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Evaluating the taphonomic consistency of microvertebrate assemblages at Natural Trap Cave, Wyoming, USA

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ABSTRACT

Paleontological sites composed of small vertebrate specimens can contain hundreds-of-thousands of identifiable fossils, which can reveal community responses to environmental and trophic changes. However, the composition of these communities may be skewed if the taphonomic signatures of the deposits change over time and across strata. Here, we discuss the taphonomic processes that led to dense deposits of microvertebrate fossils at Natural Trap Cave, Wyoming, USA. We then evaluate the nature and consistency of the taphonomic signature across stratigraphic layers using bone breakage rates and bone processing information. Natural Trap Cave is a pitfall cave that has an excellent record of vertebrate communities over the last 35,000 years. Along the North Wall of the excavation site, microvertebrate fossils form a dense accumulation, raining down from a packrat (*Neotoma*) nest located ~20 m above the floor of the cave. Using the breakage rates of micromammal limb bones, we evaluate whether the accumulation mechanism appears consistent across strata. We demonstrate that the variation in breakage rates from Natural Trap Cave's strata cluster together when compared to breakage rates for different predator types (mammalian carnivores, raptors, and owls). We then demonstrate that the variation in breakage rates from the three strata is less than would be expected if it were the result of a change in major predator type across the strata. Our analysis of depositional taphonomy at Natural Trap Cave provides confidence in the reliability of the microvertebrate community record, paving the way for future paleoecological analyses.

1. Introduction

A thorough examination of community composition through time can reveal local responses to specific events and the fundamental ecological principles that shape community compositions (Blois et al., 2010; Hadly, 1996; Terry, 2010a, 2010b; Terry et al., 2011; Terry and Rowe, 2015). An excellent microvertebrate fossil site (i.e., sites containing fossils of vertebrates with mass <5 kg) can contain hundreds of thousands of skeletal elements that accumulate over tens to hundreds of thousands of years (Barnosky et al., 2004; Toomey, 1993). When examining any new microvertebrate site, it is critical to demonstrate that observed changes in community through time are a reflection of changes in local environmental conditions, rather than an artifact of taphonomic biases (Andrews, 1990; Andrews and Nesbit Evans, 1983; Hadly, 1999; Terry, 2010a).

Here, we examine the microvertebrate communities of Natural Trap Cave, Wyoming. This fossil accumulation results from packrat (*Neotoma*) aggregation on a sill above the site and subsequent outwash, with occasional supplementation by individual falls (Williams, 2009). Packrats were the main depositional source for many late Quaternary sites that confidently use relative abundance data for microvertebrate community analyses (Barnosky et al., 2004; Blois et al., 2010; Hadly, 1996). Packrats are a source of secondary accumulation. They habitually collect bones, bird pellets, and carnivore scat from up to ~100 m of their nest (Betancourt et al., 1990; Hadly, 1999). In particular, *Neotoma cinerea*, the species found in the vicinity of Natural Trap Cave, is well known for this practice (Betancourt et al., 1990). Because it aggregates specimens from a variety of predators, a packrat accumulation more closely

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resembles the local faunal composition than any single predator accumulation (Hadly, 1999). Packrats store these specimens in or adjacent to their nests and periodically clean their nests of excess debris when it becomes crowded (Betancourt et al., 1990). However, the persistence of a particular packrat nest and the surface predators sampled by those packrats could change over millennia.

Here we assess whether depositional taphonomy (the means by which the bones were introduced into the fossil record) of the packrat-accumulated microvertebrates of Natural Trap Cave is consistent through time. To achieve this, we evaluate micromammal long bone breakage rates and acid etching to determine whether their taphonomic signatures are consistent through time. We are not trying to diagnose the exact taphonomic depositional information for these microvertebrate assemblages. Rather, the goal of this study is to assess whether the taphonomic signature is consistent enough across the strata that we can confidently assess paleoecological changes without worrying that changes in community assemblages come primarily from a major shift in predator selectivity.

2. Regional setting

2.1. Natural Trap Cave

Natural Trap Cave (NTC) is a 24-m-deep (80 ft) sinkhole cave located in Big Horn County, Wyoming east of the Big Horn River (Fig. 1). It has a single 8.5 m × 6 m diameter horizontal entrance that is difficult to see until one is quite near the edge, thus acting as a trap or pitfall for many large animals. Natural Trap Cave maintains a year-round temperature <5 °C, which provides an excellent preservational environment for bones as well as for genetic and isotopic materials. Sediments in Natural Trap Cave consist of wind- and water-borne deposits, several ashes, and roof fall (Lovelace et al., this issue).

