Comparison of Mammalian Species Richness and Community Structure in Historic and Mid-Pleistocene Times in the Colorado Rocky Mountains

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We used an exceptionally rich mid-Pleistocene paleontological sample from Porcupine Cave, South Park, Colorado, to study long-term patterns of species richness and ecological structure in local mammal communities. The fossil data were compared with historic species richness patterns (prior to impacts by humans in the last two centuries) in order to assess whether the many climatic and other environmental changes that have occurred since the mid-Pleistocene significantly affected the numbers of species in various size and trophic categories. After accounting for potential sampling biases, we found remarkable similarity in species richness and community structure between a ca. 850,000-year-old mammal community and the historic one, which suggests that this high elevation Rocky Mountain community exhibited long-term cohesiveness — on the scale of hundreds of thousands of years — in overall species richness as well as in the number of species within various size and trophic categories. Superimposed on this long-term similarity were minor fluctuations in species richness on shorter time scales and changes in species identities through time; some of these shorter-term fluctuations may have been in response to environmental fluctuations. We suggest that species richness and its distribution across size and trophic categories may be a useful metric in assessing the degree to which communities are perturbed from a long-term baseline.

The past few decades have seen significant advances in studies of Earth's biodiversity at scales ranging from genes to whole ecosystems. In part, the explosion of information has arisen from efforts to document existing diversity and to recognize or predict how humans affect ecosystems. Prediction of ecosystem response has been complicated by a lack of knowledge of how biodiversity changes in systems that are not dominated by humans. In other words, what are the normal fluctuations that non-human dominated ecosystems experience in biodiversity metrics? And is any given ecosystem now within or outside those normal fluctuations?

Here we compare paleontological and historic data to explore whether biodiversity changes or remains stable in Rocky Mountain ecosystems over ~850,000 years. We focus on mammals as our indicator of ecosystem change, regarding them as an important component of the communities of which Rocky Mountain ecosystems are composed. Hereafter, we refer to this component of the ecosystem as 'mammal communities', following Brown and Lomolino (1998:627–628) in the definition of a community as "an assemblage of organisms that live in a particular habitat and interact

with one another", and an ecosystem as "the set of biotic and abiotic components in a given environment". Other definitions of these terms differ in details, but agree in principle with the definitions we use (for example, Whittaker 1975). Our metrics for assessing biodiversity are overall species richness of mammals and species richness in various trophic and size categories within the mammal community. Results from our study area suggest that in the absence of significant human impacts, such metrics varied within a relatively small range. We discuss the implications of this finding for ecological theory and for conservation issues.

MATERIALS AND METHODS

We compared species richness, size structure, and trophic structure of two communities separated by ~850,000 years, but from the same place: South Park, Park County, Colorado, at an elevation of ~2900 m (latitude 38°43′45″N., longitude 105°51′41″W, Gribbles Park 7.5′ Quad) (Fig. 1). The ~850,000-year-old sample was derived from the mid-Pleistocene fossiliferous deposits of Porcupine Cave, a complex system of well-known localities that has been comprehensively reported elsewhere (Bell and Barnosky 2000; Barnosky 2004a; Barnosky et al. 2004a). 'Mid-Pleistocene' in this paper refers to the medial part of the Pleistocene, not to placement within formal chronostratigraphic nomenclature.

For the fossil sample, following the logic detailed in a previous publication (Barnosky et al. 2004a), we combined specimens from two of the 26 Porcupine Cave localities to generate

FIGURE 1. Site of Porcupine Cave, South Park, Park Co., Colorado.

a robust sample of mammals that lived within an 8–18 km radius of the fossil deposit. The two localities were the Badger Room and stratigraphic level 4 of the Pit Sequence. Fossils in the Pit Sequence include >7000 identifiable specimens (1154 from level 4) that are interpreted as having been accumulated primarily by wood rats (*Neotoma*) dragging in bone-laden carnivore scat and raptor pellets (Barnosky 2004b). Bones in the Badger Room (>13,000 identified specimens) accumulated in part due to the activity of wood rats, but also from the collecting activity of medium-sized carnivores such as canids and mustelids (Shabel et al. 2004), which increased the sample of larger mammals.

