Ancient bat remains illustrate the role of caves as habitat anchors in the temporally dynamic landscape of the Grand Canyon

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ABSTRACT

Globally, caves provide important refugia for bats. The Grand Canyon, more than 400 km (250 mi) long, consists of steep-sided, rocky formations with hundreds to thousands of natural caves. Two of these, Double Bopper and Leandras Caves, are remarkable because of the presence of desiccated bat carcasses, ranging in condition from skeletal to well-preserved animals identifiable to species. Both caves are complex but differ in length and structure. Double Bopper Cave, >60 km (37 mi) long, is variable with narrow passages. Leandras Cave, 24 km (15 mi) long, has wide, open passages. We surveyed both caves, collecting information for 482 specimens. We initially hypothesized that a single catastrophic event caused the deaths of many individuals or that bats died of various causes over a long period. We expected bat communities to differ between caves, since different cave structures would favor different species based on flight maneuverability. Radiocarbon dating of 67 samples found ages ranged from modern to >45,800 cal BP, spanning the Last Glacial Maximum. The dominant bat species in each cave differed, with Townsend's big-eared bat (*Corynorhinus townsendii*), a cave obligate, dominant in Double Bopper Cave and silver-haired bat (*Lasionycteris noctivagans*) dominant in Leandras Cave. Bats continue to use these caves today, as evidenced by the presence of fresh guano. The remarkable evidence of long-term continuous use of these caves by bats illustrates the importance of protection and conservation to provide habitat for them. The caves also provide an unprecedented time machine to study bat communities from the past, understand long-term patterns of habitat use, and prepare for climate change.

OVERVIEW: INVENTORY, LONG-TERM USE, AND PROTECTION

In 2006 and 2008, an ongoing cave inventory in Grand Canyon National Park led to the discovery of well-preserved vertebrate remains in two caves, including hundreds to thousands of desiccated bat carcasses. When an initial sample of nine bats representing five species was radiocarbon dated, ages ranged from 3,770 ± 80 calibrated radiocarbon years before present (cal BP) to 31,410 ± 280 cal BP (present = 1950; the calibration involves correcting for fluctuations in atmospheric carbon). Dating of additional samples has revealed ages beyond the limit of radiocarbon dating methods (>48,000 yrs BP). Subsequent inventories have highlighted the long-term continuous use of these caves by bats and the dominance of different bat species in each cave. We emphasize the importance of field inventories, uniqueness of caves, and the need for cave protection to conserve paleontological resources and protect present-day habitat for bats (Figure 1).

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FIGURE 1. A Townsend's big-eared bat in Double Bopper Cave is well preserved by desiccation. SHAWN THOMAS

SIGNIFICANCE OF BATS

Bats are of global significance because of their role in pest control, pollination, and seed dispersal. Evolving more than 52 million years ago (Eocene), bats represent the second-most diverse mammalian order with more than 1,450 species recognized today. They inhabit all continents except Antarctica. Bats are unique as the only mammals that fly, but they have other unusual life history characteristics such as nocturnality, low annual reproductive rate, small body and litter sizes, and exceptional longevity relative to their small body sizes. As nocturnal animals, many use echolocation to move in their environment and locate prey. Their volancy helps during periods of low resource availability when some species make short- or long-distance migrations to areas richer in resources; others use torpor or hibernation to avoid seasonal shifts in food availability (Kunz and Fenton 2003; Furey and Racey 2016).

ROOSTS

Roosts are critically important to bat conservation. Bats spend more than half their lives sheltering in roosts and use a variety of natural features (caves, trees, leaves) and human-made structures (buildings, bridges, mines). For these nocturnal animals, day roosts provide shelter from predators and temperature extremes, and proximity to water and foraging areas. Roosts are thus an important habitat feature and bat populations are strongly influenced by the availability and security of roosts.