In 2014, Julie Meachen and Alan Cooper resumed excavations in Natural Trap Cave with the primary goal of using modern techniques to recover ancient DNA and isotope information from recently excavated vertebrates. These excavations lasted 4 years and involved numerous volunteers from both the paleontological and the caving communities. Excavations by Meachen and others resumed again in 2021. During these excavations, we aim to create a complete picture of the environment and community around Natural Trap Cave, focusing on the last 35,000 years through many simultaneous lines of research (Grass et al., this issue; Higgins et al., this issue; Lovelace et al., this issue; Mahan et al., this issue; Meachen et al., 2016; Minckley et al., this issue; Mitchell et al., this issue; Redman et al., this issue; Schap et al., this issue; Spencer and Scott, this issue). Natural Trap Cave has incredible potential for providing insight into community dynamics across many important events in North American history and pre-history.

2.2. Taphonomic observations

Up until 1973, when a grate was fitted over the cave entrance, many large animals would fall into this “natural trap.” Very few of those animals, if any, were able to survive a 24-m fall, and even if they did, they would be unable to get back out of the cave (Wang and Martin, 1993). The megafaunal assemblage is interpreted as being an accumulative assemblage of the local community (Wang and Martin, 1993). The species accumulation curve of megafauna specimens flattened out after 10 years of sampling, indicating that the first round of excavations was sufficient to represent a complete assemblage (Wang and Martin, 1993). However, certain species are more likely to fall prone into this pitfall trap. For example, few short-faced bears or mammoths are present, but there are a large number of numerous cheetahs, lions, bighorn sheep, and horses of the genera *Equus* and *Haringtonhippus* (Grass et al., this issue; Heintzman et al., 2017; Redman et al., this issue).

Similarly, small animals fall into the cave at a fairly regular rate. From 2014 to 2017, we observed a small-animal fall rate of about six animals per year, and from 2018 to 2021, we observed a fall rate of about four animals per year (16 animals total found in 2021). Small animal falls primarily occurred in one of two “fall zones” (Fig. 2). Dead, mummifying animals in the cave consisted of snakes, packrats, deer mice, bluebirds, ravens, and rabbits. Both *Peromyscus maniculatus* (deer mice) and *Neotoma cinera* (bushy-tailed packrats) appear to either

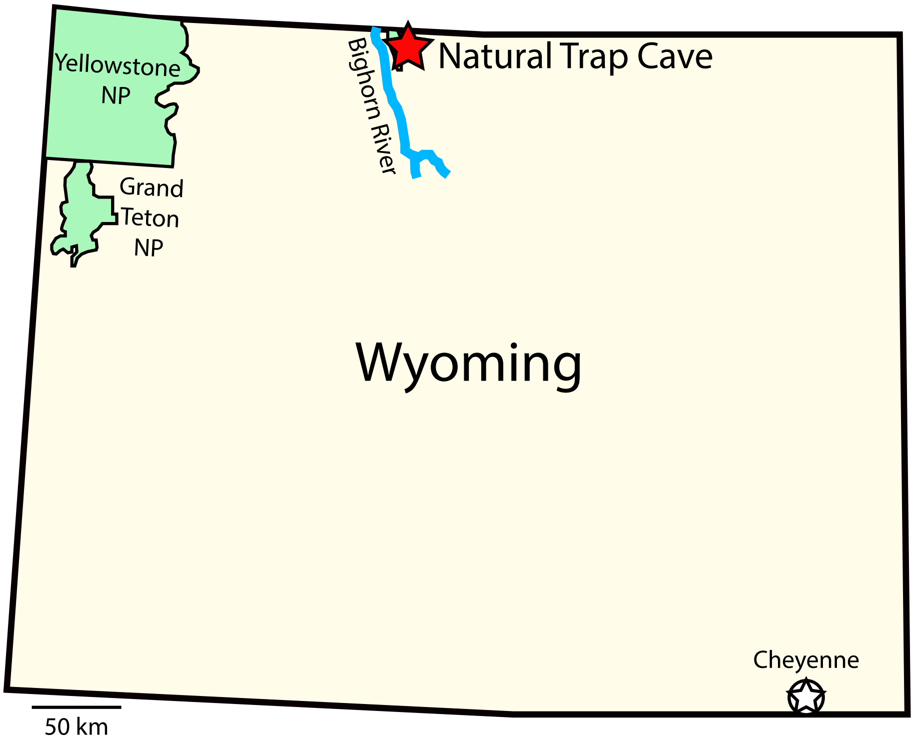

Fig. 1. Location of Natural Trap Cave, Bighorn County, Wyoming, USA.