Biostratigraphy, sedimentology, amino acid racemization, and paleomagnetic evidence indicate that the two localities are about the same age, between ~800,000 and 900,000 years old (Bell and Barnosky 2000; Barnosky and Bell 2004; Barnosky 2004a, Shabel et al. 2004). Sedimentologic and biotic evidence suggests that the fossil communities existed during a glacial episode, most likely oxygen-isotope stage 22, but possibly oxygen-isotope stage 20 (Barnosky et al. 2004a). The biostratigraphic and paleomagnetic data make it extremely unlikely that a substantially younger or older glacial stage is represented. By comparing a fossil community from a glacial time to a historic community of the present interglacial, we maximized the chances of finding differences between the communities of the two time slices. Therefore, any indications of similarity should be robust.

Detailed radiocarbon dating of fossil deposits that are younger than those of Porcupine Cave, but that are taphonomically analogous (Hadly 1999; Hadly and Maurer 2001), suggests that time-
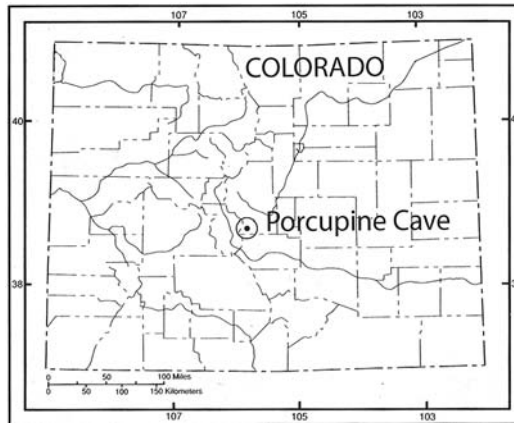
averaging in the Badger Room and Pit level 4 is less than 5000 years and potentially as little as a few hundred years. By combining the Badger Room and Pit level 4 deposits, we may increase the amount of time-averaging. However, the assemblage of mammals in the Pit is similar from level 4 through level 8, suggesting that counts of species would not be affected much even with increasing the time-averaging substantially above what we have assumed. For our purposes time-averaging is, in fact, a sampling advantage, because previous studies have shown that time-averaging of approximately 1000 years is needed to comprehensively sample all species within an 8 km radius of a site, and that fossil richness values increase only slightly with time-averaging greater than 1000 years (Hadly and Maurer 2001).

Taphonomic processes such as those that operated at Porcupine Cave have been shown to reliably sample both presence and relative abundance of most mammals that live within an ~8-18 km radius of the fossil deposit (Hadly 1999; Hadly and Maurer 2001; Porder et al. 2003). The large number of fossil specimens, combined with rarefaction analyses for the Pit Sequence (Barnosky 2004b), further justify our assumption that the fossil deposits adequately sample key aspects of the fossil community, with some caveats that we discuss in more detail below.

Given the likely sampling radius from which the fossil deposits were collected, we estimated the historic sample by counting those mammals whose historic range intersected a circle of 12.5 km radius centered on Porcupine Cave (Fig. 1). By "historic," we mean prior to significant range changes that were caused by European settlers within the last 200 years. The ranges of the historic mammals were taken from maps published by Fitzgerald et al. (1994). This radius seemed the best compromise in view of (a) its being near the midpoint of the probable minimum and maximum radius (8–18 km) from which the fossils were probably collected; (b) the resolution of available maps (Fitzgerald et al. 1994); and (c) the fact that decreasing or increasing the sampling radius by a few km would not substantially change the counts of species.

Taxonomic identifications of fossil material relied primarily on dental and cranial remains, which also are diagnostic in the extant members of the same species or congeners, and are detailed in Barnosky (2004a). The ability to recognize the involved Quaternary species reasonably consistently by using either dental-cranial criteria or soft anatomy (coat color, tail length, etc.) largely mitigates the problem that could potentially arise by comparing the list of historic species (identified largely from soft anatomy) with the list of fossil species. The same higher-level taxonomy was applied consistently to fossil and modern species, following Wilson and Reeder (1993) in most cases (Shabel et al. 2004).

Autecology of the involved species follows standard references (Fitzgerald et al. 1994; Nowak 1999; Wilson and Ruff 1999). Autecological interpretations of fossil species were detailed previously (Shabel et al. 2004). We followed the convention of defining size categories as small (average adult biomass < 0.5 kg), medium (= 0.5–8.0 kg), and large (> 8.0 kg) (Legendre 1986). Lists of taxa recovered from the fossil deposits and the historic sample, with their trophic and size categorization, are given in Appendix 1. We did not include domestic animals in the historic counts (e.g., horses, cows, sheep, domestic cats and dogs, etc.). Neither were shrews nor bats included in the study, because they are not well enough sampled to allow reasonable comparisons between the fossil and historic data sets.

