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Editorial

Natural Trap Cave, Wyoming, U.S.A. Records a Detailed Faunal, Floral, aDNA, Isotopic, and Geologic Record of the Late Quaternary

The late Pleistocene fossil site of Natural Trap Cave (NTC), Wyoming, U.S.A., has been producing fossils since its first scientific exploration in the late 1960s. This site is considered important among late Pleistocene sites in North America and is significant for several reasons. It is located just south of the confluence of the Pleistocene Cordilleran and Laurentide ice sheets, and the ice-free corridor between these two sheets that opened and closed several times over the late Pleistocene funneled fauna directly from Beringia to Natural Trap Cave. Therefore, this site holds a verifiable record of the fauna that came to North America from Eurasia and other points north, and may include some of the earliest, or latest individuals to do so (Meachen et al., 2016; Shapiro et al., 2004). Additionally, the preservation of the fossils at NTC has allowed the study of ancient DNA, including nuclear DNA, from several species that have only been found in mid-continental North America, including the American lion (*Panthera atrox*) (Barnett et al., 2009) and the American cheetah (*Miracinonyx trumani*) (Barnett et al., 2005) – only recently discovered in the Yukon (Zazula, pers comm.). The time frame captured by this cave encompasses several important climatic and ecological turnover events in the last million years, including the last glacial maximum, and the end-Pleistocene extinction events (Lovelace et al., 2023, this volume). Natural Trap Cave is also an exceptional site because of the sheer volume of fossils found there, including mammalian megafauna, microfauna from all vertebrate classes, invertebrates (mostly unstudied as of yet), and pollen. The accumulation of bones in the cave is so extensive that Wang and Martin (1993) suggested it would take over 100 years to excavate the entire deposit. The protected nature of this site also allows us to study the sediment and geology of the cave, including the deposition of the sediments, volcanic ashes in the cave, and the geological history of the cave's formation. This special volume lays the stratigraphic, taphonomic, and taxonomic groundwork for the many future analyses of environmental conditions that occurred over the past 44,000 years at NTC, and the ecological responses to those conditions.

NTC is located in north-central Wyoming, about 3 km south of the Montana border, on the western slope of the Bighorn Mountains on Little Mountain. It is a 24.5 meters-deep karst sinkhole in the Madison Limestone (Gilbert and Martin, 1984; Martin and Gilbert, 1978). The only entrance into NTC is through an oval-shaped opening on the surface, 8.5 $\times$ 6 m wide, into a bell-shaped entrance chamber, approximately 42.6 $\times$ 44.2 m in diameter. The entrance to NTC occurs in a shallow depression at the end of a long ridge, just after a small rise in the terrain, making the entrance to the cave deceptively hidden from view, and thus an excellent trap. The cave still acts as a natural trap for animals small enough to fit through the grate slats (added by the Bureau of Land Management (BLM) in 1971) and new "taphonomic" specimens are found every year, including packrats, deer mice, snakes, passerines, and rabbits (McGuire et al., 2023, this volume). The vertebrate fossils in NTC are late Pleistocene to early Holocene in age and yield radiocarbon dates between 2-9 and 23–47 cal ka BP (95% probability) (Lovelace et al., 2023, this volume). Most animals probably died on impact from the 24.5-m fall, but it is possible that some animals did not die immediately and succumbed to their wounds and starvation inside the cave. The cave was excavated in two major pulses: one from 1974 to 1985, and one from 2014-present. The fossils from both series of excavations are essential to the work conducted at NTC, and both excavation teams should be acknowledged for their work, as well as the Wyoming BLM that oversees the site. The excavational and collection history of NTC is well-documented in Meachen et al. (2022).

The works published in this special volume represent the myriad of projects that NTC provides for us to study, including the original excavations that took place from 1969 to 1985, and the second set of excavations that took place from 2014 through 2022. Most of the authors in this special volume have participated in fieldwork at NTC sometime between 2013 and the present, and this volume is the fruit of their labors.

