

TAPHONOMIC IMPLICATION OF ONTOGENETIC DISTRIBUTIONS FOR FIELD MICE (*PEROMYSCUS* spp.) POPULATIONS FROM TWO DEBRIS CONE DEPOSITS, PARKER'S PIT, BLACK HILLS, SOUTH DAKOTA, USA

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ABSTRACT

Fossils accumulate in caves in multiple ways. Each introduces biases that must be understood before interpreting the assemblage. The ontogenetic age distributions of individual specimens of field mice, *Peromyscus* spp., based on tooth wear, provides insight into taphonomic pathways for two different talus deposits in Parker's Pit, Black Hills, South Dakota. Main Cone accumulated under the modern 12 m vertical pit entrance throughout the Pleistocene and Holocene. The sink hole prohibits escape of randomly selected taxa. Red Cone formed as a talus slope in an old, now closed, entrance with a ramp-like slope that allowed animals to enter and exit the cave.

Differences in ontogenetic age distributions between these two populations are statistically significant. Main Cone individuals show a wider and generally older age distribution than those from Red Cone. The older age distribution results from individuals surviving the vertical fall and living into old age in an essentially predator-free environment. These individuals probably subsisted on organic debris washed into the cave and resident invertebrates as observed in a living population of *Peromyscus pectoralis* in Longhorn Cavern, central Texas. The Red Cone population is ontogenetically younger, as exhibited by less dental wear, than the Main Cone population but slightly older than living populations studied in Washington, USA, and British Columbia, Canada.

Bone damage indicative of predation by small carnivores, especially weasels (e.g., *Mustela frenata*) in the Red Cone sample is not apparent in the Main Cone population, reinforcing different taphonomic pathways of the two populations. The Red Cone sample is biased by predator selection. The Main Cone fossil assemblage likely represents a random, local sample of the biota around the cave that facilitates paleoecological analyses. The predator biased Red Cone sample is not amenable to reconstruction of communities but does provide insights into predator-prey interactions and selected species in the vicinity of the cave.

INTRODUCTION

Fossils provide information about the evolution of life, changes in diversity patterns, and insights into past environments and climates, to mention a few. However, the fossil record is not a snapshot of the past because it contains inherent biases that must be understood for correct interpretations. For example, fossils enter caves in a variety of ways that will introduce biases. For pit caves, animals that fall into the cave may not be able to escape. These types of cave deposits provide a relatively random sample of the biota immediately around the sink hole but not necessarily a regional perspective. However, the size of the entrance to a cave does serve as a filter. Small entrances (e.g., Don's Gooseberry Pit, South Dakota – Pardi and Graham, 2017) allows the accumulation of small animals (e.g., insectivores, rodents, lagomorphs, mustelids, etc.) but not large ones, except for fragmentary remains (e.g., isolated teeth, rib fragments, etc.). Larger entrances (e.g., Natural Trap Cave, Wyoming – Martin and Gilbert, 1978; Redman et al. 2023) permit larger animals to be sampled (e.g., mammoths, camels. Horses, etc.) more completely. The depth of a pit cave can also contribute to biases. Shallow pits will only trap animals that cannot climb out of the pit (e.g., turtles, small animals, etc.). As the pit becomes deeper, the trap becomes more effective for additional small as well as medium and larger sized animals (e.g., jack rabbits, coyotes, deer, mammoths, etc.).

Predators may contribute significant numbers of fossils to caves. Owls use caves as roosts and regurgitate pellets containing hair and bone (Andrews 1990). The size of the prey species and their proportions, as well as parts, will depend on the owl or owls that contribute to the deposits (Andrews, 1990). Owls, typically, only forage within a few square kilometers of their roost area. Thus, although prey is transported to the cave, they still represent a relatively local sample but not as localized as those animals falling into a pit.

Larger carnivores can sample larger prey over more extensive catchment areas. For example, the home ranges of foxes (e.g., *Vulpes* spp.), coyotes (*Canis latrans*), and wolves (*Canis lupus*) can vary significantly. However, there may be some overlap in diets for these carnivores. Foxes (e.g., *Vulpes* spp.) generally have smaller home ranges (ca. 0.95