Hundreds of bat species worldwide depend on natural caves as roost sites; the International Union for Conservation of Nature (IUCN) lists 49% of all bat species as cave-dwelling (Tanalgo et al. 2022). Almost half of the 45 bat species in the United States and Canada rely substantially on caves, with at least five species using caves as hibernacula. Because of cave permanency and consistent microclimates, roost fidelity is greatest for cave-roosting species, and the largest bat colonies are found in caves; for example, one cave hosts 20 million individuals. The longevity of bats that hibernate can be attributed in part to hibernation in the stable environments provided by caves, since they can be highly buffered from external climates (Podlutsky et al. 2005).

Caves are common geological features worldwide, but each is unique, and their specific characteristics influence use by bat species. Caves differ in size, shape, distribution, openness, climate, geology, and other factors. Features in caves can include caverns, passages, fissures, fractures, and tubes. Characteristics such as temperature, relative humidity, airflow, and light intensity affect roost selection, with some cave-dwelling species showing thermal preferences for hibernation or reproduction (Kunz and Fenton 2003; Furey and Racey 2016). For example, some bats in the family Mormoopidae roost in hot areas of caves where temperatures reach 40 °C (104 °F) and humidity is close to 100% (Soto-Centeno et al. 2015). In contrast, others use locations in caves where temperatures range from –10 to 21 °C (14 to 70 °F), depending on the species (Webb et al. 1996). Longer, more complex caves and those with larger entrances generally support more bat species (Furey and Racey 2016).

Variation in cave structure affects habitat selection by bats because their morphology strongly influences maneuverability. Bat species with long, narrow wings and large bodies are fast fliers but not highly maneuverable, so generally fly in open spaces. In caves, they need large chambers and have difficulty negotiating small, tight passages. Examples include the hoary bat (*Lasiurus cinereus*) and the Mexican free-tailed bat (*Tadarida brasiliensis*). In contrast, bats with short, wide wings and small bodies, although slow fliers, are highly maneuverable and able to use cluttered environments such as dense forests or narrow spaces in caves. The Townsend's big-eared bat (*Corynorhinus townsendii*) and *Myotis* species are examples. There are exceptions and some species are slower, open-air flyers with small bodies and long, narrow wings such as the silver-haired bat (*Lasionycteris noctivagans*) (Norberg 1994).

FOSSIL RECORDS OF BATS

The fossil record of bats prior to the Pleistocene is extremely limited. This record is predominantly preserved and documented in caves. The combination of use by bats and the constant internal environments of caves favors long-term preservation of organic material because fossils within caves are typically sheltered, to some degree, from the forces of weathering and erosion. Worldwide, fossil remains of bats have been discovered in caves in Brazil, the Swiss Alps, Poland, Yemen, islands in the Caribbean, and the United States. Pleistocene bats from 27 taxa were identified in caves in Brazil. Bones of one species, Peter's ghost-faced bat (*Mormoops megalophylla*), radiocarbon-dated to 20,060 ± 290 radiocarbon years (24,170 ± 800 cal BP; calibration post hoc using http://calib.org/calib/, version 8.2). Skull fragments of a common vampire bat (*Desmodus rotundus*) had adhered to the underside of a sloth coprolite with a radiometric age of 12,200 ± 120 radiocarbon years (14,315 ± 515 cal BP; calibration post hoc using http://calib.org/calib/, version 8.2) (Czaplewski and Cartelle 1998). Although changes in climate (aridification) have now eliminated the Mormoopidae from this area in modern times, many cavernicolous species considered eurytopic (able to tolerate a range of vegetation types or ecological conditions) persist today. In the Swiss Alps, fossils of bats dated to the early Holocene include species that were either cold-tolerant or warm-demanding. Community composition varied over time, and reflected climate and vegetation associated with either cooler or warmer periods. For example, Bechstein's bat (*Myotis bechsteinii*), a thermophilous species considered a tracer of Quaternary warm periods, occurred during a climate phase in central Europe that was long, warm, and dry, sandwiched between two cold-humid phases (Blant et al. 2010). In southern Poland, fossil remains of at least 246 individuals representing 24 taxa record the entire period of the Holocene (Krajcarz et al. 2020). A well-preserved early Holocene (6,669 ± 70 radiocarbon years BP [7,545 ± 515 cal BP; calibrated post hoc using http://calib.org/calib/, version 8.2]) skeleton of an Egyptian fruit bat (*Rousettus aegyptiacus*) was found in a cave in Yemen. Given its location and the apparent lack of food availability, it raised questions about the success of the species colonizing western Indian Ocean islands (Van Damme et al. 2018). Caves on several Caribbean islands have yielded thousands of bat fossils representing dozens of species that date from the Pleistocene to the late Holocene (Soto-Centeno et al. 2015, 2017; Steadman et al. 2017). These abundant fossils indicated that some 18% of bat species became extinct but at a much lower rate than non-volant species, of which 80% went extinct.