We used chi-square tests to assess the statistical significance of differences between the numbers of fossil and historic species in each trophic and size class, using algorithms in the program JMP IN 5.1 (2002, SAS Institute, Inc., Cary, North Carolina 27513).

RESULTS

Table 1 lists the numbers of species identified in each size and trophic class in the fossil com-

munity and in the historic community. The chi-square tests revealed no statistically significant differences between total historic and fossil species richness, or between any of the various pairs of size or trophic categories, with p-values for observed differences being due to chance alone ranging from 0.15 to 0.39. However, small numbers of species in some categories reduce the power of statistical comparisons, so to fully explore our data we discuss the largest qualitative differences. Two qualitative differences are obvious — small herbivores are more species-rich in the fossil community (20 versus 13 species), and large omnivores are more diverse in historic time (1 versus 3 species). In all other categories, including the total number of species, the counts are remarkably similar, given that some 850,000 years separates the two communities.

Numbers of species and genera within higher taxa exhibit both similarities and differences between the two time periods (Table 2). Similarities include stable numbers of species in Artiodactyla, and in numbers of genera of Rodentia, Artiodactyla, and all taxa combined. Differences include more fossil rodent species, more fossil lagomorph species and genera, fewer fossil Carnivora, two fossil horse species, and a fossil xenarthran.

TABLE 1. Species richness in trophic and size categories for mid-Pleistocene and historic mammal communities in the Porcupine Cave region.

In each column, the number to the left of the colon indicates the number of species in the mid-Pleistocene fossil community, and the number to the right of the colon indicates the number of species present within 12.5 km of Porcupine Cave during historic time (prior to significant European contact). The small and medium herbivore counts for the mid-Pleistocene include the rodents and lagomorphs of Pit Sequence level 4 plus taxa found in the Badger Room. All other counts for the mid-Pleistocene are exclusively from the Badger Room. Small = average adult biomass < 0.5 kg; Medium = 0.5–8.0 kg; Large = > 8.0 kg.

	Size class and trophic group			
	Small	*Medium*	*Large*	*Total*
Herbivores	20 : 13	6 : 7	8 : 7	34 : 27
Carnivores	2 : 3	4 : 4	7 : 7	13 : 14
Omnivores	2 : 2	2 : 3	1 : 3	5 : 8
TOTALS	24 : 18	12 : 14	16 : 17	52 : 49

TABLE 2. Taxonomic richness within orders for species and genera in the mid-Pleistocene and historic communities.

In each column the number to the left of the colon indicates the number of taxa in the mid-Pleistocene fossil community, and the number to the right of the colon indicates the taxa present within 12.5 km of Porcupine Cave during historic time (prior to significant European contact).

Taxon	*Species*	*Genera*
Rodentia (rodents)	24 : 20	16 : 16
Carnivora (carnivores)	15 : 19	11 : 13
Artiodactyla (deer, sheep, etc.)	5 : 5	5 : 5
Lagomorpha (rabbits, pikas)	5 : 4	5 : 3
Perissodactyla (horses, etc.)	2 : 0	1 : 0
Xenarthra (sloths)	1 : 0	1 : 0
Primates (humans)	0 : 1	0 : 1
TOTALS	52 : 49	39 : 38

For small mammals, which are represented by the most specimens and are therefore probably the most reliably sampled, the numbers of species within genera exhibit considerable stability (Table 3). The biggest difference between the communities of the two time periods is a decrease in the number of vole and lemming species, from nine in the fossil community to four in the historic one.

Within higher taxonomic groups, species composition is not stable. Some of the fossil species are extinct congeners of species currently living in the area, and others are extralimital in the sense that they are extant but do not range into our historic sampling radius (Shabel et al. 2004). Overall, about 40% of the species that compose the fossil community are not there today, although in most cases they are represented by functional analogs. For example, whereas the fossil fauna includes an extinct prairie dog species (?*Cynomys andersoni*), an extant congener is found in the historic sample (Barnosky 2004b). Lagomorphs seem to maintain approximately equal numbers of species, but those species are shifted among genera, as illustrated by the counts in Table 2.