The first article in this volume, by Lovelace et al. is a long-overdue treatise on the stratigraphy, providing an age-model of NTC. This work incorporates the original work of John Albanese, a geologist who worked in NTC in the 1970s and early 1980s, which was never previously published. This paper enmeshes the vision earlier scientists (1970s and 1980s crews) had of the cave's stratigraphy, combining all perspectives into the most accurate stratigraphic interpretation. It allows readers to incorporate data from then and now in the most functional way possible and makes a distinct blueprint for all stratigraphic work going forward at this important site. Additionally, it collates all the radiocarbon dates done on NTC specimens from the 1960s through today and creates a set of age models for the cave's sedimentary structures. Unfortunately, this work also has determined that the sediments in NTC are discontinuous and may not capture the Pleistocene-Holocene transition as completely as we would like. However, this work is seminal for this volume, and most of the other author teams penning articles in this special volume have cited Lovelace et al. (2023, this volume) herein.

The work by Mahan et al. (2023, this volume) adds to the work by Lovelace and colleagues by exploring the different age-determining techniques we can use from NTC in addition to radiometric dates. Mahan et al. (2023, this volume) use optically stimulated luminescence (OSL) dates, argon chronology, tephrochronology, and fission track chronology to better understand infilling of the cave through time.

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These techniques supplement direct radiometric dates on fauna to better resolve chronological age models. Mahan and her team confirmed that the sediments range from late Pleistocene to Holocene in age, and that the deposition in NTC was episodic and rapid, interspersed with lulls in deposition where water may have played a role in how sediments and fossils moved around or went missing. This confirms interpretations of NTC deposits as high-resolution snapshots of local environmental conditions and communities from across the late Quaternary. Additionally, this work examined the three ash samples currently known from the cave and determined these ashes may represent previously undocumented eruptions from the nearby Yellowstone caldera.

This work is followed by that of Schmitt et al. (2023, this volume) that examines zircon crystals from the ash layers at NTC. They investigated these ash layers to better refine the chronostratigraphy of the sediments at NTC. In concordance with Mahan et al. (2023, this volume), they found that one of the ash layers was from a volcanic eruption in Yellowstone approximately 138 ± 9 ka. They also found a younger ash dated to 111 ± 8 ka that likely came from Tuff of Cold Mountain Creek from the Central Plateau Member of Yellowstone. They concluded that the volcanic ashes from NTC have a high degree of usefulness to reconstruct the volcanic history at Yellowstone through the late Pleistocene.

As we move further into this volume, we shift from geology to biology. The papers by Redman et al. (2023, this volume), Schap et al. (2023, this volume), and McGuire et al. (2023, this volume) examine vertebrate abundance through time at NTC in megafauna and microfauna, respectively. Redman et al. (2023, this volume) uses the previously collected fossil specimens (1974–1985) housed at the University of Kansas to determine how rank abundance distributions (RAD) of large vertebrates change through time to assess the faunal stability at NTC through the late Pleistocene, and into the Pleistocene-Holocene transition. Additionally, taphonomic metrics were used to better understand depositional biases in the fossil record. This work found little bias in taphonomic processes, suggesting that all differences in RADs were due to ecosystem changes, and not taphonomic biases. Results show that large-bodied vertebrates at NTC remained consistent in species composition and did not change abundance structure prior to or during the last glacial maximum. The environment at NTC was consistently dominated by large open-habitat grazers, some of which are still on the landscape today (e.g., pronghorn antelopes and bighorn sheep).