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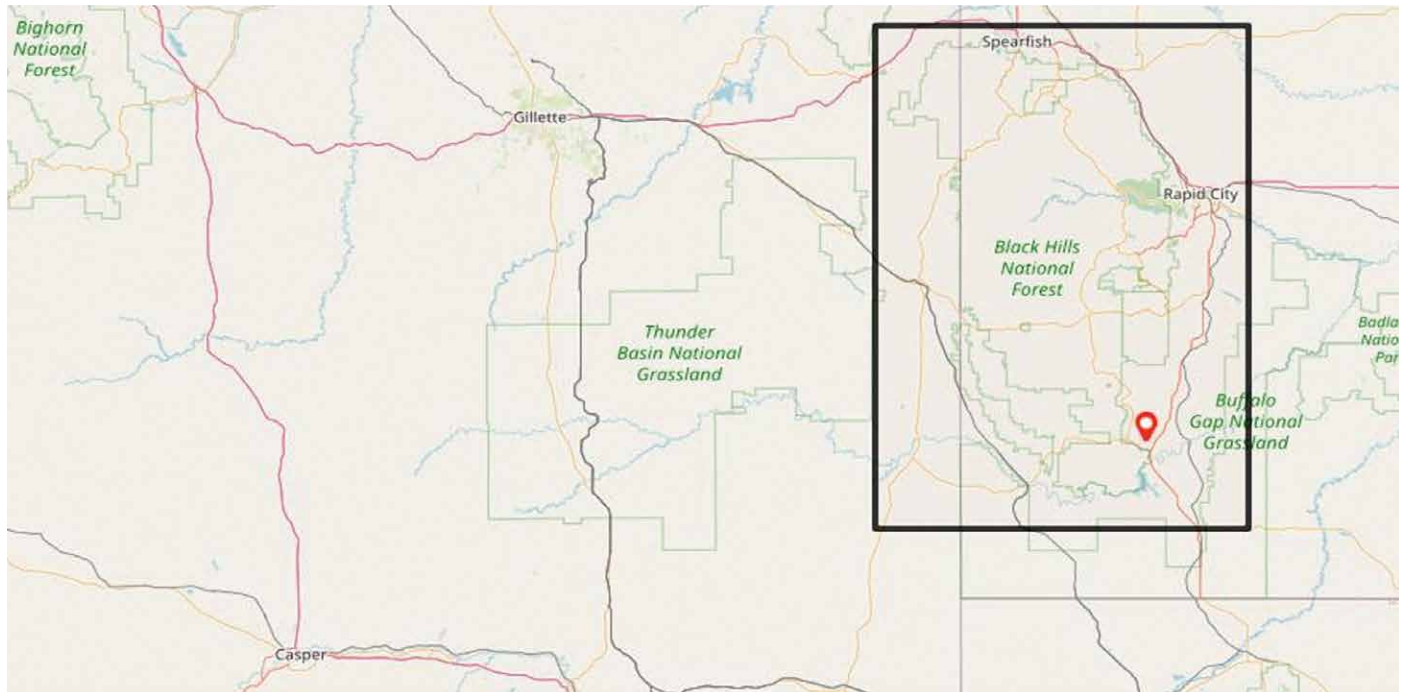


Figure 1. Location of Parker's Pit and Don's Gooseberry Pit (within 30 meters of each other) in the Black Hills (in rectangle, southwestern SD, USA). Longitudinal line in western portion of rectangle is the state line between SD on the right and WY on the left.

km² – 44 km²) (Walton et al., 2017), sampling more local environments, and eat smaller mammalian prey (e.g., insectivores, rodents, lagomorphs, small carnivores) (Casteñeda et al., 2022). Coyotes and wolves may range over hundreds to tens of thousands km² in their search for prey. Wolves have home ranges between 130 km² – 13,000 km² (Mech, 1974) and the home ranges of coyotes may range from 5.4 – 39.2 km² (Ward et al., 2018). Coyotes' mammalian prey may contain a similar size range as the fox but include some larger items like hares (*Lepus* spp.). Wolves may sample prey as large as deer, caribou, and bison.

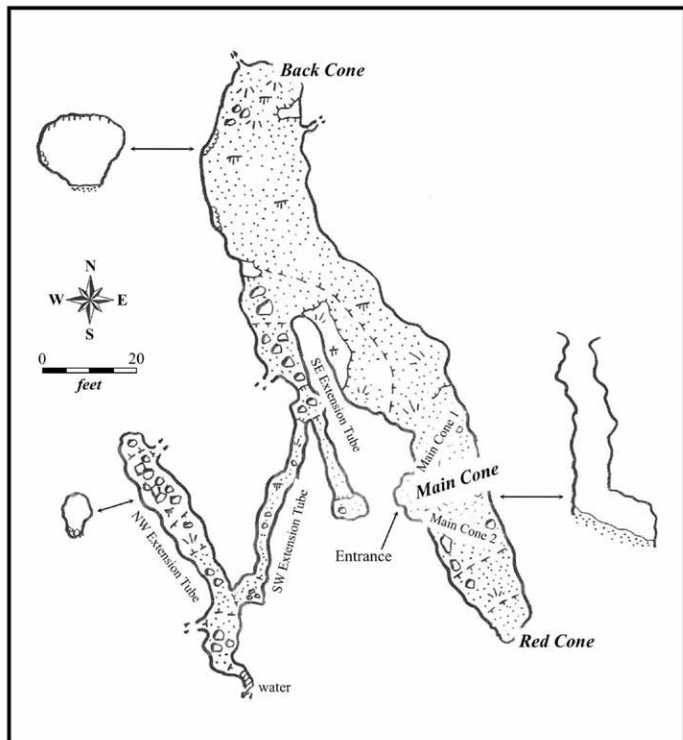


Figure 2. Plan view map of Parker's Pit.

Parker's Pit is a fossiliferous cave in the southeastern section of the Black Hills National Forest, South Dakota. It is located about 16 km north of the town of Hot Springs (Fig. 1). The cave is formed in the Mississippian-aged Pahasapa Limestone (Madison Group) (Petty, 2003). The cave opens just below the top of a northeast-southwest oriented ridge at ca. 1422 m elevation. There is a small intermittent stream below the ridge. The current sink hole entrance is 0.5 m x 1m with a 12 m vertical drop that ends at the top of a large debris cone (Figs. 2 and 3). This cone is referred to as the Main Cone. The cone is composed of stratified deposits of heterogeneous and unsorted angular to sub-rounded limestone rocks (generally smaller than 20 cm in diameter) intermixed with finer grained matrix. The current entrance was also open during the late Pleistocene as well as throughout the Holocene. It served as an effective trap for all animals, including many snakes, that fell into it. Most of the animals from Main Cone are smaller than black-tailed jack rabbits (*Lepus californicus*) that have an average weight of 11-15 kg (Jones et al., 1983) (Table 1).