Discussion

The difference in small herbivore richness appears to be due, in part, to the fact that a glacial community (the fossil one) is being compared to an interglacial one (the historic sample). Previous work has documented that in this part of Colorado, fewer species of small herbivores are present in the comparatively xeric interglacials than in the more mesic glacials (Barnosky 2004b; Barnosky et al. 2004a). That pattern seems to repeat in the Great Basin where mid-Holocene xeric episodes feature fewer species of small herbivores than more mesic times (Grayson 1998). At Porcupine Cave, the transition from the glacial-age fossil community we analyzed here (that of Pit Sequence level 4) to the superjacent xeric interglacial (Pit levels 3, 2, and 1) that we have reported in previous publications (Barnosky 2004b; Barnosky et al. 2004a) is marked by a drop in small herbivore richness from 20 to 16 species, compared to the 13 species present in historic time. Three of the small herbivore species lost at this time were voles (*Allophaiomys, Phenacomys gryci, Mimomys*), and one is a pocket gopher (*Thomomys*) — all are taxa that prefer relatively mesic microhabitats (Fitzgerald *et al.* 1994; Hadly 1999; Wilson and Ruff 1999). On this basis we infer that climatic events such as glacial-interglacial transitions cause numbers of small herbivores to fluctuate, but that the number of species that characterize similar climatic intervals are not dramatically different. Climatic effects on the geographic ranges of small herbivores have been widely reported for other glacial-interglacial transitions as well (Graham and Grimm 1990).

Some of the other differences in small and medium herbivore counts can also be explained by the fact that we are comparing a fossil glacial with a historic interglacial. In interglacial mid-Pleistocene levels of Porcupine Cave (Barnosky 2004b; Barnosky et al. 2004a), the count for overall numbers of Rodentia and Lagomorpha are 20 and 4, respectively, as they are for the historic sample. Within genera or families, the ancient and historic tallies for *Thomomys* and leporids reach parity when the mid-Pleistocene interglacial samples are used (Barnosky 2004b; Barnosky et al. 2004a).

A second possibility for enhanced mid-Pleistocene species richness of small herbivores is that time-averaging has inflated the species count. Whereas the modern counts are based on a temporal snapshot that encompasses less than a century, the fossil counts are based on samples that accumulated over hundreds or perhaps a few thousand years.

In view of these two confounding factors (comparing a glacial with an interglacial, and the potential for time-averaging to inflate our estimates), it is difficult to confidently interpret the differences between the counts in fossil and modern species of small herbivores. However, our conservative assessment is that there are fewer small herbivore species in the historic sample, and that it is in this size category that most fluctuation takes place in species numbers through time, largely in response to climatic fluctuations. Species of arvicolines and *Neotoma* account for most of the reduction (Barnosky 2004b; Barnosky et al. 2004a; and Table 3).

Counts for fossil Carnivora are very likely too low because of sampling considerations.

Carnivorans (especially large-bodied species) typically occur in low abundance in living communities, and unless they utilize caves as dens or hibernacula, their chances of preservation in places like Porcupine Cave are further reduced. That these effects may depress the fossil carnivoran counts in the Badger Room and Pit is illustrated by the situation for bears (ursids). Two species of *Ursus* are present in the historic sample, whereas no ursids occur in the fossil sample from the Badger Room or the Pit Sequence. However, ursids are known from other localities in Porcupine Cave (Barnosky 2004a; Barnosky et al. 2004a), suggesting that they could have been present in South Park at the time the Badger Room and Pit samples were accumulating. This would close the gap between the fossil and historic carnivoran sample. The only other histori-cally present carnivoran lacking in the fossil sample is the rac-coon (a procyonid). Members of this family tend to be rare in the

TABLE 3. Species richness within genera of small mammals in mid-Pleistocene and historic mammal communities in the Porcupine Cave region.

The mid-Pleistocene list is a composite of the Badger Room and Pit level 4 localities, and the historic list represents the taxa that were reported within a 12.5-km radius of Porcupine Cave during historic time (prior to significant European contact).