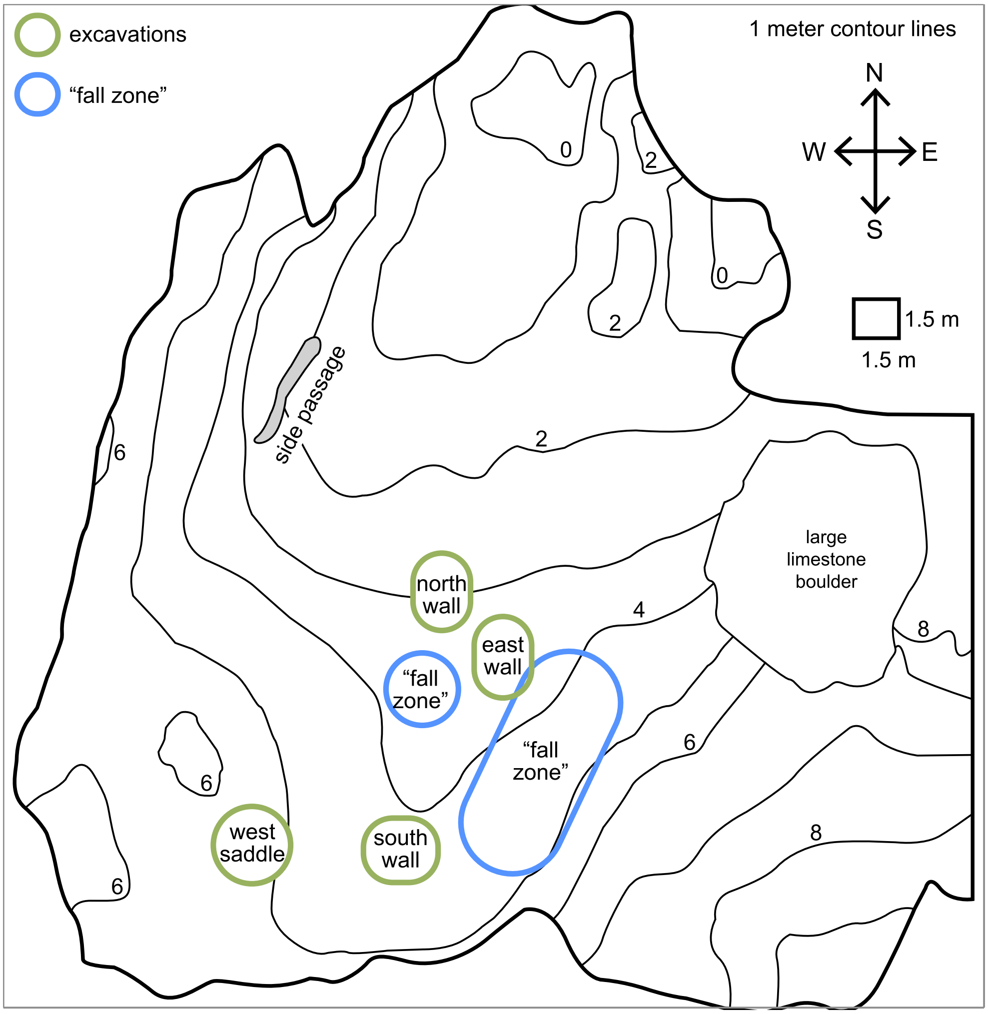

Fig. 2. A top-down map of Natural Trap Cave. The "fall zone" is where we most frequently find fallen microvertebrates. Specimens for this paper were collected from the north wall.

survive falls or enter the cave through an unknown entrance. Both these species have been found throughout the cave, and both species intermittently establish populations in the cave.

After evaluating microvertebrates from the previous excavations, Williams (2009) identified packrats as the primary means of bone concentration at Natural Trap Cave, supplemented by individual falls. To do so, Williams (2009) assessed the sizes and abundances of microvertebrate fossils, examined the fossils for wear, fragmentation, and gnawing, and classified weathering extents. Throughout these most recent excavations, we agree that this is the most likely explanation of the dense depositional pockets of microvertebrates. Packrat nests line the upper rim of the cave, with a notably large nest just above the microvertebrate-rich north wall of the cave (Figs. 2 and 3). Modern, active packrat middens are located ~20 m (65 feet) above the excavation pit (Figs. 2 and 3), and debris regularly rains down from these nests and into the excavation site. Upon re-opening the cave in 2021, packrat feces and debris from their nests were observed to lightly cover the surfaces of the tarps used to cover excavations along the north wall. All specimens evaluated herein were collected from strata in this portion of the cave, with packrat accumulation identified as the primary source of these accumulations. These north-wall strata visibly differ from the stratigraphy in the rest of the cave (see Lovelace et al., this issue for a detailed stratigraphic analysis), possessing little visible layering and exhibiting a relatively uniform dark brown-red hue. Characteristics of these strata include a large abundance of *Neotoma* fossils and coprolites found throughout. Also, based on identification of cranial material collected in these strata, community composition of the micromammals collected throughout these strata are most similar to the late Quaternary accumulations of Samwell Cave, California, also the result of packrat accumulation, when compared with two owl-accumulated Holocene fossil sites (see Schap et al., this issue). Although packrat middens built on ledges can be ephemeral, frequently washed away by rainstorms or abandoned by their occupants, the presence of active middens indicates the appropriate environmental conditions for frequent packrat reoccupation (Betancourt et al., 1990). However, others have also hypothesized that there may have been raven (Martin and Gilbert, 1978) or owl (Wang and Martin, 1993) nests along the rim of the cave, potentially contributing to deposition.