The Red Cone is about 10 m to the southeast of the base of the Main Cone (Fig. 2). It is a filled former entrance without a surface exposure at present. Red Cone is a stratified talus slope with red to brown gravel to sand-size sediments. Unlike the vertical entrance of the

Table 1. Taxa identified from Parker’s Pit.

| Red Cone (N=7) | Red Cone | Main Cone |
|----------------------------------|----------|-----------|
| <i>Cryptotis parva</i> | X | |
| <i>Vulpes velox</i> | X | |
| <i>Mustela</i> spp. | X | |
| <i>Mustela nigripes</i> | X | |
| <i>Spermophilus</i> sp. | X | |
| <i>Reithrodontomys</i> sp. | X | |
| <i>Odocoileus</i> sp. | X | |
| Red and Main cones (N=15) | | |
| <i>Sorex</i> sp. | X | X |
| Chiroptera | X | X |
| <i>Mustela frenata</i> | X | X |
| <i>Sylvilagus audbonii</i> | X | X |
| <i>Sylvilagus</i> spp. | X | X |
| <i>Lepus californicus</i> | X | X |
| <i>Tamias minimus</i> | X | X |
| <i>Tamiasciurus hudsonicus</i> | X | X |
| <i>Marmota flaviventris</i> | X | X |
| <i>Thomomys</i> sp. | X | X |
| <i>Peromyscus</i> spp. | X | X |
| <i>Neotoma cinerea</i> | X | X |
| <i>Neotoma</i> sp. | X | X |
| * <i>Microtus</i> sp. | X | X |
| ** <i>Microtus</i> sp. | X | X |
| Main Cone (N=9) | | |
| <i>Sorex palustris</i> | | X |
| <i>Sorex arcticus</i> | | X |
| <i>Canis latrans</i> | | X |
| <i>Perognathus</i> sp. (small) | | X |
| <i>Phenacomys intermedius</i> | | X |
| <i>Myodes gapperi</i> | | X |
| <i>Synaptomys cooperi</i> | | X |
| <i>Zapus</i> sp. | | X |
| <i>Bison</i> sp. | | X |

**Microtus* sp. (three closed triangle clade)

***Microtus* sp. (5-7 closed triangle clade)

Main Cone, the Red Cone appears to have an acute slope that allowed easy entrance and egress from the cave (Fig. 3). This would have made Red Cone useful for small predators but not an effective trap (Fig. 2). Since the stratified deposits of the Red Cone only contain small animals (e.g., smaller than black-tailed jack rabbits) (Table 1), the entrance was probably quite small.

One of the most abundant animals represented in both cones is the “field mouse” (*Peromyscus* spp.). The respective accumulations of *Peromyscus* spp. remains at each entrance’s debris cone provided an opportunity to test for different taphonomic pathways for specimens from a single source. Our hypothesis is that the *Peromyscus* spp. populations at Main and Red cones are different in their ontogenetic age distributions. Red Cone will have predominantly younger individuals because it reflects a predator accumulation, whereas Main Cone will have older mice that were trapped but survived the fall; and consequently, lived in a predator-free environment within the cave.

To this end, we compared the ontogenetic age distributions for individuals of *Peromyscus* spp. from the two different cone deposits. For small mammals like rodents, the durability and distinctiveness of teeth make them a useful, and sometimes preferred, choice for age determinations (Bryant, 1991; Macêdo, et al., 1987; Morris, 1972; de Oliveira, et al., 1998; Sheppe, 1963). The null hypothesis in this study was that the two sample populations, Main Cone and Red Cone, would show no significant differences in their age distributions and physical conditions. The alternative hypothesis was that Main Cone and Red Cone would have a statistically significant difference in their respective age distributions, which would reflect differing taphonomic processes. A similar set of null and alternative hypotheses were devised for comparisons between Main and Red cones and the Sheppe’s (1963) wear stage data for wild populations of *Peromyscus ar-eas* and *P. maniculatus*.

In addition, during excavations for fossils in 1957, Holmes A. Semken, Jr. collected data on *Peromyscus pectoralis* populations living inside and outside Longhorn Cavern in central Texas. Although these data (body length, tail length, weight, etc.) are not directly comparable to the other data sets in this study, they do provide insight into how mice can survive in a cave environment for an extend-

ed time and reflect an older population that has relevance to the Main Cone *Peromyscus* spp. population.

METHODS

Excavations of both cones were conducted with trowels in 10 cm and 5 cm intervals within natural stratigraphic units that were defined by sediment types and other stratigraphic data (Graham, 2008). A single relative elevation datum was arbitrarily set at 1000 m in the cave. The same datum was used to measure relative elevation of excavation units for both cones. Excavated sediments were placed in individually numbered bags, labeled with cone name, stratum, excavation level, and excavator. Large pieces of rock were removed and discarded in the cave. The bags were then transported to a location for wet screening. Each bag of sediment was weighed before it was processed. Sediments were placed in screens (3-mm mesh) and then sprayed with water to remove the clays, silts and fine sands. Conspicuous jaws and individual teeth were removed from the screen and placed in labeled vials to avoid further damage. The

Table 2: Criteria for identifying relative ages of individual *Peromyscus* using lower jaw molars (modified from Sheppe, 1963; m1 = 1st molar, m2 = 2nd molar, m3 = 3rd molar).

| WEAR STAGE | DESCRIPTION OF LOWER MOLAR WEAR |
|------------|--|
| Stage I | m3 not fully erupted and without wear, m1 and m2 without wear |
| Stage II | m3 fully erupted, m3 without wear or slightly worn, m1 and m2 with very little wear (wear forms narrow bands of dentine linking cuspids, cuspids distinct) |
| Stage III | m3 basined but cuspids still apparent, m1 and m2 worn with dentine band forming lophids between cuspids |
| Stage IV | all molars basined, cuspids of m3 worn away but re-entrant angles still apparent |
| Stage V | cuspids and re-entrant angles of m1 and m2 worn away, roots usually protruding beyond the alveoli |

residue was then placed on canvas tarps and allowed to dry. Smaller pieces of limestone and chert were examined for signs of human workmanship and then discarded. The dried matrix was collected and placed in resealable plastic bags with interior and exterior labels. These bags were also weighed.

