternary Studies in Eastern California and Southwestern Nevada. San Bernardino County Museum Association, Redlands, pp. 107–109.
Rickart, E.A., Robson, S.L., Heaney, L.R., 2008. Mammals of Great Basin National Park, Nevada: comparitive field surveys and assessment of faunal change. Monographs of the Western North American Naturalist 4, 77–114.
Stirton, R.A., 1938. UCMP Field Notes.
Stuiver, M., Polcah, H.A., 1977. Reporting of ^{14}C data. Radiocarbon 19, 355–363.
The IUCN Red List of Threatened Species, 2014. Version 2014.3 (<iucnredlist.org > Downloaded on 17 November 2014).
USGCRP, 2009. Global climate change impacts in the United States. In: Karl, T.R., Melillo, J.M., Peterson, T.C. (Eds.), United States Global Change Research Program. Cambridge University Press, New York, NY, USA.
Van Vuren, D., Armitage, K.B., 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? Oikos 69, 179–181.
VertNet database, 2014. Version 2014–09–26. http://portal.vertnet.org/search (Downloaded on 17 November 2014).
Vogel, J.S., Southon, J.R., Nelson, D.E., 1987. Catalyst and binder effects in the use of filamentos graphite for AMS. Nuclear Instruments and Methods in Physics Research B29, 50–56.
von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin 1. Harvard University, Peabody Museum of Archaeology and Ethnology.