Caves with low humidity can preserve animal remains through desiccation, thereby retaining tissues and hair. Animals conserved in this manner are remarkably well preserved; however, desiccation is a very rare form of fossilization. One such specimen of the spotted bat (*Euderma maculatum*) was found in a cave in the Navajo Nation near the Grand Canyon (Mead and Mikesic 2001). The limestone cave contained at least 20 bat carcasses of five or more species. The desiccated spotted bat, easily identifiable from its pelage, dated to approximately 10,500 cal BP (9,180 ± 50 radiocarbon years BP).

Despite offering some degree of shelter from weathering and erosion, most caves do not harbor ideal conditions for preservation. Cave microclimates result from a complex interaction of factors, including latitude, elevation, entrance size and orientation, number of entrances, cave length and volume, passage morphology, hydrology, and airflow. Caves with ideal preservation conditions are exceedingly rare. Even in the arid southwestern United States, caves often function as moisture traps and present elevated relative humidity levels that can rapidly degrade soft tissues. Climate stability is likely a very important preservation factor, and smaller caves typically have limited areas of long-term (year-round, multi-year) stability. Large caves, which are rare, are more likely to harbor well-preserved remains, but only under very stable conditions, especially in respect to relative humidity. Not all large caves receive use by wildlife, especially in the dark zone beyond the reach of ambient light. With few caves offering suitable preservation conditions and even fewer among those receiving consistent visitation by bats and other wildlife, well-preserved desiccated animal remains are a rare find.

A UNIQUE FIND IN GRAND CANYON NATIONAL PARK

In the Grand Canyon, arid conditions and the variety of biological life zones along a steep altitudinal gradient combine to create an area rich in bat species diversity that is also capable of exceptional preservation of remains. Arizona has the second highest number of bat species in the United States with 28 recorded, and 20 of those species occur in Grand Canyon National Park. Although hundreds to thousands of caves are estimated to exist in the Grand Canyon, including many in the Redwall Limestone, not all are used by bats and not all offer suitable preservation conditions. However, two caves identified during a research and exploration project in the 2000s were unique in having thousands of bat carcasses. These caves are difficult to access, requiring backcountry travel, route finding, and technical ropework during multi-day expeditions. With inhospitable surface weather conditions during much of the year, the caves are rarely accessible, so inventory and mapping occurs slowly, typically limited to a single annual expedition.

Double Bopper and Leandras Caves occur between 1,400 and 1,700 m (4,600 to 5,600 ft) elevation in desert scrub vegetation. They have north-facing entrances and are complex. Both caves display passage morphologies such as maze cave development and mineralogy consistent with hypogene (subsurface) cave formation and sulfuric acid speleogenesis (Heimel 2023: 1–105). The caves are notable for their size (length and volume) and complexity as three-dimensional maze caves as well as for their outstanding displays and abundance of gypsum flowers, a speleothem (secondary cave deposit) extruded from cave walls. The age of these caves has been inferred from dating of mammilaries, a cave deposit that forms as a coating on cave surfaces as the water table drops due to incision, such as through canyon formation. Uranium-series dating of mammilaries from Leandras Cave indicates the upper Redwall Limestone caves in this part of the Grand Canyon formed more than 3 million years ago (Polyak et al. 2008), and the caves would have drained soon after as the water table continued lowering. Thus, these caves have been available as potential bat habitat for far longer than the upper limit of radiocarbon dating.