Taxon	mid-Pleistocene	Historic
Ochotonids (pika)	1	1
Leporids (rabbit)	4	3
Marmota (marmot)	1	1
Spermophilus (ground squirrel)	2	3
Cynomys (prairie dog)	2	1
Tamiasciurus (red squirrel)	1	1
Tamias (chipmunk)	1	2
Sciurus (gray squrrel)	0	1
Thomomys (pocket gopher)	2	1
Neotoma (wood rat)	3	1
Peromyscus (deer mouse)	1	1
Arvicolines (voles, lemmings)	9	4
Ondatra (muskrat)	1	1
Zapus (jumping mouse	0	1
Erethizon (porcupine)	1	1
Castor (beaver)	0	1
TOTALS	29	24

fossil record, and it is unclear whether their absence from the fossil fauna from Porcupine Cave is biologically meaningful, or if it is a sampling artifact.

These taphonomic considerations suggest that the gap in species richness between the fossil and historic communities may be even narrower than Table 1 indicates. In the large omnivore category, humans are counted in the historic sample, which we considered valid in view of Native American use of the landscape. Others might argue that humans should not be included in the overall mammal tally. Deleting humans would make the historic and fossil counts closer.

A fluctuation in species richness that may be obscured by the nature of our data is the end-Pleistocene extinction of very large mammals (those > 44 kg) (Martin and Klein 1984; Barnosky 1989; Alroy 1999; Grayson and Meltzer 2003; Barnosky et al. 2004a,b). Our sample is from a time at least 800,000 years before the end-Pleistocene event, and includes at least four species that disappeared from North America at the end of the Pleistocene: the two species of horse, the peccary, and the xenarthran (Table 2 and Appendix 1). A species of mammoth (*Mammuthus*) was not present in our sample (perhaps for taphonomic reasons) but was present in Colorado at the end-Pleistocene (FAUNMAP Working Group 1994). Elsewhere, we (Barnosky 1989; Barnosky et al. 2004b) and many others (Martin and Klein 1984; Alroy 1999; Martin and Steadman 1999; Alroy

2001) have argued that humans influenced species richness at the end of the Pleistocene in North America through interactions with megafauna such that many large-bodied species were deleted from communities. The absence of horses and sloths from around Porcupine Cave may well reflect this end-Pleistocene effect. If so, it is striking that compensations since the Late Pleistocene have resulted in a net loss of only one large herbivore species in historic time relative to the mid-Pleistocene fossil sample. If mammoths were present and not sampled in the mid-Pleistocene, this net loss of large herbivores would climb to two species, and a more striking community difference would be evident in the total absence of elephant-sized species historically.

Conclusions

When we account for the biases intrinsic to the fossil record, we find surprisingly little difference in overall species richness, or in species richness within major trophic and size categories, between a mid-Pleistocene mammal community and a historic one in the high elevation environment at South Park, Colorado. Total numbers of species in the two time slices are close (52 and 49, respectively), with the main differences accounted for by a decrease in the number of small herbivore species, which we attribute to the effects of climatic fluctuations, and the loss of one or perhaps two large herbivore species, which may have been related to interactions with human immigrants in the late Pleistocene. In view of the major environmental perturbations — including six glacial-interglacial cycles and the immigration of human hunters — that affected the South Park area in the ~850,000 years since our fossil community lived, the similarity between ancient and historic species richness patterns appears more striking than the differences. These results suggest that in communities like the one we studied, there is long-term stability in overall species richness, and structural similarity in how richness is parsed across broad trophic and size categories. Put another way, even in the face of a series of dramatic environmental changes and the first-time introduction of humans into the ecosystem, the South Park mammal community responded with a change in overall species richness that was at most 10% (and probably closer to 5%).

We do not mean to imply that communities do not change through time — they clearly do. In South Park, these changes included a 40% turnover in the species that were present in the mid-Pleistocene, in addition to the relatively minor adjustments in species richness patterns we noted above. What we do suggest, however, is that in our study area species richness exhibited long-term stability, evidenced by a similar total number of species in the fossil and historic samples, and similarity in numbers of species in trophic and size categories. That species richness is so similar across these trophic and size categories, even though the two communities are separated by some 850,000 years, suggests long-term stability in the functional links between constituent species, even though the species may change through time. By "functional links" we mean the way species in one size and trophic category are connected to those in other trophic and size categories, for example, the number of small herbivore species that are available for consumption by medium size carnivore species. Clearly such links between size and trophic categories can change in many different ways, for example, by one species dropping out and the number of individuals of a different species in that category simultaneously increasing in abundance. However, our data suggest that one way that mammalian communities do not change much through time is by fluctuation in numbers of species within different trophic and size categories. This conception of stability in community structure (not in species composition) is consistent with observations of nestedness through time in montane mammal communities (Hadly and Maurer 2001), fluidity of mammalian species ranges at times of climatic change (Graham and Grimm 1990; FAUNMAP Working Group 1996), and constancy in mammalian species richness in communities through tens, hundreds, and thousands of years (Brown et al. 2001).