These materials were transported to a field lab where additional specimens were removed from the matrix. These specimens were put in bags or vials that were labeled with all provenience data. All material was transported back to the vertebrate paleontology laboratory at the Pennsylvania State University. Students and other volunteers then picked the matrix for all bones and teeth and these materials were then reunited with specimens previously sorted in the field laboratory. Using synoptic collections and identification keys, Russell Graham and students supervised by him identified teeth, mandibles, maxilla and other identifiable bones to the lowest taxonomic unit possible. These data were then entered into an EXCEL database.

Peromyscus maniculatus and *P. leucopus* both occur in the Black Hills today with *P. maniculatus* being the most abundant and widespread (Turner, 1974). Because these two species are difficult, if not impossible, to identify based upon their dental structure (Semken and Falk, 2014), specific separation was not attempted. The referral of specimens only to genus should not affect our longevity analyses.

Lower jaws of *Peromyscus* spp. with complete molar dentitions were selected at random from both the Main and Red cones. A binocular microscope with adjustable magnification and lighting was used to examine the degree of molar wear of each specimen. To categorize wear, we employed five wear stages used by Sheppe, (1963) who had studied live populations of *P. areas* (N= 274) and *P. maniculatus* (N= 376) from both British Columbia, Canada and the northwestern US. Sheppe's (1963) system had five stages of wear ranging from Stage 1 (essentially no wear on cusps) for the youngest to Stage 5 (cusps on molars obliterated) for the oldest. His system, like other similar systems for rodent age determination, used upper molars. Since fewer upper jaws than mandibles of *Peromyscus* spp. are preserved in Parker's Pit, we applied comparable wear stages to the lower jaws (Table 2). This significantly increased the sample size of specimens analyzed. In cases where the tooth wear appeared to be between two stages, the youngest age stage was selected.

Twenty-three specimens were used from Main cone and another 22 for Red Cone. Specimens were selected from different stratigraphic and elevation levels to get a more representative sample from each cone. All provenience data for each specimen were recorded in an EXCEL file along with the assigned wear stage. Graphing functions from EXCEL were used to compare samples.

Since Sheppe's (1963) samples for his living populations were orders of magnitude larger than our samples from Parker's Pit, we averaged the data for Sheppe's wild populations. The averaged sample's total size was 320.5, much larger than the Parker's Pit samples of 23 (Main Cone) and 22 (Red Cone). To make comparisons easier, we adjusted or "normalized" the averaged Sheppe population by using percentages to create a total closer in size to the average number of individuals (21) from Main and Red cones. A Student's *t*-test was used to evaluate statistical significance. Histograms of age classes permitted easy comparison of age structures for each of the three populations.

For the study of *P. pectoralis* populations in Longhorn Cavern, 10 traps were evenly distributed throughout the cave between the entrance just beyond the twilight zone to the beginning of the Hall of Marble (Semken 1961: Fig. 2) well within the dark zone. All traps were baited with Baby Ruth candy chips. Five additional traps were placed on the surface above the cave. Captured specimens were subdued with ether, uniquely marked for individual identification by toe clipping, weighed, measured, and released. Traps in the cave were checked three times per night, those on the surface in the morning. A flash flood in the cave removed all underground traps and none were recovered. Thus, no study skins or skulls are available. Because only three mice were captured on the surface, additional proxy data were taken from museum specimens collected from Burnet and surrounding counties housed in the Department of Zoology Collection, University of Texas at Austin (now in the Texas Memorial Museum). Standard measurements (weight, body length, tail length, hind foot length and ear length) were taken of the 32 individuals trapped in the cave and compared to measurements of 27 University of Texas Repository specimens that served as proxies for the Longhorn surface sample.

Table 3. A summary of the molar wear stage data from Main Cone, Red Cone and Sheppe’s 1963 paper on live *Peromyscus* populations. The Sheppe data in this table, derived from a study of two different populations, is an average that was “normalized” to a size comparable with Main and Red Cone samples (see text for methods).

| SOURCE | STAGE I | STAGE II | STAGE III | STAGE IV | STAGE V | TOTAL |
|-------------|---------|----------|-----------|----------|---------|-------|
| Main Cone | 0 | 5 | 13 | 3 | 2 | 23 |
| Red Cone | 0 | 8 | 13 | 1 | 0 | 22 |
| Sheppe Data | 1 | 14 | 4 | 2 | 0 | 21 |

RESULTS

In inspecting the results for the Main and Red cone samples, there are both obvious similarities and differences (Figs. 4 and 5; Table 3). Both cones consist primarily of Stage 3 individuals (13 for each site), neither exhibited Stage 1 individuals, and both showed more Stage 2s than either Stage 4 or Stage 5. But Main Cone has only five Stage 2s with three Stage 4s and two Stage 5s. The Red Cone had eight Stage 2s and a single Stage 4 and no Stage 5 individuals. Clearly, the population at Red Cone is younger overall than that at Main Cone.

