The dead do not lie: using skeletal remains for rapid assessment of historical small-mammal community baselines

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Conservation and restoration efforts are often hindered by a lack of historical baselines that pre-date intense anthropogenic environmental change. In this paper I document that natural accumulations of skeletal remains represent a potential source of high-quality data on the historical composition and structure of small-mammal communities. I do so by assessing the fidelity of modern, decadal and centennial-scale time-averaged samples of skeletal remains (concentrated by raptor predation) to the living small-mammal communities from which they are derived. To test the power of skeletal remains to reveal baseline shifts, I employ the design of a natural experiment, comparing two taphonomically similar Great Basin cave localities in areas where anthropogenic land-use practices have diverged within the last century. I find relative stasis at the undisturbed site, but document rapid restructuring of the small-mammal community at the site subjected to recent disturbance. I independently validate this result using historical trapping records to show that dead remains accurately capture both the magnitude and direction of this baseline shift. Surveys of skeletal remains therefore provide a simple, powerful and rapid alternative approach for gaining insight into the historical structure and dynamics of modern small-mammal communities.

Keywords: conservation palaeobiology; taphonomy; live-dead analysis; baselines; Great Basin; small mammals

1. INTRODUCTION

To establish meaningful targets for conservation and restoration ecology, there is a critical need for baseline information on the status of ecological communities from before the onset of recent and rapid anthropogenic environmental change (National Research Council 2005). Typically, however, historical biological survey data that pre-date the onset of intense human activity are scarce, and the vast majority of available population assessments address current conditions shaped by a century of intense modification to the environment (Vitousek *et al.* 1997; Swetnam *et al.* 1999; Jackson *et al.* 2001; National Research Council 2005; Jackson 2007; Kidwell 2007; Jackson & Hobbs 2009). Thus we urgently need alternative sources of data to fill in the decadal to millennial-scale gaps in our knowledge of the histories of ecosystems. Here I show that, for communities of terrestrial small mammals, such data can be readily obtained from natural accumulations of their dead remains.

Insights gained from accumulations of skeletal remains ('death-assemblages') are limited only by the fidelity with which these modern, subfossil and fossil deposits reflect the structure of their contemporaneous living source communities. Establishing the magnitude and direction of such bias in death-assemblages serves as a foundation

for palaeoecological reconstruction and analysis (e.g. Kidwell 2001). Palaeoecologists have shown that naturally occurring death-assemblages are rich sources of ecological information in both terrestrial and marine systems alike (Behrensmeyer & Dechant Boaz 1980; Kidwell & Bosence 1991; Burnham *et al.* 1992; Sept 1994; Tappen 1995; Jackson & Kearsley 1998; Kidwell 2001, 2002; Behrensmeyer *et al.* 2003; Liebig *et al.* 2003; Lockwood & Chastant 2006; Olszewski & Kidwell 2007; Western & Behrensmeyer 2009). However, the implications of these results have typically focused on millennial to million-year time scales. Despite the urgent need to reconstruct more recent community responses to environmental change, the use of such archives to assess modern ecosystems has barely been explored (but see Kidwell 2007).

In this study, I combine ecological and palaeontological techniques to demonstrate that such critically needed biodiversity baseline data can be obtained from the modern skeletal and subfossil archives of the recent past—the last 100 years. More specifically, I use two fossil cave localities in the Great Basin deserts of North America to test whether small-mammal death-assemblages concentrated via raptor predation can provide historical baseline information on the temporal dynamics of community composition and structure equivalent to or exceeding the quality of modern surveys. The land-use histories of these two sites have diverged markedly in the last half century, with one site now located on a military test and training range that has been active since the mid-1960s. Using this comparative natural experiment, I then test the degree to which the ecological memory

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of dead remains can be used to detect and reconstruct the relatively rapid (decadal-scale) baseline shift that has occurred at the recently disturbed site. I independently validate this analysis using pre-disturbance historical trapping records. If small-mammal death-assemblages are to be useful in the reconstruction of historical baselines, then the time-averaged surface accumulation of skeletal remains must correspond to the historical trapping records at Homestead Cave, thus preserving the magnitude and direction of the observed baseline shift within the last century.