If it is true that under natural conditions species richness and community structure remain relatively stable through long periods of time, there are important implications for conservation biology. Species richness could provide a simple yet effective metric for assessing whether the functional properties of communities had been perturbed off of a long-term baseline. For example, in South Park, Colorado, we would interpret future changes in species richness to signal an unusual perturbation to the mammalian community if future overall richness deviated in excess of 10% relative to historic richness, because changes of that magnitude would exceed the differences between the ~850,000-year-old fossil community and the historic one. Particularly informative would be changes in the distribution of species richness among size and trophic categories, as that distribution seemed to have remained relatively stable in the absence of significant human impacts, and changes in it signify modification of functional links between species. Such changes now are taking place in the mammal community around Porcupine Cave, as demonstrated by the reduction of species in the large and medium carnivore categories in the past several decades (Barnosky et al. 2004a). As has been suggested elsewhere (Barnosky et al. 2003), changes in species richness are probably preceded by changes in relative abundance of individuals within species; thus, changes in species richness should be regarded as signs of major ecosystem perturbation, the early signs of which might be detected by detailed monitoring of population sizes and geographic range fluctuations.

We emphasize that our results so far apply only to the specific ecological system that we studied — high-elevation mammal communities in the central Rocky Mountains. However, several of North America's major nature preserves exist in similar settings, for example, Rocky Mountain National Park, the Greater Yellowstone ecosystem, and the Glacier-Waterton ecosystem, all of which are characterized by a core National Park surrounded by National Forest and private lands that are used for ranching, agricultural and silvicultural activities, and ecotourism. Thus, monitoring mammalian species richness in such areas may prove a fruitful exercise.

Other pertinent caveats to our suggestion about the stability of species richness include the sampling issues inherent in making comparisons between the fossil record and historic data, the fact that we have compared only two widely separated time slices, and that we have sorted trophic and size categories into conservatively large bins. In view of these caveats, our observations are offered not as a firm conclusion, but as a suggestion that the metric of species richness, especially as distributed across various size and trophic categories, will prove valuable in assessing the degree to which future perturbations shift communities from a long-term functional baseline. The ideas we put forth here can be fruitfully tested by comparing species richness patterns in fossil communities with historic and modern ones in a variety of ecological settings, where sampling issues have been treated appropriately. We note that this approach has been applied with success to both vertebrate (Hadly 1996; Hadly and Maurer 2001; Hadly 2003; Hadly et al. 2003) and invertebrate communities (Tang 2001; Jablonski et al. 2003; Alin and Cohen 2004), and suggest that it can provide a valuable merger between paleontologists, ecologists, and conservation biologists.

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APPENDIX

LIST OF FOSSIL AND MODERN SPECIES USED IN THIS ANALYSIS,
SORTED INTO SIZE AND TROPHIC CATEGORIES.

Small and medium herbivore count for mid-Pleistocene includes rodents and lagomorphs of Pit Sequence level 4 plus taxa found in the Badger Room; all other counts for mid-Pleistocene are exclusively from the Badger Room. Small = average adult biomass < 0.5 kg; Medium = 0.5–8.0 kg; Large = > 8.0 kg. In the right column, where two different English names apply to the same row, the English name for the mid-Pleistocene taxon is given to the left of the comma, and the name for the historic taxon appears to the right of the comma.