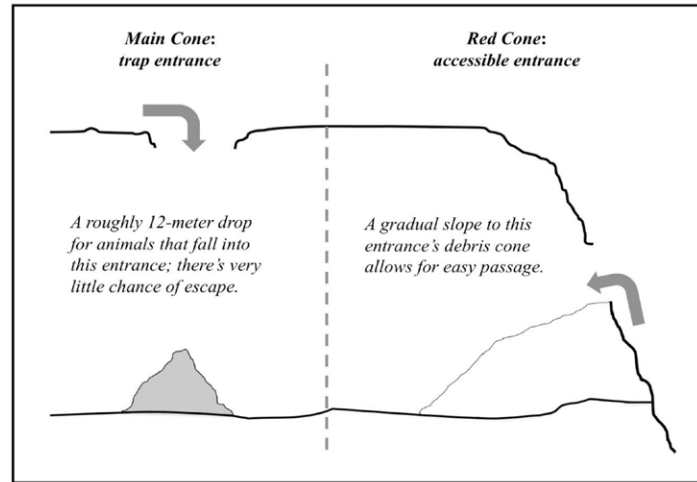


Figure 3. Comparison of cones and entrances to Parker’s Pit. The Red Cone is depicted as open but it is currently a sealed entrance without a surface expression.

The averaged wild *Peromyscus* populations from Sheppe’s (1963) study show yet another variation in age distribution (Table 3, Figure 6). Red and Main cones have no Stage 1 specimens, whereas, Sheppe’s (1963) sample had one. Sheppe’s (1963) deer mice populations are composed of younger individuals than Red or Main cone samples with Stage 2 being the most abundant (N=14). Stages 3 and 4 have four and two, respectively and no Stage 5s (this last result is due to a rounding issue in proportionally reducing the sample size). So Sheppe’s (1963) deer mice populations were generally younger than those found in either of Parker’s Pit cones (Fig. 6).

The Student’s- *t* test results showed that all three populations were significantly (at $p < .05$) different than alike in their age distribution patterns (Table 3). The comparison of the Main Cone sample to that of the Red Cone demonstrated to a 95.5% confidence level that they were statistically dissimilar to each other (Table 4). This suggests that they represent either samples from different populations or the results document different processes of accumulation. Likewise, in comparing Main Cone to Sheppe (99.8% confidence level) and Red Cone to Sheppe (91.8% confidence level), the differences in age distribution outweighed the similarities. This result also suggests either difference source populations or different taphonomic processes.

In Longhorn Cavern, only three individuals were captured on the surface over eight trap nights. Although the surface sample above the cave was small, no surface mice were captured inside the cave and no cave mice were documented on the surface. Hence, the cave mice and surface mice populations appear distinct with little, if any, interchange between populations. All traps throughout the cave attracted mice and illustrated that the mice occupied the entire cave

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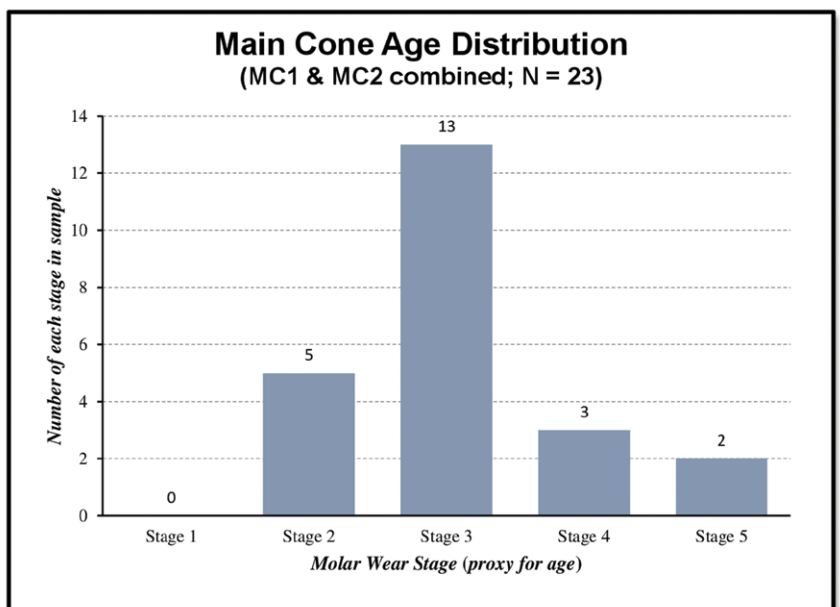


Figure 4. Histogram showing the distribution of the five age categories for *Peromyscus* spp. from Main Cone.

system. Mice were usually captured in the same or juxtaposed traps. As a commercial cave, Longhorn Cavern had a food concession area. Although the presence of food in the concession area could have served as a resource for the cave mice, it was clear that the distribution of cave mice was independent of the concession area because the mice inhabited the entire cave. Furthermore, no concession food was left in the cave overnight. Mice living in the cave probably were feeding on cave crickets that are abundant in the cave.

Table 4: A summary of the Student's *t*-test results for the Main Cone (MC), Red Cone (RC) and the "normalized" Sheppe data, showing confidence levels.

| PAIRS TESTED | NULL REJECTED | CONFIDENCE LEVEL |
|-------------------|---------------|------------------|
| MC vs RC | YES | 95.5% |
| MC vs Sheppe Data | YES | 99.8% |
| RC vs Sheppe Data | YES | 91.3% |