Natural accumulations of recent dead remains are common across landscapes worldwide and are easily collected in the field over the course of a single day. As such, these types of deposits are uniquely suited for biomonitoring surveys and the rapid establishment of historical baselines. By integrating skeletal remains into our biodiversity analyses through a merging of palaeontological and ecological techniques, we can begin to realize the important task of filling in the gaps in our temporal understanding of ecosystems and their communities.

2. STUDY SYSTEM

Small mammals are sensitive indicators of climatic change over both recent and palaeontological time scales (Brown 1995; Barnosky *et al.* 2003). Furthermore, small-mammals are considered the 'survivors' of the highly size-selective terminal Pleistocene extinction (Lyons *et al.* 2004). The Pleistocene extinction is of particular interest because it was the only other time in the Earth's history where novel anthropogenic pressures (e.g. hunting) intersected with climatic variability and warming (Koch & Barnosky 2006). Thus small mammals have much to tell us about community and ecosystem resilience in the face of modern and future environmental change.

Caves and rock shelters represent rich sources of small-mammal skeletal remains. Raptors (e.g. owls, hawks, eagles and falcons) often establish long-term roosts in such protected sites and regurgitate masses of hair (pellets) that include the undigested bones of their small-mammal prey. Raptor roosts can be active for decades to millennia, leading to significant build-up of skeletal remains (Andrews 1990). While these archives often incorporate skeletal remains from centuries to millennia into a single stratigraphic horizon ('time-averaging'), Terry (2008) showed that the majority of bones in a time-averaged assemblage come from a restricted window of time, increasing their use for examining population dynamics by an order of magnitude. Despite the potential for these deposits to yield high-quality data, evaluation of the ecological fidelity of small-mammal death-assemblages to their living source communities is virtually absent (but see Terry 2010). Previous explorations of such assemblages have been conducted without data from the local living community (Hadly 1999; Reed 2007). As a result, we have little insight into the general use of such time-averaged death-assemblages as sources of ecological baseline information.

Desert ecosystems are also considered to be sensitive indicators of environmental change. The Great Basin of the Western USA in particular is considered one of the

most threatened ecosystems in North America (Noss *et al.* 1995), as climate change, land use and invasive species continue to alter the structure and dynamics of native communities (Miller & Wigand 1994; Knapp 1996; Rowe 2007). By comparing two cave roosts in the Great Basin with similar taphonomic and geomorphologic histories, I control for variation in the accumulation and preservation of skeletal remains. Both caves were formed by wave incision during the highstands of Pleistocene pluvial lakes. When the lakes receded, they eventually became long-term roosts for large-bodied owls, accumulating stratified skeletal death-assemblages extending back through the Holocene (Hockett 1993; Madsen 2000; see the electronic supplementary material for details). Over the past century, however, the land-use histories of these two sites have diverged. Two Ledges Chamber, located on the western margin of the Smoke Creek Desert (NV), is currently characterized by limited anthropogenic activity and a diverse sagebrush steppe habitat. By contrast, the vicinity of Homestead Cave, located on the northern end of the Lakeside Mountains (UT) just west of the Great Salt Lake, has been used by the United States Air Force as a weapons test and operations training range since the mid-1960s (Powell 1994). Today this area shows high levels of landscape modification and has a plant community dominated by the invasive cheatgrass (*Bromus tectorum*). I use this contrast between taphonomically similar sites to test the degree to which palaeoecological techniques can be used to detect rapid and recent shifts in community baselines.

3. SOURCES OF DATA

My analyses compare data on small-mammal communities from (i) modern trapping surveys with (ii) skeletal remains recovered from three different stages in the natural dissociation process of raptor pellets: samples from modern intact pellets, the time-averaged surface debris and late Holocene fossil deposits. At Homestead Cave, I also compare these data from skeletal remains with (iii) historical trapping records from 1950 to 1968.