Despite its massive entrance, Leandras Cave was not discovered until 2006, due to its remote and obscure location (Figure 2) (Rice 2012). The cave has more than 15 km (9 mi) of passages with five parallel borehole passages that are enormous (30 m [98 ft] high, 24 m [79 ft] wide), with an average passage diameter greater than 11 m (36 ft) (Figure 3) (Mead et al. 2021; Tobin et al. 2021). While mapping Leandras Cave, the entrance to Double Bopper Cave was spotted; exploration and mapping began in 2008. Like Leandras, Double Bopper Cave is characterized as a maze cave with rectilinear joint-controlled passage development. Double Bopper, however, is significantly more extensive, and its network of passage development connects entrances in two canyons. It is the 12th longest cave in the United States and among the 60 longest caves in the world. Currently, the known extent of Double Bopper Cave is 66 km (41 mi) long with three levels and more than 180 m (590 ft) of vertical development. Though considerably longer, its passages are not as large as those in Leandras Cave and average 5 m (16 ft) in diameter (Figure 4). Volumetrically, though, the two caves are similar in magnitude. Double Bopper Cave is still being mapped and will increase in mapped length as exploration continues. Temperatures vary between 14–17 °C (57–63 °F) and relative humidity is low (usually 35–45%) (Mead et al. 2021; Tobin et al. 2021). Though climate data have not been collected in Leandras Cave, conditions there are very similar to those in Double Bopper Cave.

Knowledge of current bat use of Double Bopper and Leandras Caves is limited, largely based on observations by cavers only in autumn. During September and October visits, a few Townsend's big-eared bats were documented in torpor in Double Bopper Cave; these bats were observed in a portion of the cave that contains dripstone speleothems and is higher in relative humidity due to presence of infiltrating water. This is consistent with hibernation preferences of Townsend's big-eared bats selecting for cool, humid conditions (Gillies et al. 2014). However, the caves have never been visited by cavers during winter, so the extent of hibernation use is unknown. Active bats have also been observed exiting the main Double Bopper entrance in autumn, despite no live bats being seen in the main part of the cave. Bats may roost out of view on high ceilings or in inaccessible portions of the cave such as in cracks or fissures. Signs of bats are common throughout Double Bopper Cave, found as scattered guano along long stretches of passage that appear to serve as flyways. This guano has not been dated, so it is unknown whether it is modern or from the past, and only scattered guano is present; no guano piles occur in the caves and no associated staining has been observed that might indicate large roosts. These factors indicate that colonial or maternity use during the warm season does not occur in these caves; the measured temperature ranges in the caves also support that conditions are not suitable for maternity use.

Arid conditions have preserved a few other vertebrates in these two caves, including ringtails (*Bassariscus astutus*), raccoons (*Procyon lotor*), foxes (*Urocyon cinereoargenteus*), and woodrats (*Neotoma* spp.) (Figure 5). These non-bat mammal remains are rare, and non-bat mammalian use of the caves appears to be opportunistic or accidental. The cave location and entrances on vertical Redwall Limestone cliff faces make the caves inaccessible to most wildlife. A gray fox skeleton is conspicuously located directly below a tall ceiling dome greater than 45 m (148 ft) high, suggesting this animal may have fallen into the cave from above. Bat carcasses occur

FIGURE 2. A member of the science team accesses the cave entrance to Leandras Cave. The remote locations of Double Bopper and Leandras Caves make them difficult to reach and although their entrances are large, access is arduous, requiring a rappel into each. SHAWN THOMAS

▼ **FIGURE 3.** Leandras Cave is large with passages up to 24 m wide and 30 m tall. BRANDON KOWALLIS

▼▼ **FIGURE 4.** Although passages are smaller in Double Bopper Cave compared to Leandras Cave, the two caves may have similar volumes because of the longer length of Double Bopper. BRANDON KOWALLIS