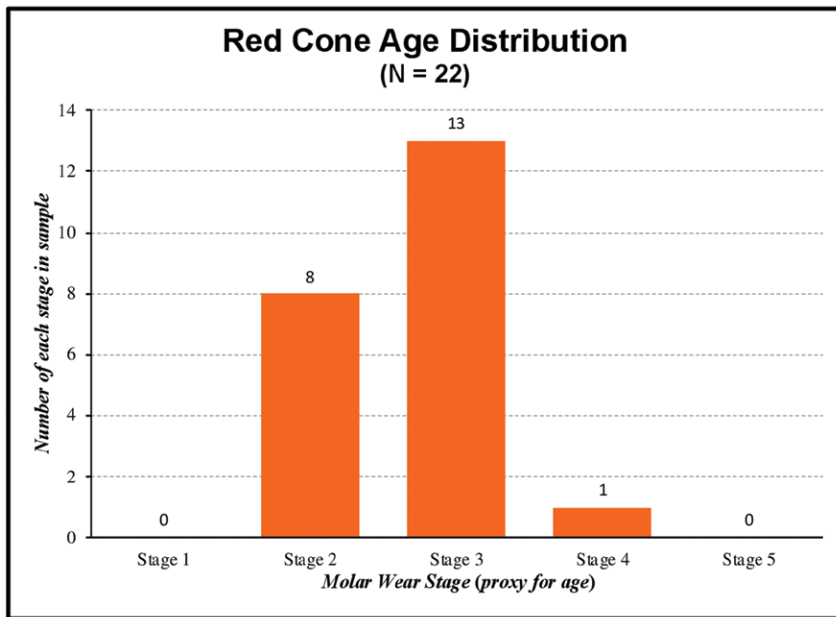


Figure 5. Histogram showing the distribution of the five age categories for *Peromyscus* spp. from Red Cone.

ten, perhaps due their greater experience (Andrews, 1990). Therefore, the presence of older deer mice in Main Cone seems somewhat enigmatic with regards to a standard pit trap sample. However, once the entire process of entrapment is understood (i.e., mice living in the cave), the older ages of individuals is explained.

Peromyscus is a relatively small rodent (in Colorado *P. leucopus* ranges from 20-36 grams and *P. maniculatus* is from 14-27 grams – Fitzgerald et al., 1994). Therefore, as noted in the quote by Haldane (1926) at the beginning of this paper, the terminal velocity of a mouse (i.e., *Peromyscus* spp.) is low, so it could survive a fall of 12 m. Voles, for instance, have been observed living on the floor of a 30 m shaft in Britain (Andrews, 1990). Blaine Schubert (personal communication) has also documented living *Peromyscus* individuals in Natural Trap Cave that has a vertical fall of about 30 m. Furthermore, abundant organic debris washes into Parker's Pit regularly. Since *Peromyscus* is omnivorous, able to eat a variety of plant and animal materials (Reid, 2006), the organic debris could provide adequate food for the trapped individuals after they had survived their fall. Finally, since the mice cannot escape and there are not any predators in the cave, the trapped individuals can live until they die naturally. Hence, the trapped population would tend to be composed of older individuals.

These data are consistent with a study of mice living inside and outside of Longhorn Cavern conducted by Holmes A. Semken, Jr. in 1957. His study documented that the mice could survive in the dark zone of the cave and that there was

Data comparisons verified that the mice living in the cave were larger than those living on the surface (Fig. 7). Although there was broad overlap in all the measurements for the two populations, body weight was the most significant. All measurements showed a trend in larger size for the population that lived in the cave (Fig. 7). Because the specimens were lost when Longhorn Cavern flooded, skins and skulls were not collected and dental wear could not be documented.

DISCUSSION

At Parker's Pit there are no Stage 1 individuals recovered from either entrance's debris cone. In Sheppe's (1963) study populations, he found that Stage 1 mice were never very abundant. These observations are not surprising. They can be explained by the prolonged time for young deer mice to stay in their mother's nest as they develop physical skills before setting up in a territory of their own (Vestal, et al., 1980; Lyman et al., 2001). The presence of this "training period" in their early days would tend to exclude these mice from being caught by traps and most accumulation processes.

The Main Cone sample of *Peromyscus* spp. should represent individuals that randomly fall into the pit. Based on research into small animals recovered from natural pitfall traps, it has been shown that the older individuals tend not to fall in as of-

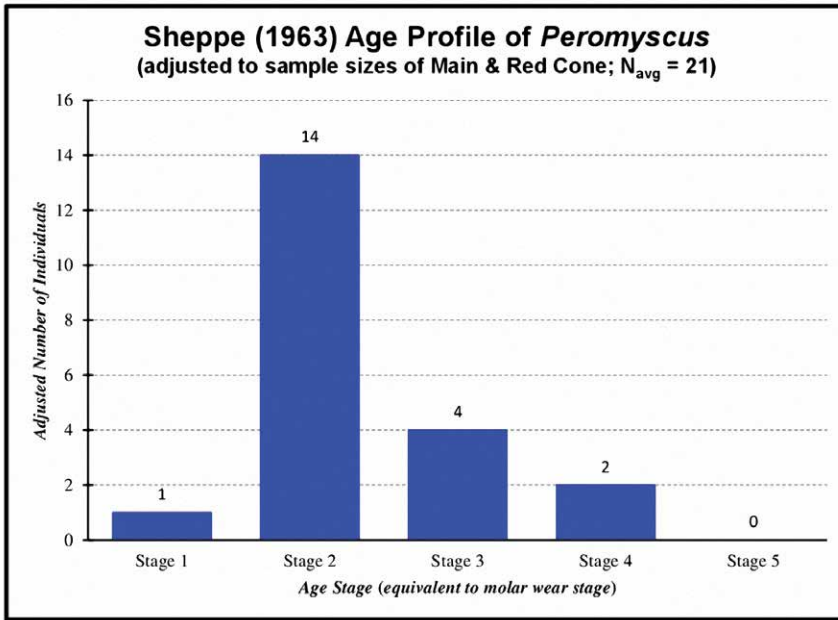


Figure 6. Histogram showing the distribution of the five “normalized” age categories for *Peromyscus* sp. from Sheppe’s (1963) study.

an vicar for *Peromyscus*, were significantly older in ontogenetic age distributions from excavations of Neolithic village sites on Orkney Islands, Scotland than in living populations. The Neolithic vole population was decidedly younger than that of the associated wood mice. Romanuik et al. (2016) felt that voles preferred open habitats to human habitations, whereas door mice are frequently commensal in human structures. Therefore, like the *Peromyscus* from North Dakota villages and Main Cone, the Orkney door mice are indicative of protected and predator-free environments.