(a) *The modern living community*

'Modern live' trapping surveys were conducted semi-annually for 3 years at both Homestead Cave (2004–2005, $n = 200$ total captures) and Two Ledges Chamber (2005–2007, $n = 652$ total captures) (table S1 in the electronic supplementary material). Trapping employed a targeted transect approach with lines of 25–30 traps established and revisited in all microhabitats present within 0.5 km of each cave entrance. Sherman Live Traps, Museum Specials and Victor Rat Traps were used, and were double-baited with a peanut butter-oat mixture and with bird seed. Each survey lasted for four nights (one survey at Homestead Cave (December 2004) was three nights owing to inclement weather), with traps checked in the early morning and reset in the late afternoon. Trap success rates ranged from approximately 5 to 45 per cent. Specimens caught in live traps were marked before release to avoid re-counting. Trap types differ in their success rates for catching different species (Pizzimenti 1979; Drickamer & Mikesic 1993; Wilson *et al.* 1996), and were deployed in varying proportions within a given survey. I therefore standardized

species-specific catch data to an equal number of each trap type using the probability of catching each species in each trap type (Terry 2010; see the electronic supplementary material for details).

(b) *Natural archives of the dead*

'Modern dead' data were collected from fresh intact raptor pellets that rained down on cave floors between trapping surveys. Comparing the modern live and dead communities is necessary to test for bias in the death-assemblage owing to predator selectivity. Pellets were collected semi-annually from 2004 to 2005 at Homestead Cave and 2005 to 2007 at Two Ledges Chamber (table S2 in the electronic supplementary material). All pellet debris found below each roost was removed prior to the initiation of semi-annual pellet collections, thus modern dead data reflect time-averaging over only 3–12 months. Pellets were frozen for two weeks, soaked in water and dilute hydrogen peroxide to loosen the hair, then manually separated using forceps and a magnifying lens. Skeletal remains were passed through nested screens (one-quarter, one-eighth and one-sixteenth of an inch = 6.4, 3.2 and 1.6 mm, respectively) to separate size fractions. Craniomandibular elements, humeri, femora and tibiae from the 6.4 and 3.2 mm size fractions were identified to species by comparison with reference material in combination with species-specific measurements of skeletal features (Homestead Cave: $n = 481$; Two Ledges Chamber: $n = 2778$ total identified specimens). The minimum number of individuals (MNI) of each species in a sample was calculated by incorporating information on side (left versus right), breakage and age (juvenile versus adult).

'Historical dead' data were collected from replicate bulk samples (approx. $25 \times 25 \times 1\text{--}2$ cm) of skeletal debris and partially dissociated pellets swept from the cave floors at the start of this study (table S2 in the electronic supplementary material). At Two Ledges Chamber, pellet debris on the accumulation surfaces had previously been collected in 1988–1989 by Hockett prior to his excavation of the site (Hockett 1991). The historical dead samples thus reflect 20 years of time-averaged pellet rain. At Homestead Cave, 18 of 20 dated bones from the surface debris provided accelerator mass spectrometry (AMS) ^{14}C dates of no older than 50 years before present (BP; with the remaining two bones at 75 ± 35 and 220 ± 35 ^{14}C years BP). These historical dead samples thus reflect time-averaging on the order of 50 years (table S3 in the electronic supplementary material). Samples were frozen for two weeks, passed through nested screens (see above), then picked manually to separate skeletal material from any remaining host sediment. Any material still bound up in pellet hair was processed wet (see above) and re-screened. Identification of skeletal remains and generation of MNI estimates followed the same procedure as used for modern pellets described above. (Homestead Cave: $n = 1128$; Two Ledges Chamber: $n = 2023$ total identified specimens.)

'Fossil dead' data from Two Ledges Chamber were generated from material excavated by Hockett in 1993. Skeletal specimens from samples from the top two levels of the record were screened to separate out size fractions (6.4 and 3.2 mm only), then identified and counted as

above (table S2 in the electronic supplementary material). AMS ^{14}C dating of five bones from these top two levels indicates that samples are time-averaged over approximately 300 years (oldest date = 300 ± 35 ^{14}C years BP; table S3 in the electronic supplementary material). Fossil specimens from Homestead Cave (6.4 and 3.2 mm size fractions) were originally collected by D. K. Grayson in 1993 and, based both on AMS and conventional radiocarbon dating, represent approximately 800 years worth of averaged time (1020 ± 40 to 1854 ± 47 ^{14}C years BP; Madsen 2000). Because left–right data were not collected for the original analysis of these samples, MNI estimates were generated by dividing counts of skeletal elements by the number of times that skeletal element appears in the mammalian body (e.g. femora count/2). (Homestead Cave: $n = 11132$; Two Ledges Chamber: $n = 1885$ total identified specimens).

