

## Dung, diet, and the paleoenvironment of the extinct shrub-ox (*Euceratherium collinum*) on the Colorado Plateau, USA

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### Abstract

Fossil remains of *Euceratherium collinum* (extinct shrub-ox) have been found throughout North America, including the Grand Canyon. Recent finds from the Escalante River Basin in southern Utah further extend the animal's range into the heart of the Colorado Plateau. *E. collinum* teeth and a metapodial condyle (foot bone) have been recovered in association with large distinctively shaped dung pellets, a morphology similar to a 'Hershey's Kiss' (HK), from a late Pleistocene dung layer in Bechan Cave. HK dung pellets have also been recovered from other alcoves in the Escalante River Basin including Willow and Fortymile canyons. Detailed analyses of the HK pellets confirmed them to be *E. collinum* and indicate a browser-type diet dominated (>95%) by trees and shrubs: *Artemisia tridentata* (big sagebrush), *Acacia* sp. (acacia), *Quercus* (oak), and *Chrysothamnus* (rabbit brush). The retrieval of spring and fall pollen suggests *E. collinum* was a year-round resident in the Escalante River Basin. © 2006 University of Washington. All rights reserved.

**Keywords:** Pleistocene; Dung; Bechan Cave; Escalante River Basin; *Euceratherium*; Paleoenvironment; Microhistology; Pollen

### Introduction

The shrub-ox, *Euceratherium collinum* (Artiodactyla, Ruminantia, Bovidae, Ovibovini), along with several related taxa, represent a little studied and poorly understood group of extinct North American ovibovids (Frick, 1937; Scott, 1962; Martin and Wright, 1967; Nelson and Neas, 1980; Harris, 1985). *Euceratherium* is the earliest known ovibovid to enter North America, appearing in the early Irvingtonian Land Mammal Age of the Pleistocene, possibly 1.1 Ma (Kurtén and Anderson, 1980). The morphology of the animal and its relationship to other bovids is inferred from a moderate amount of skeletal material found in two caves, including the type locality in northern California (Sinclair and Furlong, 1904; Furlong, 1905; Sinclair, 1905). Radiocarbon dates taken on dung pellets, having a distinctive shape resembling a 'Hershey's Kiss' (HK) and assumed by Mead and Agenbroad (1992) to belong to *Euceratherium*, indicate extinction as late as 11,500 <sup>14</sup>C yr BP.

However, the rationale for the identification of the dung has not been presented until now.

One of the most remarkable finds in the American Southwest has been the preservation of dung remains from Pleistocene animals such as *Mammuthus* (mammoth; Mead et al., 1986a), *Nothrotheriops* (ground sloth; Martin et al., 1961), and various pellet-producing artiodactyls, including *Oreamnos harringtoni* (Harrington's mountain goat; Mead et al., 1986c) in dry caves (Davis et al., 1984; Mead et al., 1984; Agenbroad et al., 1989; Mead and Agenbroad, 1992; Mead et al., 2003). Large distinctively shaped dung pellets (HK pellets), with an average cylindrical diameter of 14.5 mm and length of 19.3 mm, tapered on one end only, with a flat to concave shape on the opposite end (giving them their distinctive 'Hershey's Kiss' morphology), are located in numerous alcoves and caves within the Escalante River Basin, southern Colorado Plateau (Table 1; Mead and Agenbroad, 1992). The purpose of this study is to characterize and identify the HK dung pellets, previously assumed to belong to *Euceratherium collinum*, and to describe the diet from extracted microhistological remains and pollen preserved in the pellets. This study permits a better understanding of the natural history of an extinct and enigmatic herbivore.

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Table 1  
Locations of *Euceratherium* remains in the Intermountain West