The age distribution for the Red Cone population of *Peromyscus* is significantly different from either the Main Cone or surface populations studied by Sheppe (1963). Red Cone has but 1 mouse older than Stage 3 versus 5 in the Main Cone sample. The age distribution of *Peromyscus* from Red Cone is significantly younger than the population from Main Cone (Table 3). Furthermore, the Red Cone population is significantly older than the samples of *Peromyscus* studied by Sheppe (1963) that were derived from living populations from the surface.

One of the primary causes of mortality in small mammal populations is predation, which is also a major source for small mammal bone accumulations in caves (Andrews, 1990). Studies have revealed that predators can be selective for a particular prey type (e.g., Andrews, 1990; Brain, 1981; Lyman and Power, 2001; Mushtaq-ul-Hassan, et al., 2007) as well as age group. Different predators will exhibit different preferences or “tastes” in their prey choices. Thus, accumulations of bones by predators will reflect their preferences (Korth, 1979) more than the composite biological community living around the cave. A predator’s success can depend upon the age, and thus, the experience level of

little, if any, interchange with the surface population. Furthermore, the larger body size of the cave population in comparison to the surface population is attributed to lack of predation, as was older age for the Main Cone population in Parker’s Pit. Unfortunately, as noted before, it was not possible to conduct age studies based on tooth wear on the Longhorn Cavern population.

Semken and Falk (2014:255) found a preponderance of aged *Peromyscus* (“completely worn dentitions”) preserved in late Holocene earth lodges in North Dakota. They interpreted this older population as indicating “... that the village supported a resident population of *Peromyscus* that was enabled by a stable food supply and a reduced chance of predation.” Main Cone represents a similar situation. Likewise, Romanuik et al. (2016) found that the age distributions between voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*), the Europe-

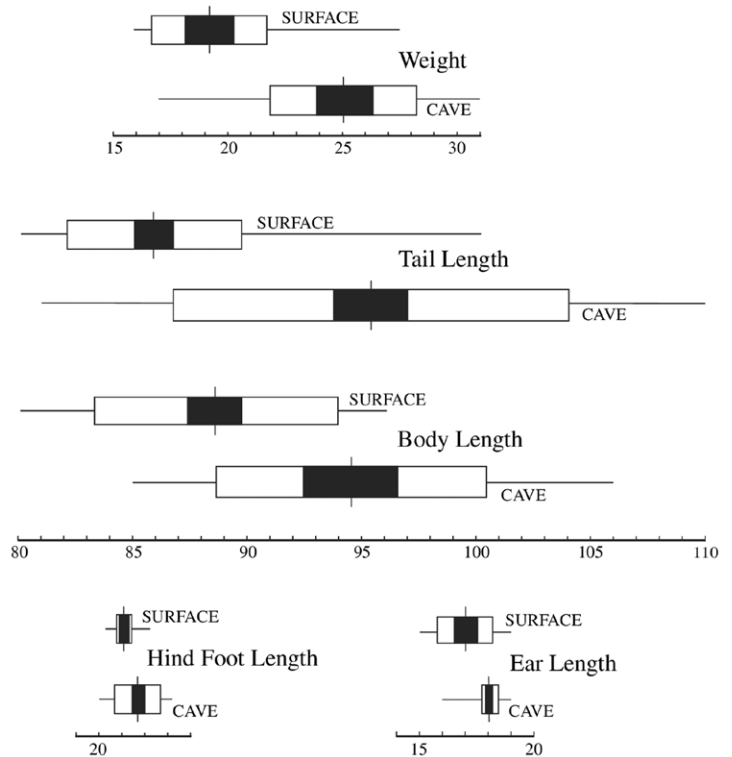


Figure 7. Summary statistics for measurements of *Peromyscus pectoralis* that lived inside Longhorn Cavern in comparison to *P. pectoralis* from the University of Texas Department of Zoology repository that served as a proxy for the surface population at Longhorn Cavern. Lengths are in millimeters and weight is in grams. The vertical line is the mean, the black box is one standard deviation, and the white box is two. The central horizontal line is the range.

its target prey. This age preference can show up in the remains left behind (Bryant, 1991; Lyman and Power., 2001), and can be detected by examination of the ontogenetic age of the animal remains (Lyman and Power, 2001; Morris, 1972). Because of predator selection, any small mammal accumulation found in the fossil record should be considered a possible predator accumulation until it has been demonstrated to be otherwise (Andrews, 1990).

Red Cone, which had a small ramp-like entrance into Parker's Pit, would have allowed a variety of differently sized animals to enter and leave at will. In other words, it was not a trap. It would have been easy for deer mice to come and go, but not likely that they would choose to live in the cave where resources were limited, unless they were trapped. Hence, it is unlikely that the *Peromyscus* in Red Cone represent a resident population in the cave. Thus, it is more probable that the *Peromyscus* found at Red Cone are the result of predators using the cave as a den. Predators actively prey on *Peromyscus*, catching almost exclusively the less experienced younger individuals. The result would be a selectively produced accumulation of *Peromyscus* remains in the debris pile at Red Cone, uniquely biased in the selection of prey and the ages of individuals based upon the preferences and abilities of the predator.