(c) *Historical trapping records: an independent test*

The Great Basin has a long history of research on the biogeography and ecology of mammals, generating a wealth of historical trapping data preserved in natural history collections. I used this 'historical live' data as an independent assessment of the reliability of historical data generated from time-averaged skeletal remains at Homestead Cave. To do this, I obtained a total of 219 historical records from the last 60 years within a 50 km radius of Homestead Cave through the Mammal Networked Information System (MaNIS—<http://manisnet.org>; table S4 in the electronic supplementary material) that met the following criteria: (i) more than three individuals present per site; and (ii) locality elevation below 1463 m (to ensure desert habitat). These records were collected from 1950 to 1968, thus they represent a sample of 'live' data from just prior to and overlapping with the intensification of anthropogenic disturbance around Homestead Cave. The Utah Test and Training Range that surrounds Homestead Cave was completed and became active in 1964 (Powell 1994).

4. ANALYTICAL APPROACH

I employ a 'live–dead' approach developed by palaeoecologists to compare community information from modern surveys ('modern live') to the three different sources of 'dead' data at each cave: modern, historical and fossil. Using this set of live–dead comparisons, I assess five well-known community metrics of applied ecological interest: (i) species richness (number of species, using rarefaction curves following Raup (1975)); (ii) evenness (the uniformity of the distribution of taxonomic abundances, using probability of interspecific encounter (PIE) following Hurlbert (1971)); (iii) taxonomic composition (species presence/absence, using the Jaccard Similarity Index with sample-size standardized data, following Magurran (2004)); (iv) species rank abundance (using Spearman's rho, following Sokal & Rohlf (1995) and Davis (2002)); and (v) species proportional abundance (using the Bray–Curtis Similarity Index with sample-size standardized data, following Gotelli & Ellison (2004), which is sensitive to both species presence/absence and relative abundance).

At Homestead Cave, I also compare the historical live data to the community as reconstructed from the

Figure 1. Rarefaction analysis for (a) Two Ledges Chamber and (b) Homestead Cave. (a) Analyses indicate that at Two Ledges Chamber, pooled data from modern trapping surveys (modern live), modern pellet collections (modern dead) and replicate bulk samples of the time-averaged surficial death-assemblage (historical dead) are indistinguishable from one another in terms of species richness and evenness at this relatively undisturbed site. (b) By contrast, at Homestead Cave, a site characterized by significant anthropogenic impact, both modern live and modern dead data are species poor and highly uneven relative to samples of the historical dead. Blue, historical dead; green, modern dead; yellow, modern live.

Table 1. Rarefied richness (*S*) and evenness (PIE) $\pm$ 95% CI for samples pooled by data type.

data type	Two Ledges Chamber		Homestead Cave	
	<i>S</i> (<i>n</i> = 100)	PIE	<i>S</i> (<i>n</i> = 100)	PIE
modern live	10.5 $\pm$ 1.4	0.78 $\pm$ 0.07	4.9 $\pm$ 0.6	0.45 $\pm$ 0.12
modern dead	10.4 $\pm$ 1.4	0.81 $\pm$ 0.04	6.9 $\pm$ 0.3	0.65 $\pm$ 0.07
historical dead	11.7 $\pm$ 1.8	0.81 $\pm$ 0.04	9.5 $\pm$ 1.7	0.79 $\pm$ 0.04
historical live	—	—	10.4 $\pm$ 1.9	0.78 $\pm$ 0.07

historical dead. This comparison allows me to independently assess the degree to which the data from dead remains accurately capture the magnitude and direction of the observed community baseline shift at this site.