FIGURE 5. Arid conditions have preserved other vertebrates in these two caves, including this ringtail; however, non-bat mammal remains are rare, and mammal use of the caves appears to be opportunistic or accidental. SHAWN THOMAS

throughout the caves on both cave walls and floors and many individuals are so extraordinarily well preserved that they can be identified to species and sex; many carcasses are fully articulated and have intact skin and fur. Bat carcasses on cave walls are difficult to distinguish from live bats without close inspection (Tobin et al. 2021). The primary distinction between the carcasses and live bats is fading of pelage coloration, which seems to be more pronounced with time since death. Brittleness also increases with age. During initial explorations, the dominant bat species observed among carcasses in Leandras Cave and Double Bopper Cave appeared to be the silver-haired bat and Townsend's big-eared bat, respectively (Figure 6). In 2010, 170 bat carcasses were opportunistically inventoried and mapped, and tissue samples collected from a small subset in Double Bopper Cave; 60% were Townsend's big-eared bats with the remaining 40% representing at least 11 additional species. Because some species like those in the genus *Myotis* are difficult to differentiate, more than 12 species may be represented (Table 1). All identified species are still extant. In 2019, samples from 12 individuals representing five species were radiocarbon dated and ages ranged from 3,770 to 38,470 cal BP. Inventorying bats in these caves became a priority, and an independent team focused on sampling bats in each cave. Unfortunately, field work was halted for several years by the COVID-19 pandemic and park closures to wildfires.

FIGURE 6. From a survey of bat carcasses, the dominant species observed in Leandras Cave is the silver-haired bat while the dominant species in Double Bopper is the Townsend's big-eared bat.
SHAWN THOMAS

In 2021, our inventory of bats resumed, and we returned to Double Bopper Cave in October of that year and to Leandras Cave in October 2022. Our priority was to describe the bat community in both caves, so we systematically sampled three areas in each. We searched each area, recording start and stop times and locations. When we located a bat, we numbered and photographed it, recorded its location (ceiling, wall, floor), and measured forearm length. As in 2010, for a subset of bats we collected samples for radiocarbon dating, stable isotope analysis, and future analysis of ancient DNA.

Our inventory to date includes 482 bats of at least 12 species (Table 1). In 2021 and 2022, we sampled 147 bats in Double Bopper Cave and 165 in Leandras Cave, respectively. Townsend's big-eared bat, an agile flyer, was most common in the more confined spaces of Double Bopper Cave, while the silver-haired bat, a less maneuverable flyer, was more common in the wide passages of Leandras Cave. Although this confirms that bats select caves depending at least in part on maneuverability, we were surprised to find silver-haired bats so abundant in Leandras Cave. Unlike Townsend's big-eared bats, silver-haired bats are not cave obligates and do not commonly roost in caves (Table 1). Silver-haired bats, western red bats, and hoary bats are considered tree-roosting species, settling among needles or

TABLE 1. Bat carcasses inventoried during two surveys in Double Bopper Cave, in October 2010 and October 2021 (DB-2010, DB-2021), and one survey in Leandras Cave, in October 2022 (LC-2022), Grand Canyon National Park, Arizona. Roost types used vary by species and include C = cave, H = human structures (buildings, bridges, tunnels), M = mines, T = trees or snags, R = rock crevices or ledges.

Scientific name	Common name	Number sampled DB-2010	DB-2021	LC-2022	Roost type
Corynorhinus townsendii	Townsend's big eared bat	98	91	10	C,H,M
Eptesicus fuscus	big brown bat	6	9	10	C,H,M,T,R
Lasionycteris noctivagans	silver-haired bat	7	2	89	H,T,R
Myotis californicus or *ciliolabrum*[1]	California or western small footed myotis	8	1	7	C,H,M,T,R
Antrozous pallidus	pallid bat	6	1	7	C,H,R
Parastrellus hesperus	canyon bat	7	0	0	C,H,M,R
Lasiurus cinereus	*hoary bat*	6	0	8	T
Myotis thysanodes	fringed myotis	5	0	0	C,H,M,T,R
Lasiurus blossevillii	western red bat	1	0	0	T
Myotis volans	long-legged myotis	1	0	0	H,T,R
Tadarida brasiliensis	Mexican free-tailed bat	1	0	0	C,H,T
Myotis species, further unidentified[2]	*Myotis* spp.	8	34	17	
Unknown	unidentified	16	9	17	
	TOTAL	170	147	165	