Many animals (small to medium mammal carnivores, owls and other raptors, as well as snakes) prey on *Peromyscus*. Snakes can be eliminated as the primary predator for the Red Cone accumulation since none of the *Peromyscus* bones exhibit extensive erosion and pitting characteristic of bones from a serpentine's digestive system (Doherty, 2009), if they even survive the digestive process (Secor, 2009). The restricted nature of the entrance for the Red Cone is not conducive to raptor access. Furthermore, raptors also leave diagnostic damage patterns on bones (Andrews, 1990; McGuire et al., 2023), none of which have been observed on specimens from Red Cone. To this end, small mammal carnivores are most likely the source of the Red Cone *Peromyscus*.

Weasels (*Mustela* spp.), especially the long-tailed weasel (*Mustela frenata*), are generalist predators on rodents and smaller lagomorphs (King, 1990). Weasels have been referred to as "hair-trigger mouse traps with teeth." (King, 1990: 4). At least two species of weasels are relatively abundant in Red Cone (Table 1). Weasel remains are rare in Main Cone. The weasels from Red Cone can be divided into two groups based on size. There is a small weasel that could be *M. erminea* and/or *M. nivalis*. The other weasel is significantly larger and can be assigned to *M. frenata* unequivocally (Sheffield and Thomas, 1997) and it is the most common weasel in Red Cone. The tubular shape of weasels allows them to navigate small narrow passages like the entrance to Red Cone.

Several *Peromyscus* skulls from Red Cone exhibit small puncture marks, which is the strongest evidence for predation. The size of these punctures is consistent with the morphology of the canine of *M. frenata*. While trapping small mammals in Laguna B lgica Educational Park, Chiapas, Mexico, Vaca-Leon et al. (2019) captured one male *M. frenata* along with a dead Mexican deer mouse (*Peromyscus mexicanus*) in the same trap. The *Peromyscus* had incision marks on the skull indicative of capture by the weasel. Therefore, it is most likely that a large part of the *Peromyscus* accumulation in Red Cone has been derived by predation of *M. frenata*.

Micromammal bones that pass through small mustelids and felids are generally fragmented and consist of largely unidentifiable bone flakes (Andrews and Evans, 1983; Mellet, 1974). There are lots of unidentifiable bone fragments of small mammals from both cones in Parker's Pit. Some of this damage may be due to mustelid predation but there is also fragmentation by trampling, sediment compaction, transport, etc. Many of the *Peromyscus* mandibles from Red Cone are complete. These mandibles and the numerous other complete bones could result from forgotten food caches that weasels are known to create (King, 1990: 83-84). As King (1990:83) states, "A typical [weasel] cache would contain 40-50 freshly killed mice with the typical puncture marks of the weasel's teeth in the neck."

According to Korth, (1979:249) any coprocoenosis from both avian and mammalian carnivores "... should give a relatively close approximation to the living population of mammals. From the descriptions of fecal and pellet material... it should be possible to determine if a single type of predator or a combination of predators has contributed to an assemblage" Finally, the difference in age distributions between Red Cone and Sheppe's (1963) modern samples strongly suggest that the predator also has a proclivity for mice of a particular age. Sheppe's (1963) samples were significantly younger than the Red Cone population (Table 3) and much younger than that of the Main Cone. One possibility for this difference is that dispersing individuals are more vulnerable to predation than resident individuals (Jamison, 1975). The difference between Sheppe's (1963) sample and Red Cone may, therefore, indicate that mice need to reach a certain age before they disperse and are captured by predators.

CONCLUSION

Parker's Pit has two different fossiliferous debris cone deposits. Main Cone is at the bottom of the 12 m modern vertical shaft with an entrance 0.5 m in circumference. Red Cone is a closed, small entrance with a ramp-like approach into the cave. That the taphonomy of these cones varied is documented by different ontogenetic age structures for their fossil samples of *Peromyscus* spp. Mice from the Main Cone are significantly ontogenetically older than those from the Red Cone. It appears that after falling, mice in Main Cone survived and were able to live in a predator-free environment feeding on organic material that washed into the cave. These mice died of natural causes as older individuals.

On the other hand, the ontogenetically younger *Peromyscus* sample from the Red Cone were victims of predation presumably by the long-tailed weasel (*M. frenata*). Evidence of predation is suggested by puncture marks the size of canines of *M. frenata* on some *Peromyscus* skulls. In addition, observations of predator induced modification on some other *Peromyscus* bones are consistent with the damage documented on bones that have been fed upon by predators: tooth marks, bone removal and exposure to stomach acid while passing through a predator's digestive tract (Andrews, 1990). Also, the Red Cone population is older than the populations of living *Peromyscus* monitored by Sheppe (1963) in the Pacific northwest. The very young mice are missing, presumably because they were nursing or still developing in their nest. Furthermore, the lack of very young mice may result from the fact that transient mice composed of slightly older individuals are more vulnerable to predation than are resident mice (Jamison, 1975). Mice may need to reach a certain age before they are able to disperse.

The differing ontogenetic age structures and taphonomic pathways for the Main and Red cones has significant implications for interpretations of fossil remains from these deposits. The older age structure of the Main Cone population suggests that *Peromyscus*, as well as other faunal components, fell into the pit and could not get out. Also, animals are more randomly selected by pit traps than in other cave entrances. Therefore, the Main Cone fossil record is more representative of the community surrounding the cave and can be used for paleoecological analyses, assuming other taphonomic signals are not red flags for different biases. On the other hand, the Red Cone was not an effective trap because animals could enter and leave at will unless they were brought into the cave dead or severely injured. In addition, predators can be very selective with regards to their choice of prey and their age. Hence, Red Cone deposits have a strong bias and do not effectively represent the relative abundance of species in communities around the cave and are less useful for paleoecological interpretations, especially where the faunal list is limited. However, they do provide a good record for predator-prey interactions.

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