5. RESULTS

Modern live and dead samples from Two Ledges Chamber show high similarity to one another in species richness, evenness (figure 1a and table 1), and taxonomic composition (figure 2a and table 2). Agreement between modern live and dead species lists is statistically indistinguishable from the average taxonomic similarity of repeated modern live surveys ($p > 0.99$, Tukey HSD). This also holds true for the rank order abundance of species (non-parametric Spearman rank tests, $p = 0.86$; table 2), and for their proportional abundances (Bray-Curtis Index, $p > 0.99$; figure 2c; table 2). High live–dead agreement persists at this site for all ecological metrics even as the temporal extent of the live–dead comparisons is expanded to include time-averaged historical dead and fossil dead samples (figure 2a,c and table 2).

By contrast, richness and evenness at Homestead Cave are both significantly higher in the historical dead samples than in the modern live and modern dead data (figure 1b and table 1). Modern live and dead species lists at Homestead Cave show high taxonomic similarity indistinguishable from levels found both at Two Ledges Chamber and between repeat live surveys at Homestead Cave

($p = 0.84$ and 0.99 , respectively; figure 2b and table 2). However, similarity of species’ proportional abundances decreases markedly between modern live–live and modern live–dead comparisons at Homestead Cave ($p = 0.02$; figure 2d and table 2). Taxonomic similarity also decreases dramatically when the modern dead species list at Homestead Cave is compared with historical and fossil dead samples (all $p < 0.05$; for Bray-Curtis modern dead versus historical dead $p = 0.104$; modern dead versus fossil dead $p = 0.003$; figure 2b,d and table 2). Spearman rho metrics of rank order agreement are unreliable for species lists as short as the modern community at Homestead Cave, and thus are not included (Kowalewski *et al.* 2003).

6. DISCUSSION

The agreement between modern live and modern dead data at Two Ledges Chamber is remarkable given the array of biological and taphonomic factors that could decrease the ecological fidelity of skeletal remains to their living source community. While predators and traps are in no doubt selective at some level, the agreement between modern live surveys and the community reconstructed from modern owl pellets is indistinguishable from the agreement found between repeat surveys of the living community (figure 2a,c). Thus the variability observed in live–dead agreement of modern samples is within the range of variation expected owing to

Figure 2. Live–dead agreement for all pairwise comparisons at (a,c) Two Ledges Chamber and (b,d) Homestead Cave. All comparisons are shown relative to modern live samples. Boxplots represent the median, upper and lower quartiles, with boxplot width proportional to sample size. Whiskers include the most extreme values within 1.5 times the interquartile range. Comparison tables next to graphs show significance of Tukey HSD posterior pairwise comparisons following analysis of variance. * $p < 0.05$; ** $p < 0.01$. (a,b) Taxonomic similarity (Jaccard Index). (c,d) Proportional abundance similarity (Bray–Curtis Index). All metrics reveal consistently high live–dead agreement across the range of temporal comparisons at Two Ledges Chamber. Modern live–dead mismatch in proportional abundance at Homestead Cave reflects a predation/trapping bias. Agreement also drops as the temporal depth of the comparisons increases at Homestead Cave, suggesting community change over time. ML, modern live (trapping surveys); MD, modern dead (modern pellets); HD, historical dead (time-averaged surface samples); FD, fossil dead (late Holocene strata); HL, historical live (historical trapping records).

Table 2. Mean $\pm$ 95% CI (calculated on the s.e.m.) and median (in parentheses) live–dead agreement for all possible pairwise comparisons to modern live data. All comparisons were sample-size standardized to the smaller sample.