Schap et al. (2023, this volume) and McGuire et al. (2023, this volume) examine similar questions in the microfauna of NTC. Schap et al. (2023, this volume) examines relative abundance, evenness, and richness of microfaunal species from three time-bins at NTC: late Pleistocene, middle Holocene, and late Holocene. They found that changes in community composition were not driven by species extirpations, but rather by abundances of each taxon examined. The late Pleistocene had high evenness and high standardized richness being driven by horned lizards (*Phrynosoma*), rabbits (Lagomorphs) and western pocket gophers (*Thomomys*). The middle Holocene was marked by high raw richness with the inclusion of prairie dogs (*Cynomys*) and pocket mice (*Perognathus*). Like the late Pleistocene, the late Holocene at NTC was also marked with high levels of evenness. Schap et al. (2023, this volume) determined that NTC most closely resembles Samwell Cave in California, as both cave deposits are better grouped by age, rather than cave location when compared with other similar cave deposits in the western U.S. McGuire et al. (2023, this volume) examine the taphonomic signatures of the microfauna from NTC. They examine bone breakage rates and look for evidence of digestion of microfaunal elements by predators across the same three time-bins used by Schap et al. (2023, this volume). McGuire and her team conclude that the large quantity of microfaunal fossils were collected and curated by the resident group of packrats that resides in the cave, similar to Samwell Cave. Unlike Samwell Cave, the NTC packrats lived high above the floor and have likely resided there for hundreds of millennia. When the packrat nests are flooded out, their treasures rain down upon the cave floor and are then preserved there in distinct faunal layers. McGuire and colleagues also determined that the breakage rates and types are consistent across time, suggesting that the community signals of the small vertebrates entombed in NTC, collected by the industrious packrats, are not affected by any shifts in predators. The predators who killed the NTC microfauna were likely mammalian carnivores or avian raptors but were unlikely to be owls or corvids.

Other papers in the special feature place populations of animals at NTC in the broader North American biogeographic context. The Laurentide-Cordilleran migration corridor and the fortuitous geography of NTC play a large role in the paper by Mitchell et al. (2023, this volume). His team used ancient (mitochondrial) DNA from the two genera of horses at NTC: *Equus* and *Haringtonhippus*, as well as camels (*Camelops*) to examine migration patterns and biogeographic relationships of the individuals from NTC to the same species in Beringia, and the rest of mid-continental North America. Results from this work highlights the importance of the location of NTC adjacent to the ice-free corridor, showing that the individuals from NTC were more closely related to individuals from Beringia than to individuals nearby in Nevada or Idaho. These results comport with those from another genetic study on bison (Shapiro et al., 2004), and a morphological study of wolves (Meachen et al., 2016) that suggest these species were also migrating from Beringia to what is now the lower 48 U.S. states, passing through NTC on their way to points south.

Another species that likely moved between the ice-free corridor and one of the most common, and interesting carnivores found at NTC is the American Cheetah (*Miracinonyx trumani*). This extinct cat has been postulated to be the reason for speed in living pronghorn antelopes (*Antilocapra americana*) (which are also found in some abundance at NTC). The abundance of both *Miracinonyx* and pronghorns at NTC made this site a prime test spot for this just-so story, which Higgins et al. (2023, this volume) presents here. Using stable carbon and nitrogen isotopes, a proxy for diet, Higgins and her team show who is eating whom at NTC. Unfortunately, the just-so stories are much simpler and more straightforward than reality. The data in Higgins et al. (2023, this volume) suggest that American cheetahs were eating pronghorn antelopes – but they were also eating other species too, such as the local horses and the occasional bighorn sheep. Additionally, they were not the only species partaking in the pronghorn buffet. American lions (*Panthera atrox*) also show a strong signal of pronghorn in their diet as well. These data suggest that pronghorns were a favorite of multiple big cats at NTC, not just American cheetahs, suggesting that their speed was needed on multiple fronts. Additionally, wolves ate a varied diet at NTC, with no strong preference for any of the sampled herbivores. The abundant horses at NTC seemed to be on everyone's menu at NTC.