3. Materials and methods

3.1. Micromammal material from Natural Trap Cave

Natural Trap Cave microvertebrate specimens were collected during three field seasons from 2014 to 2016, over a total of 12 weeks. Excavation methods closely aligned with those of the previous excavations (Martin and Gilbert, 1978), using a 1.5 × 1.5 m archeological grid system. Matrix has been collected from three regions of the cave: the southeast portion of the pit, the northeast wall, and the north wall (Fig. 2). Matrix was screenwashed onsite in stacked sieves with a minimum screen size of 850 μm (20 mesh). Washed concentrate was then brought back to either the Georgia Institute of Technology or Des Moines

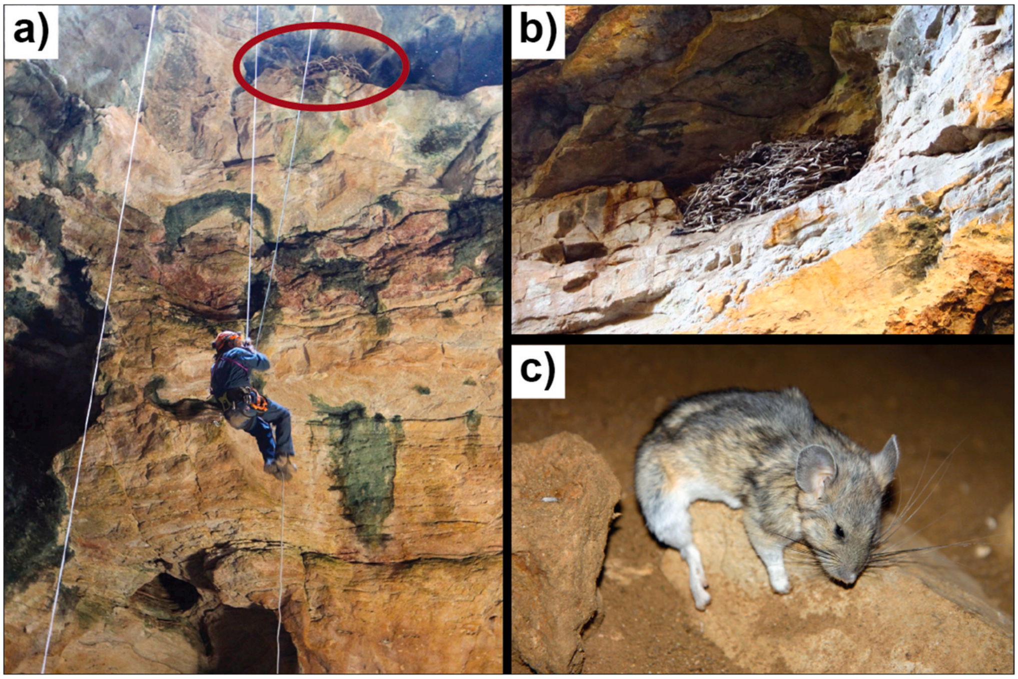

Fig. 3. Source material for north wall microvertebrate deposit. a) and b) *Neotoma* (packrat) nests located along the rim of Natural Trap Cave, just above the highest concentration of microvertebrate fossils (see Fig. 3). c) a fallen packrat (*Neotoma cinerea*).

University where microvertebrate fossils were systematically picked out of the matrix. In addition, 47 radiocarbon dates are associated with 2014–2017 excavations (Lovelace et al., this issue).

Only matrix from the north wall had sufficient concentrations of micromammal specimens for analysis (Fig. 2). Herein, we use 1061 micromammal limb bones collected from three stratigraphic layers along the north wall that have confident temporal resolution, as indicated by stratigraphic depths and radiocarbon dating: late Holocene (2.5-5ka; n = 582), middle Holocene (~7ka; n = 432), and late Pleistocene (~19.5ka; n = 47) (dates and dating methods described in Schap et al., this issue). All micromammal limb bones are identified only to Mammalia. Taxonomic identifications based on craniodental material include Anura, Aves, Serpentes, cf. *Phrynosoma*, Lagomorph, *Lemmiscus*, *Microtus*, *Neotoma*, *Peromyscus*, *Thomomys*, *Perognathus*, *Marmota*, *Cynomys*, and *Tamias* and are discussed elsewhere in this volume (Schap et al., this issue).