[1] *Myotis californicus* and *M. ciliolabrum* are small (4 g [0.14 oz]) *Myotis* species and cannot be differentiated visually.
[2] These examples of *Myotis* species are larger (7 g [0.25 oz]) than *M. californicus* and *M. ciliolabrum* but are difficult to differentiate visually.

leaves of trees. Leandras Cave contains a number of paleo pool basins; these pool basins are currently dry, but cave pool precipitates such as mineralized water lines on cave walls and calcite rafts indicate presence of fresh water from meteoric infiltration at some point in the past. All species inventoried in Leandras were present within one of the paleo pool basins, including hoary bats, another species not associated with caves. It is possible that silver-haired bats and other species used the cave because of this important water resource. Accessing this water would have required bats flying approximately between 1–2 km (0.6–1.2 mi) through a series of passages in Leandras Cave. The discovery of this water source by bat species that typically do not use caves is intriguing; however, once the pools became known, they may have served as long-term sources of drinking water that required less energy to access and fewer threats relative to accessing sources of surface water. Other species occurred in both caves in smaller numbers; to date we have not identified all species, but overlap is high, with seven of eight species groups common between the caves. However, a community comparison metric that combines species richness with relative abundance resulted in a Similarity Index of just 0.31 for the two bat communities, indicating the unequal number of the two dominant species between the caves, as evident in Table 1.

LONG-TERM USE OF CAVES

During inventories, we collected samples for radiocarbon dating from 160 bats, 82 for DNA analysis, and 120 for stable isotope analysis. Currently, we have radiocarbon ages for 67 bats from Double Bopper Cave representing six species and one species group (*Myotis*) (Table 2). All AMS ^{14}C dates are reported in calendrically calibrated years before present (cal BP). Townsend's big-eared bats have occupied the cave continuously over the past 50,000 years; ages of bats ranged from 100 (modern) to >45,800 cal BP. Although silver-haired bats are less abundant in Double Bopper Cave, they have also used the cave both in the Holocene and Pleistocene. Radiocarbon dates for eight silver-haired bat carcasses were 5120 ± 70, 10,035 ± 140, 10,320 ± 85, 10,600 ± 90, 11,300 ± 60, 31,410 ± 275, 33,500 ± 480, and 42,240 ± 335 cal BP.

One question that puzzled the cave research crew was the cause or causes of mortality for the hundreds of bats they observed. Did animals die from one catastrophic event, such as naturally occurring environmental toxins that might be produced by a volcanic eruption or an outbreak of a disease, or did they die over millennia from natural causes? Many bats appeared to have died while roosting on breakdown blocks on the cave floor, an unusual roost site for

TABLE 2. Number of bat carcasses radiocarbon-dated to 10,000-year period sampled from Double Bopper Cave in October 2010 and October 2021, Grand Canyon National Park, Arizona. *Myotis* species represent multiple species (*M. californicus, M. ciliolabrum, M. thysanodes,* and others).

	Cal age (ka)					
Species	**0–10**	**11–20**	**21–30**	**31–40**	**41–50**	**Total**
Corynorhinus townsendii	3	5	5	4	15	32
Myotis species	4	2	1	0	3	10
Eptesicus fuscus	4	3	0	1	1	9
Lasionycteris noctivagans	1	4	0	2	1	8
Lasiurus cinereus	1	0	0	2	2	5
Antrozous pallidus	2	0	0	0	0	2
Tadarida brasiliensis	1	0	0	0	0	1
TOTAL	16	14	6	9	22	67