data type	Two Ledges Chamber			Homestead Cave	
	Jaccard	Spearman	Bray–Curtis	Jaccard	Bray–Curtis
modern live	0.69 ± 0.08 (0.67)	0.42 ± 0.08 (0.49)	0.58 ± 0.06 (0.57)	0.63 ± 0.18 (0.60)	0.80 ± 0.05 (0.79)
modern dead	0.68 ± 0.04 (0.67)	0.36 ± 0.09 (0.42)	0.57 ± 0.03 (0.58)	0.69 ± 0.13 (0.60)	0.50 ± 0.16 (0.60)
historical dead	0.61 ± 0.03 (0.62)	0.49 ± 0.04 (0.49)	0.61 ± 0.02 (0.62)	0.49 ± 0.06 (0.50)	0.35 ± 0.03 (0.35)
fossil dead	0.56 ± 0.03 (0.56)	0.52 ± 0.12 (0.52)	0.52 ± 0.04 (0.51)	0.46 ± 0.06 (0.50)	0.22 ± 0.02 (0.22)
historical live	—	—	—	0.46 ± 0.09 (0.38)	0.38 ± 0.09 (0.39)

fluctuations in the living community and sampling error of modern surveys. Predator selectivity at this site is neither strong enough to exclude species from the diet of the raptors completely, nor does it substantially alter the community composition and species abundances in the death-assemblage. Furthermore, community composition and structure at Two Ledges Chamber show excellent agreement across the full temporal extent of live–dead comparisons (from decades to centuries). This is despite the greater time-averaging of the historical and fossil dead samples. These results suggest that the small-mammal fauna at this relatively ‘pristine’ desert location has shown marked stability over the last century.

At the recently disturbed Homestead Cave site, however, the modern small-mammal community is species poor and highly uneven compared with its recent past (figure 1a). While the similarity of modern live and dead species lists is high and within the range seen between repeat modern trapping surveys, agreement drops when species abundance information is included (figure 2b,d). This suggests a stronger predator or trapping bias that may arise at Homestead Cave because of its shorter species list, less even distribution of species abundances, and/or the avoidance of specific habitats

(such as dense cheatgrass) during hunting by the raptors. Whatever the underlying cause, the raptors at Homestead Cave select species from the modern living small-mammal community in different proportions than are caught by trapping. However, this selectivity is not strong enough to result in species being completely excluded from the raptor’s diet.

As comparisons with the modern live community at Homestead Cave are expanded to include historical and fossil dead data, live–dead agreement drops significantly (figure 2b,d and table 2). This is a strikingly different pattern than the relatively stable signal seen at Two Ledges Chamber, indicating a recent and rapid shift in the ecological baseline at Homestead Cave. Alternative taphonomic processes that could potentially drive this pattern are unlikely. In theory, owls might hunt outside of their local habitat, but studies using isotopic tracers have shown that raptors consume small mammals from within an approximately 7 km radius of their roost (Hadly 1999; Porder *et al.* 2003; Feranec *et al.* 2007). Furthermore, Terry (2010) has shown that the owls at Two Ledges Chamber provide a spatially integrated picture of the small-mammal community at the local scale. Thus, raptor-generated death-

Figure 3. Comparison of historical dead (time-averaged surface samples) and historical live data (historical trapping records) at Homestead Cave. (a) Rarefaction analysis of historical live data from 1950 to 1968 shows that richness and evenness are indistinguishable between historical live and dead samples. (b) Species proportional abundances are also remarkably similar in these two different sources of historical data, indicating that surficial death-assemblages (historical dead) contain high-quality ecological information on past living communities. Pink, historical live; blue, historical dead.

assemblages record a reliable local signal, especially for small-bodied taxa.

Occupation of Homestead Cave by different raptor species over time, particularly by diurnal hawks that preferentially hunt a different prey community owing to diel activity patterns, could also result in an apparent pattern of community turnover (Grayson 1981; Terry 2007). However, death-assemblages at Homestead Cave are consistently dominated by nocturnal small-mammal species and lack the taphonomic signatures of diurnal raptor predation (Terry 2007; see figure S2 in the electronic supplementary material for details). Evidence suggests, therefore, that the observed patterns of community restructuring are not artefacts of how the skeletal remains accumulated or how they were preserved, but instead reflect true biological signals of small-mammal community response to environmental change.

Figure 4. Rarefaction analysis of modern and historical trapping data, including 21 additional trapping records from 1995. Pooling the historical trapping data at a decadal scale indicates that the drop in richness and evenness occurred post late-1960s. Black, 1950s; dark brown, 1960–1964; light brown, 1966–1968; red, 1995; yellow, 2004–2005.