3.2. Limb bone breakage

We use limb bone breakage rates as a means of examining the taphonomic signature of the small mammal record. This has previously been done to identify the predator signature for microvertebrate-containing strata (Andrews, 1990; Terry, 2007). We adapt a method developed by Terry (2007) that uses long bone breakage rates from known predator assemblages to discriminate between three major predator types known to concentrate fossil specimens: mammalian carnivorans, owls, and raptors. This method uses the breakage rates of four individual long bone types (femur, humerus, tibia, and ulna). Although, we recognize that *Neotoma* serves as a primary collector, we wish to evaluate whether the breakage-based taphonomic signature of the main predators represented in the assemblage changes significantly between the three layers.

Although it may be concerning to use breakage rates at a fall site such as Natural Trap Cave, upon examination, recent fall specimens have exhibited no limb bone breakage. Given the relatively small body masses of the individual animals, the force with which a small animal hits the ground is rarely sufficient to cause limb bone breaks. Rather, the deaths of these fall-based microvertebrate specimens appear to be the result of soft tissue damage, hypothermia, or shock, based on our observations. As the famous evolutionary biologist, J.B.S Haldane (1926) once wrote, "You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away … A rat is killed, a man is broken, a horse splashes."

3.2.1. Predator signatures

To examine the predator signatures present in Natural Trap Cave specimens, we performed a discriminant analysis using the R package MASS (Venables and Ripley, 2002). Statistical analyses are performed in R (R Found, 2018) through RStudio (2016). We trained the discriminant analysis using known predator assemblage data from Terry (2007), supplemented with breakage data from raven pellets (Laudet and Selva, 2005) and data published since Terry (2007) (Table S1). Training data consist of the percent breakage rate of each of the four major limb bones (femur, humerus, radius, ulna) gathered by known predator species. Each predator species is assigned to one of three predator types (mammalian carnivorans, owls, or raptors). Passerines (i.e., ravens) are excluded here because there is only one assemblage represented in our dataset. We then use this discriminant analysis to predict the posterior probabilities of predator types represented in the Natural Trap Cave layers.

Predator analyses are performed at the predator-type level, because, after a thorough literature review, we have determined that there are not sufficient studies performed at the predator-species level to assess the variation in intraspecific breakage rates. This is in agreement with previous analyses (Terry, 2007). To sufficiently discriminate between individual species' breakage patterns, one would need many independent samples of breakage rates attributable to each predator species. For a more in-depth analysis and discussion of discriminant analyses, sample sizes, and statistical strength see McGuire (2011).

3.2.2. Taphonomic consistency through time

Next, we assess whether there is an apparent change in taphonomic signature in the Natural Trap Cave specimens between our three stratigraphic layers (late Holocene, middle Holocene, and late Pleistocene;

Table S2). To do this, we use the breakage rates of assemblages gathered by known predator types (mammalian carnivorans, owls, and raptors) to examine two complementary hypotheses.

First, we tested the hypothesis that the three Natural Trap Cave layers possess the equivalent variance in breakage rates as a single predator type (either mammalian carnivorans, owls, or raptors). We created a distribution of variation in breakage rates that would be expected to occur if three assemblages were gathered by the same predator type. To calculate variation, we randomly draw three assemblages from a single predator type and calculate their average Euclidean distances. This is a calculation of the spread of the points. We calculate the variation between three known assemblages because we are comparing them to fossil assemblages from the three layers at Natural Trap Cave. We resample with replacement 10,000 times to create the distribution.

Simultaneously, we test the hypothesis that all three Natural Trap Cave layers result from at least two predator types. To do so, we created a distribution of variation in breakage rates that would be expected to occur when three assemblages from more than one predator type were randomly drawn. Again, we calculate the variation between three known assemblages because we have fossil assemblages from three layers at Natural Trap Cave. To calculate variation, we calculate the average Euclidean distance of breakage rates between three assemblages randomly drawn from two or three of the predator types, including all predator-type combinations. We resample with replacement 10,000 times to create a null distribution. By directly comparing these complimentary breakage rate distributions, we can assess the likelihood that fossils from Natural Trap Cave contain the breakage signature of a single predator type rather than multiple predator types.

3.3. Acid etching and gnaw marks

As is often requested for taphonomic analyses, we also examine the same set of limb bones for indications of acid etching and/or gnaw marks using a light microscope at 100× magnification. This additional information is intended to provide additional context. Specifically, owl-predated long bones typically exhibit less damage from stomach acid than those processed by raptors or mammalian predators (Andrews, 1990). Gnaw marks can be indicative of either predation or packrat-caused damage.