bats to choose since they prefer to roost in high locations that offer protection from predation. Could mortality from an endemic disease such as rabies explain unusual roost behavior? Radiocarbon dates from Double Bopper Cave indicate there was not a single die-off, but instead, that the cave had been used for thousands of years with animal carcasses accumulating over time. If the explanation is simply death by natural causes, then this seemingly extraordinary collection of carcasses becomes less so when considered through the lens of deep time. If, for example, just one bat died every decade in a cave with the cool, dry environment of Double Bopper or Leandras, 5,000 bats could accumulate over a 50,000-year period. This hypothetical scenario is very feasible and quite conservative, as recently deceased bats are commonly observed by cavers and researchers working in caves, so it is likely that with steady, continuous use, more than one bat would accumulate per decade. Most caves are not amenable to long-term preservation of carcasses, and modern observations of deceased bats in caves with typically elevated relative humidity are often accompanied by descriptions of fungal invasion and decay leading to unidentifiable species and eventually complete decomposition within a few months or years. The unique climatic conditions and long-term stability of these Grand Canyon caves are responsible for preserving this exceptional bat fauna and represent the truly extraordinary takeaway of this discovery: these caves are not only serving as habitat anchors—important roost sites across epochal changes in climate—but also acting as museum-caliber archives of the past. Thus, the long-term use of these caves documents the change in bat communities and dominance of individual bat species across the past, helping us understand how changing climate altered species composition, and allowing us to predict how climate will affect bat communities into the future.

CAVE PROTECTION CAN SUPPORT LONG-TERM INVENTORIES

Inventories document important cave features and aid in management decisions. Many cave-roosting bat species now face the risk of extinction (Tanalgo et al. 2022). Caves are thermally stable, relatively permanent environments that help reduce energy loss in and provide safety to bats. Many caves have long histories of human use such as recreation and commercialization, harvesting of minerals and guano, production of construction materials, and use as dump sites. Unfortunately, human uses are often incompatible with wildlife needs and may interrupt and displace long-term use by bats and other animals. In one recent study, bat use and species richness were negatively correlated with human disturbance, and the authors found that, if left unchecked, disturbance can reduce bat use by 80% or more (Furey and Racey 2016). Although caves are fragile environments, if protected, they allow for paleo-environmental and paleo-climatic reconstruction.

Fortunately, most Grand Canyon caves have been spared from modern human disturbance. While many caves in the Grand Canyon contain cultural artifacts attesting to Indigenous use, there is no evidence that Double Bopper or Leandras Caves were entered by humans prior to modern discovery and exploration commencing in the 2000s. This is not surprising, considering that the entrances are located on vertical cliff faces and can only be accessed via technical ropework. The cave exploration teams documenting these caves are transient visitors, and minimal impact is a key tenet of the inventory and mapping work. As such, these caves will hopefully continue to be used by bats in the absence of any significant disturbance from humans. Accordingly, we expect that these caves should continue to serve as habitat anchors and natural museums, accumulating and preserving the occasional bat that comes to roost in them as its final resting place, deep within the dark zone and within the long-term stable climate that is unique to these large, complex systems.

Work in Double Bopper and Leandras Caves will continue. Additional inventories will help us understand changes in bat communities through time. From the description of the spotted bat by Mead and Mikesic (2001), we have been able to model Holocene biogeography for the species (Sanchez et al. 2023). Although Mexico was within the Pleistocene-era range for spotted bats, the species expanded into the United States throughout the Holocene and climate space contracted in Mexico. Bats are remarkably vagile and can alter their ranges with changing climate. Additional opportunities with these cave inventories include use of ancient DNA to compare modern and Pleistocene and Early- to Mid-Holocene bat communities. Given the state of desiccation and preservation of many specimens, it may be possible to examine the diet of these bats, identify invertebrates associated with them, and describe climate change and its effect on bat communities. These caves are remarkable in containing abundant evidence of long-term continuous use by bats, indicating the importance of modern-day protection and conservation to provide habitat for them. They also provide an unprecedented time machine to study bat communities from the past and understand long-term patterns of habitat use. In terms of paleontological resources, cave inventories pose unique challenges but also provide opportunities to uncover unique rewards (e.g., Santucci et al. 2001), such as have been found in these Grand Canyon caves. Without inventorying, these sites and their information will remain unknown.

Collectively, the desiccated bat specimens from these caves in Grand Canyon National Park span more than 40,000 years during a period of extreme climate change both before and after the Last Glacial Maximum (approximately 23,000–21,000 years BP). What questions may yet be addressed by evidence preserved within this biogeochronological assemblage?

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