Mid-Pleistocene	Historic 12.5 km radius	English name(s)
Large carnivores		
Canis sp. "small canid" †		Small canid sp.
Canis latrans	*Canis latrans*	Coyote
Canis edwardii †	*Canis lupus***	Edward's wolf, Gray wolf
Lynx rufus	*Lynx rufus*	Bobcat
	*Lynx lynx***	Lynx
Taxidea taxus	*Taxidea taxus*	American badger
Miracinonyx cf. *M. inexpectatus*†	*Felis concolor*	Irvingtonian cheetah, Puma
Lutrinae, indet. †	*Gulu gulo***	Otter, Wolverine
Medium carnivores		
Mustela nigripes	*Mustela nigripes***	Black-footed ferret
Mustela sp. nov. †	*Mustela vison*	Mustelid sp. nov., American mink
Martes diluviana †	*Martes americana*	Extinct fisher, American marten
Vulpes vulpes	*Vulpes vulpes*	Red fox
Small carnivores		
Spilogale putorius	*Spilogale gracilis*	Eastern and Western spotted skunks
Mustela frenata	*Mustela frenata*	Long-tailed weasel
	Mustela erminea	Ermine
Large herbivores		
Erethizon dorsatum	*Erethizon dorsatum*	Porcupine
Antilocapra/Tetrameryx	*Antilocapra americana*	Pronghorn spp.
Antilocapridae, indet.	*Odocoileus hemionus*	Pronghorn indet., White-tailed deer
Equus sp. "small" †	*Cervus elaphus*	Small horse, Elk
Equus sp. "large" †	*Bison bison***	Large horse, Bison
Ovibovini, indet.	*Ovis canadensis***	Muskox sp., Bighorn sheep
Ovis sp. †	*Castor canadensis*	Sheep sp., Beaver
Paramylodon harlani †		Ground sloth
Medium herbivores		
Ondatra annectens †	*Ondatra zibethicus*	Extinct muskrat, Extant muskrat
Marmota sp.	*Marmota flaviventris*	Marmot sp., Yellow-bellied marmot
Cynomys cf. *C. leucurus**	*Cynomys gunnisoni*	Prairie dog sp., Gunnison's prairie dog

	Sciurus aberti	Abert's squirrel
Lepus sp.	*Lepus townsendii*	Jackrabbit sp., White-tailed jackrabbit
Sylvilagus sp.	*Sylvilagus nuttallii*	Cottontail sp., Mountain cottontail
Aztlanolagus sp. †	*Lepus americanus*	Aztlan rabbit, Snowshoe hare

Small herbivores

Spermophilus cf. *S. elegans* †	*Spermophilus elegans*	Wyoming ground squirrel
?*Cynomys andersoni,* sp. nov. †	*Spermophilus tridecemlineatus*	Prairie dog, Ground squirrel
*Tamiasciurus hudsonicus**	*Tamiasciurus hudsonicus*	Red squirrel
Tamias cf. *T. minimus**	*Tamias minimus*	Chipmunk sp., Least chipmunk
	Tamias quadrivittatus	Colorado chipmunk
Allophaiomys pliocaenicus †		Extinct vole
Phenacomys gryci †	*Clethrionomys gapperi*	Gryci's vole, Southern red-backed vole
Phenacomys sp. (not *gryci*)*	*Phenacomys intermedius*	Western heather vole
*Microtus paroperarius** †	*Microtus longicaudus*	Extinct microtus, Long-tailed vole
*Microtus meadensis** †	*Microtus pennsylvanicus*	Extinct microtus, Meadow vole
Microtus "5T form" †		"5T" vole
Mimomys virginianus †		Virginia mimomys
Lemmiscus sp.*		Sagebrush vole sp.
Mictomys kansasensis/meltoni †		Bog lemming sp.
Neotoma cinerea	*Neotoma cinerea*	Bushy-tailed woodrat
*Neotoma floridana**		Eastern woodrat
*Neotoma micropus**		Southern plains woodrat
Brachylagus sp.		Pygmy rabbit sp.
Ochotona cf. *O. princeps*	*Ochotona princeps*	Pika sp., American pika
Thomomys sp.	*Thomomys talpoides*	Pocket gophers
Thomomys cf. *T. bottae**		Pocket gopher sp.
	Zapus princeps	Western jumping mouse

Small omnivores

Spermophilus lateralis	*Spermophilus lateralis*	Golden-mantled ground squirrel
Peromyscus sp.	*Peromyscus maniculatus*	Deer mice

Medium omnivores

Mephitis mephitis	*Mephitis mephitis*	Striped skunk
Brachyprotoma obtusata †	*Bassariscus astutus*	Short-faced skunk, Ringtail
	Procyon lotor	Raccoon

Large omnivores

Platygonus sp. †	*Ursus americanus*	Peccary, American black bear
	*Ursus arctos***	Brown bear
	Homo sapiens	Human

Small insectivores

Sorex sp.	*Sorex* spp.	Shrews
Chiroptera, indet.	*Chiroptera* spp.	Bats

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* = added from Pit Level 4   ** = extirpated since Historic   † = extinct