4. Results

4.1. Specimen breakage rates and predator contributions

If we average the breakage rates of all long bones examined, owls break very few long bones while eating (mean = 20% broken) and mammals and raptors break the most long bones (means = 81% and 86% broken, respectively). The single raven sample is most similar to owls (mean = 49% broken; owl posterior probability = 0.90; Fig. 4). The three stratigraphic layers at Natural Trap Cave exhibit 79–89% breakage rates (Table 1). Posterior probabilities indicate that these layers group most closely with mammals or raptors, although these two predator types are indistinguishable using breakage rates alone (Table 1; Fig. 4). We can, however, confidently reject a previously proposed hypotheses that these specimens might represent owl assemblages (Wang and Martin, 1993). Given current data, it seems unlikely that they result from raven assemblages either (Martin and Gilbert, 1978), though more raven breakage data are necessary to confidently reject this hypothesis (Fig. 4).

4.2. Consistency in predator signatures

We created two resampled distributions, one depicting the variance in breakage that would result from a single predator type (either mammalian carnivorans, owls, or raptors). This distribution was created by randomly sampling three assemblages gathered by the same predator type and has a mean variance in breakage rate of 1.77 (sd = 0.55). The variance in breakage rates between Natural Trap Cave's stratigraphic layers (NTC variance = 1.57) is not significantly larger than the variance in breakage rates of three assemblages from the same predator type ($p = 0.47$; Fig. 5). We then compare the single-predator-type distribution with a multiple-predator-type distribution. This distribution was created by randomly sampling three assemblages gathered by at least two different predator types and has a mean variance in breakage rate of 3.40 (sd = 0.87). When predator combinations are drawn from multiple predator types, limb bone breakage rates result in higher variation than

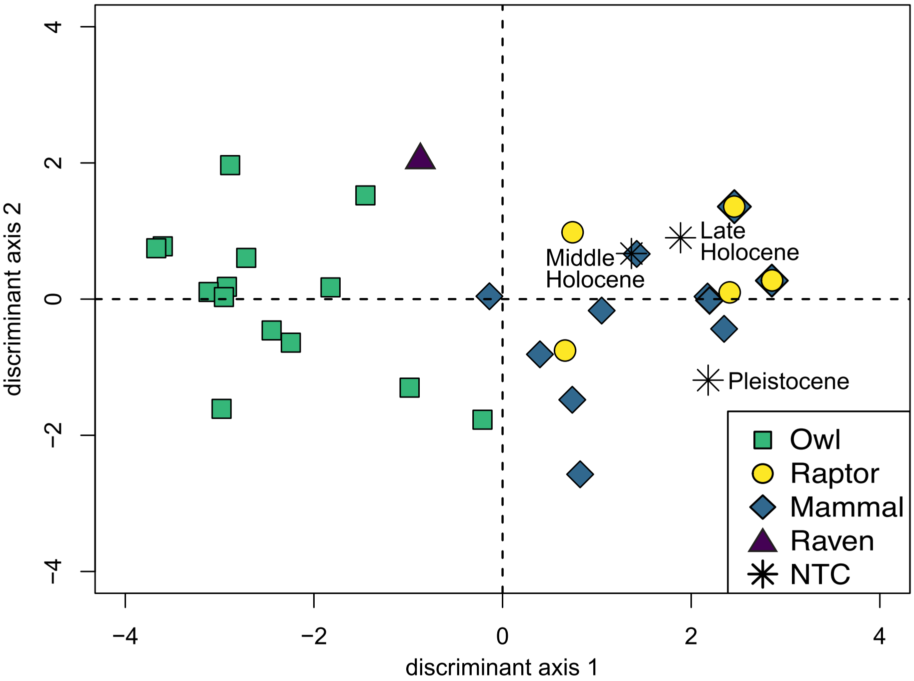

Fig. 4. Two discriminant axes trained using the breakage rates of modern limb bone elements collected from the scat and pellets of known predators (Table S1). Natural Trap Cave (NTC) specimens cluster with mammal and raptor deposits and clearly away from owls or the raven.