We now know who was eating the horses at NTC, but the diet of the horses is the subject of the next work by Spencer and Scott (2023, this volume). This team examines the mesowear (occlusal tooth wear) of the cheek teeth of bighorn sheep (*Ovis canadensis*) and horses (*Haringtonhippus francisci* and *Equus* sp.) at NTC to determine the types of vegetation each species was consuming. Interestingly, this study finds active niche partitioning between the horses and the sheep. Unsurprisingly, both genera of horses are grazers, grinding their cheek teeth down with an abrasive diet; whereas the sheep at NTC preferred a less abrasive diet, which could indicate sheep and horses may have been partitioning their diets much like the wildebeest and zebras of the modern African Serengeti. NTC sheep (comparable to African wildebeest) come through first and eat the new vegetation growth that is softer and younger, and horses (comparable to African zebras) come through later eating the tough, older grass. This analogous niche partitioning is exciting, since this gives us new insights into the ecosystem surrounding NTC during the Pleistocene.

Having two genera of horses at NTC makes niche distinction difficult between these two species. In fact, distinguishing *Haringtonhippus* and *Equus* at all using cranial morphology has been a challenge for all previous researchers, but Grass et al. (2023, this volume) tackle that challenge here. Genetic analyses have shown *Haringtonhippus* to be more common than *Equus* at NTC (Heintzman et al., 2017; Mitchell et al., 2023, this volume), but how does one differentiate these two species based on cranial morphology, and specifically teeth? Grass and his colleagues approach this problem by examining the occlusal surface of molars and premolars of both horse genera using 2D geometric morphometrics. They showed that these two genera can be distinguished using the enamel patterns on the tooth occlusal surface. Additionally, they found that a landmark scheme using fewer points was better at this discrimination, due to the noise incorporated by using a greater number of landmarks (which capture mostly individual variation). Their findings also mirror those of the genetic analyses – that *Haringtonhippus* outnumbered *Equus* at NTC.

Rounding out this special volume is the work by Minckley et al. (2023, this volume) on pollen and carbonate isotope data at NTC. Like the work by Lovelace et al. (2023, this volume) this paper is much-anticipated and sorely needed. Pollen was originally examined at NTC by Johnson and Fredlund (1982), but with the techniques used to isolate and examine pollen in the early 1980s, very little was found. Minckley and colleagues changed that when they examined pollen collected from NTC in 2015. They analyzed pollen from three time-intervals: 151.1 to 132.2 cal ka BP, 51.8 to 17.4 cal ka BP, and 10.4 cal ka BP to present. Using the combination of pollen counts and carbonate values they determined that the earliest time interval was indicative of relatively wet summers, whereas the interval during the Last Glacial Maximum (~21 cal ka BP) was indicative of steppe-like, cold and dry conditions. The final Holocene interval showed a shift to a short-term humid interval with abundant pine pollen and woodland expansion before the drying that occurred closer to the recent. Minckley et al. (2023, this volume) also captured the Pleistocene-Holocene transition in their pollen samples – something that has yet to be done with mega- or microfauna at NTC, with a clear delineation and change in pollen abundance and types at this juncture. This seminal work will be the basis for future environmental change studies at NTC.

Like this fossil site, this volume of papers reflects the richness of projects possible to study at NTC. However, this volume is only the beginning of many of these studies and with further data collection and analysis, NTC will continue to change our view of the Pleistocene world. Some of the projects that are currently in progress at NTC, but not included in the volume, include the ancient DNA of the large canids at NTC, which include the dire wolf (*Aenocyon dirus*) and another mysterious wolf (*Canis)* species; a study of aridity through time and the resultant effects on the fauna; and a continuation of data collection on some of these papers contained herein (e.g., more pronghorn stable isotopes). Additionally, the surface has not even been scratched for some possible projects at NTC, for example, an analysis of the terrestrial invertebrates in the cave. This site will continue to inspire endless projects for the scientists of the future. We hope to be part of this exciting venture for years to come.

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Julie A. Meachen*
Department of Anatomy, Des Moines University, Des Moines, IA, USA

Jenny L. McGuire
School of Biological Sciences, School of Earth & Atmospheric Sciences, Interdisciplinary Graduate Program in Quantitative Biosciences, Georgia Institute of Technology, Atlanta, GA, USA

* Corresponding author.
E-mail address: julie.meachen@dmu.edu (J.A. Meachen).
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