Pre-disturbance historical trapping records confirm the signal of an abrupt baseline shift in small-mammal community structure at Homestead Cave and provide a test of using skeletal remains to reveal the magnitude and direction of this shift. Results indicate that the time-averaged surface death-assemblage (the historical dead samples) provide a remarkable match in overall species richness and evenness to the historical living community of Homestead Cave (figure 3a and table 1; see electronic supplementary material for details). Furthermore, there is no significant difference in the taxonomic composition or the proportional representation of species between the historical live and historical dead communities ($p > 0.99$ and $p = 0.97$, respectively; figures 2b,d and 3b; table 2). Analysis of historical records by distance from the cave, as well as assessment of habitat heterogeneity using satellite land-cover data, indicate that spatial averaging is not a significant driver of these observed community-level patterns (see electronic supplementary material for details). Partitioning the historical live data by decades, and adding 21 more historical trapping records collected in 1995 (table S4 in the electronic supplementary material), further constrains the timing of the significant decline in richness and evenness at Homestead Cave: it occurred after the 1960s but before the mid-1990s (figure 4), bracketing with the completion of the military proving ground.

Unlike Two Ledges Chamber, the vegetation around Homestead Cave today is dominated by cheatgrass (*B. tectorum*). The spread of this annual invasive grass is a probable proximate driver of the observed baseline shift at this site. Cheatgrass is inferred to have spread to the area near Homestead Cave in the 1930s (Mack 1981), although when it became dominant is unknown. While anthropogenic activities on military proving grounds typically occur in localized areas, disturbance and fire regimes in this ecosystem were certainly altered—conditions that are well known to facilitate the spread of cheatgrass across the landscape (Mack 1981; Knapp 1996; Novak & Mack 2001). Heteromyid rodents,

which prefer open ground and move via saltatory locomotion, appear to have been negatively affected by dense grass cover at Homestead Cave (proportional abundances fell from 55% to 7% between historical dead and modern live samples (tables S1 and S2 in the electronic supplementary materials)). Concomitantly, the population of the habitat generalist *Peromyscus* spp. at Homestead Cave has thrived (proportional abundances rose from 21% to 72% between historical dead and modern live samples (tables S1 and S2 in the electronic supplementary materials)). Similar patterns have been noted at Camel's Back Cave, a Holocene deposit located on the Dugway proving ground approximately 80 miles to the south of Homestead cave (Schmitt 2004), as well as in several modern ecological studies of small mammals (Gano & Rickard 1982; Foster & Gaines 1991).

7. CONCLUSIONS

Today we are witnessing unprecedented rates of anthropogenic environmental change. Understanding how communities and ecosystems have responded to environmental pressure in the past is of the utmost importance for predicting how they are likely to respond in the future. This study demonstrates that modern and subfossil skeletal remains clearly retain an ecological memory owing to their time-averaged nature, and thus provide a simple, powerful and rapid means to obtain historical insights into community and ecosystem restructuring at precisely the time scales (decades to centuries to millennia) needed to inform long-term conservation and restoration efforts.

Despite their importance as indicators of ecosystem health and environmental change, the reliability of the ecological information recorded in the small-mammal fossil record has been poorly understood. This study shows that small-mammal skeletal death-assemblages accurately capture the composition and structure of their corresponding living communities. This has important implications for both neontologists and palaeontologists alike. For neontologists interested in non-invasive community survey methods, natural accumulations of skeletal remains offer a rapid viable alternative. For palaeontologists, the high fidelity of small mammal skeletal remains to their living source community indicates that ecological information can be extracted from fossil deposits with a high degree of confidence. Natural accumulations of predator-derived skeletal remains in caves and rock shelters are common worldwide and, given their relatively protected depositional setting, have a high potential for preservation in the permanent sedimentary record. Thus, not only can such sites provide information from historical times, excavation of older strata can yield additional insight into earlier pre-historic time periods characterized by dramatically different climate regimes, non-analogue communities and significantly lower human population densities. By unlocking these invaluable storehouses of information, we can better understand the natural range of variability for ecosystems and trace the origins, as well as the impacts, of recent climatic change and human activities on species and their communities.

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