Table 1

Natural Trap Cave limb bone breakage data. Sample sizes of limb bones analyzed for each stratigraphic layer; breakage rates of limb elements for each stratigraphic layer; mean breakage rate of all limb elements; and the posterior probability of the predator source for each stratigraphic deposit based upon the discriminant analysis. Note that raptors and mammals are not distinguishable based on the data presented.

	sample sizes	prevalence of broken				mean breakage	mammal posterior probability	raptor posterior probability
		humeri	ulnae	femora	tibiae			
Late Holocene	582	84%	90%	83%	93%	87%	0.51	0.49
Mid Holocene	432	80%	83%	71%	83%	79%	0.61	0.39
Pleistocene	47	100%	67%	100%	88%	89%	0.75	0.25

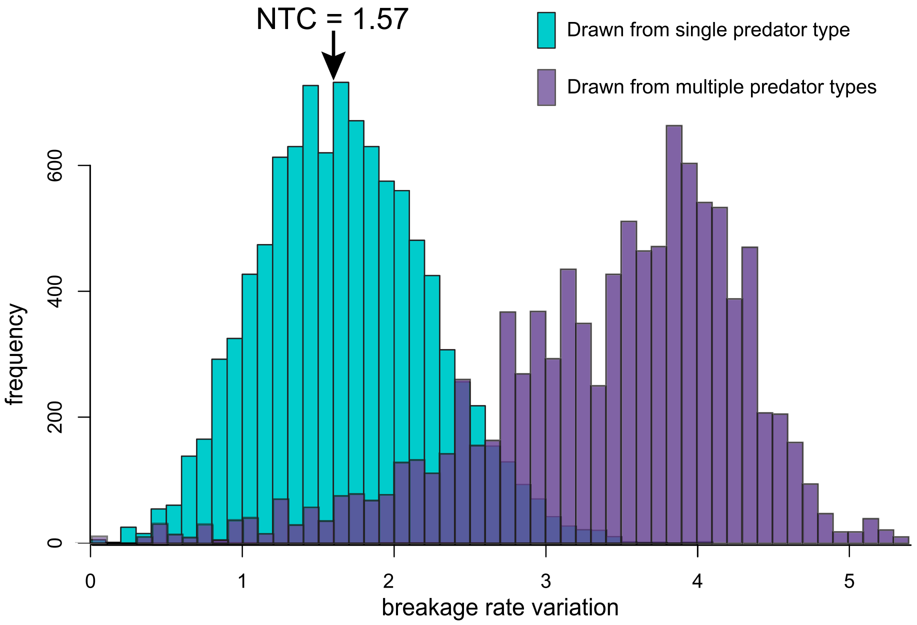

Fig. 5. Breakage rate variation is most consistent with a single predator type resulting in Natural Trap Cave (NTC) microvertebrate accumulations. The teal curve (left) depicts the variation in breakage rates resulting from randomly sampling three assemblages gathered by the same predator type. The purple curve (right) depicts the variation in breakage rates resulting from randomly sampling three assemblages gathered by predators representing at least two different predator types. When predator combinations are drawn from multiple predator types, limb bone breakage rates result in higher variation than is found at Natural Trap Cave 94% of the time. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

is found at Natural Trap Cave 94% of the time (Fig. 5). When compared to these two curves, we see that breakage rate variation is most consistent with a single predator type resulting in the Natural Trap Cave microvertebrate accumulations (Fig. 5).

4.3. Acid etching and gnaw mark prevalence

Evidence of acid etching was found on 76% of limb bones examined, including 88% of femora, 63% of tibiae, 80% of humeri, and 63% of tibiae (Table 2; Table S2). According to past work on North American predators, the few evaluations of raptor digestive effects demonstrate an average of 81% of digested femora (Andrews, 1990: kestrel = 82%; Armstrong, 2016: bald eagle = 80%). For mammals, the average percent of digested femora is 56% (Andrews, 1990: coyote = 67%, red fox = 50%, pine marten = 50%; Armstrong, 2016: coyote = 100%). For owls, the average percent of digested femora is 16% (Andrews, 1990: barn owl = 11%, snowy owl = 12%, long-eared owl = 14%, short-eared owl = 11%, great grey owl = 18%; Armstrong, 2016: great horned owl = 18%). Again, although we can confidently say that these limb bones are unlikely to have resulted from owl digestion, given inter- and intra-specific variation, it is impossible to distinguish between mammalian carnivorans and raptors. Finally, gnaw mark prevalence varied from 42% in large limb bones (femora and humeri) to 19% on the less robust limb bones (ulnae and tibiae).

5. Discussion

Breakage rates and bone processing evidence of Natural Trap Cave's micromammals indicate that the fossils are likely the result of a mammalian predator and/or raptor predators whose prey remains were secondarily concentrated by packrats (Schap et al., this issue; Williams, 2009). With the addition of more predator limb bone breakage rates, we can no longer confidently discriminate mammalian predators and raptors (unlike Terry, 2007). However, by evaluating the variances in breakage rates within and between predator types, we are able to determine that a predator signature is relatively consistent across the stratigraphic layers of Natural Trap Cave.

Natural Trap Cave's microvertebrate accumulations cannot be confidently assigned to any single predator type based upon long bone breakage rates alone. Breakage rates from all three stratigraphic layers group with mammalian carnivores and raptors (Table 1). The inability to distinguish between these predator types results from the combination

Table 2

Natural Trap Cave acid etching and gnaw mark prevalence.

	sample sizes	acid etching prevalence				gnaw mark prevalence			
		humeri	ulnae	femora	tibiae	humeri	ulnae	femora	tibiae
Late Holocene	582	83%	75%	86%	74%	54%	23%	40%	19%
Mid Holocene	432	76%	79%	79%	72%	47%	12%	35%	36%
Pleistocene	47	80%	67%	100%	44%	50%	11%	25%	19%

of a high variance in mammalian carnivore breakage rates and a relatively small sample size of raptor species' breakage rates. However, the breakage rates of owls and ravens are distinctly different from those of the Natural Trap Cave layers (Table 1; Fig. 4), contrary to previous suggestions (Martin and Gilbert, 1978; Wang and Martin, 1993). Both ravens and owls minimally process their prey, often swallowing them whole (Andrews, 1990; Laudet and Selva, 2005). As a result, both these predators have lower breakage rates than were observed in any of the layers or elements found in the Natural Trap Cave deposits.

Variation in breakage rates in Natural Trap Cave's three depositional layers is sufficiently low to suggest that predator signatures have remained relatively stable over time (Fig. 5). In fact, the variation in breakage rates falls solidly within the normal range of variation calculated from three assemblages drawn from a single predator type (mammalian carnivore, raptor, or owl), implying that the main predator signature likely results from either mammalian carnivores or raptors, but not both. The variance of 94% of the assemblages drawn from multiple predator types is higher than the variance of bone breakage rates of these three layers. This indicates that we can have confidence that the relative abundances of microvertebrates represent true ecological responses rather than a shifting predator signature.

The relatively high prevalence of acid etching confirms the finding that the Natural Trap Cave microvertebrate assemblages are likely the result of mammalian carnivorans or raptors. While raptors exhibit higher levels of acid digestion than owls (Duke et al., 1975, 1976; Terry, 2007), mammalian carnivorans process bones through the entirety of their digestive tracts (Terry, 2007). However, it is nonetheless difficult to distinguish between mammalian carnivorans and raptors based on acid etching (Andrews, 1990; Andrews and Nesbit Evans, 1983; Terry, 2007). Long bones from Natural Trap Cave do exhibit a relatively consistent prevalence of acid etching except for Pleistocene tibiae (Table 2).

Using taxonomy, it is difficult to discriminate between community changes that result from paleoenvironmental change versus a change in predator identity. One strength of this approach is that, by using limb elements, it is independent of taxonomic identity, so that any environmentally-driven shifts in species composition remain independent of the taphonomic analyses. Simultaneously considering the breakage rates of these individual long bones provides a nuanced means for discriminating between predator types, because the predators differentially process different limb elements (Andrews, 1990; Terry, 2007). However, this method is not yet sufficient to statistically discriminate specific predator type, nor is it yet able to fully and consistently discriminate between mammalian carnivorans and raptors as primary predators.

A full analysis of the taphonomic processes that resulted in the deposition of the microvertebrate fossils of Natural Trap Cave from initial death, to accumulation and transport, to burial and preservation is beyond the scope of this paper. However, some work to this end is in the works. We have collected a recent packrat midden from the surface adjacent to the cave, which we can use to assess the extent to which the microvertebrates on the north wall of Natural Trap Cave represent extant midden collections versus individual fall. Additionally, we are performing a mark-recapture study adjacent to the cave to assess the relative abundances of modern taxa and compare them to the fossil abundances at Natural Trap Cave. Using these data, we can compare fossil communities, modern middens, and modern communities and assess biases. For now, however, we can feel confident that the stratigraphic layers possess a consistent predator signature that will allow us to confidently evaluate changes in community composition that may have resulted from environmental changes rather than shifts in predator preference.

6. Conclusions

Overall, we find that the taphonomic signature of Natural Trap Cave is relatively consistent through time. Changes in community composition can result from depositional taphonomy or from community responses to environmental changes. Here, we demonstrate a framework for establishing confidence in our ability to interpret the relative abundances of microvertebrates that have accumulated over long timescales. Having confidence in the depositional taphonomy of the site allows us to address fundamental ecological questions by observing the community responses of the species living around Natural Trap Cave as ecological and environmental changes took place.

Author contributions

Conceptualization, JLM; Methodology, JLM; Formal analysis, JLM; Data collection, JLM, CMR, JI, JAM, JMS, &; AW; Data Curation, JLM & AW; Visualization and Writing (Original draft), JLM; Writing (Review and editing) all authors; Funding acquisition, JAM, JLM.

Data availability

All data used in this research can be found in the affiliated supplementary table.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2022.02.009.

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