Location	Deposit	Remains	Age	Reference/Species
(1) Bechan Cave, UT	Cave	Tooth, dung	11,630±150 yr*	Mead and Agenbroad, 1992, <i>E. collinum</i>
(2) Cottonwood Alcove, UT Site 42SA20858	Alcove	Dung	12,510±190 yr*	Mead and Agenbroad, 1992, <i>E. collinum</i>
(3) Grobot Grotto, 40 Mile Canyon, UT	Alcove	Dung	20,930±400 yr* 18,320±290 yr*	Mead and Agenbroad, 1992, <i>E. collinum</i>
(4) Hooper's Hollow, 40 Mile Canyon, UT	Alcove	Dung	18,840±350 yr dated by assoc.	Mead and Agenbroad, 1992, <i>E. collinum</i>
(5) Oak Haven, Willow Gulch, UT	Alcove	Dung	9169±100 yr to 11,690±660 yr dated by assoc.	Mead and Agenbroad, 1992, <i>E. collinum</i>
(6) Shrub-ox Alcove, Willow Gulch, UT	Alcove	Dung	12,690±180 yr to 23,100±660 yr dated by assoc.	Mead and Agenbroad, 1992, <i>E. collinum</i>
(7) Eastern Grand Canyon Caves AZ; CB:8:1 CC:5:3	Cave	– Phalanx calcaneus	Late Pleistocene	Mead et al., 2003 <i>E. collinum</i>
(8) Rio Arriba County, NM	Valley deposits	Cranial fragment, part horn core	Pleistocene	Simpson, 1963 <i>E. collinum</i>
(9) Deadman Cave, Pima County, AZ	Cave, pebbly silt	Mandible with teeth	8000–12,000 yr BP	Mead et al., 1984 <i>E. collinum</i>
(10) Anza Borrego State Park, CA	Sands, muds, silts and clays	No bones described	1.7–2.0 Ma	Downs and White, 1968, Opdyke et al., 1977 mentioned <i>E. collinum</i>
(11) Muskox Cave, Eddy County, NM	Cave	No bones described	Pleistocene	Logan, 1981 mentioned <i>Preptoceras sinclairi</i> (Bush-ox)
(12) Burnet Cave, Carlsbad, NM	Aeolian and colluvial deposits	Cranium with horn cores, palate with teeth, metacarpal, 1st and 2nd phalanx, astragalus	Rancholabrean	Shultz and Howard, 1935, assigned to <i>E. collinum morrisoni</i> and <i>Preptoceras sinclairi neomexicana</i>
(13) Mineral Hill Cave, Carlin, NV	Mixed gravel and rocks	Phalange	not mentioned	McGuire, 1980 <i>E. collinum</i>

\* = direct radiocarbon analysis.

HK pellets are represented in six alcoves on the Colorado Plateau (Table 1; Fig. 1). Excavations completed in the early 1980s at Bechan Cave first revealed the presence of a stratum, up to 40 cm thick (>300 m<sup>3</sup>), containing dung (predominantly *Mammuthus*) and skeletal remains of Pleistocene mammals dating between 14,700 and 11,000 <sup>14</sup>C yr BP (Mead et al., 1986a). The HK dung pellets were found in loose association with *E. collinum* skeletal remains (a dentary second molar (M<sub>2</sub>) and a metapodial condyle; Kropf, 2005).

Surveys conducted in Fortymile Canyon and Willow Gulch in the middle to late 1980s recovered HK pellets, similar in morphology and size to those found in Bechan Cave (Mead and Agenbroad, 1992). HK pellet samples were collected from the loosely compacted flat surface sediments within alcoves and from sloping erosional deposits. Table 1 presents the alcoves containing these distinctive dung pellets. HK dung pellets were dated directly and by stratigraphic association by Mead and Agenbroad (1992).

#### Study area

The Escalante River Basin, located in southern Utah at the center of the Colorado Plateau, contains countless deeply entrenched canyons formed predominantly in the Navajo Sandstone. The formation has numerous alcoves and caves that provide a unique arid habitat for the preservation of late

Pleistocene deposits containing the dry-preserved remains of plant macrofossils, pollen, dung, and skeletal material (Agenbroad et al., 1989).

Climate in the Escalante River Basin today is semiarid with seasonal rains and a mean annual temperature of 10–12°C. Vegetation communities in the Escalante River Basin include desert scrub along slick rock areas, riparian vegetation along permanent stream beds, hanging gardens near seeps, sagebrush along the dry sandy areas just above the stream beds, and a xeric landscape dominated by an open pinyon–juniper woodland above the canyon walls (Withers and Mead, 1993).

Bechan Cave is located in a semiarid tributary of the Colorado River just north of the confluence with the Escalante River in southern Utah. The cave, carved into the Navajo and Kayenta sandstone formations, is a single large room approximately 53 m deep. Fortymile Canyon and Willow Gulch are western tributaries of the Escalante River located less than 10 km west of Bechan Cave (Fig. 1). The numerous alcoves within the two entrenched canyons are shallow yet long, with high cliff overhangs.

#### Shrub-ox dung and diet

#### Dung morphology

Dung can be identified in several ways, including determining the morphological differences between whole dung

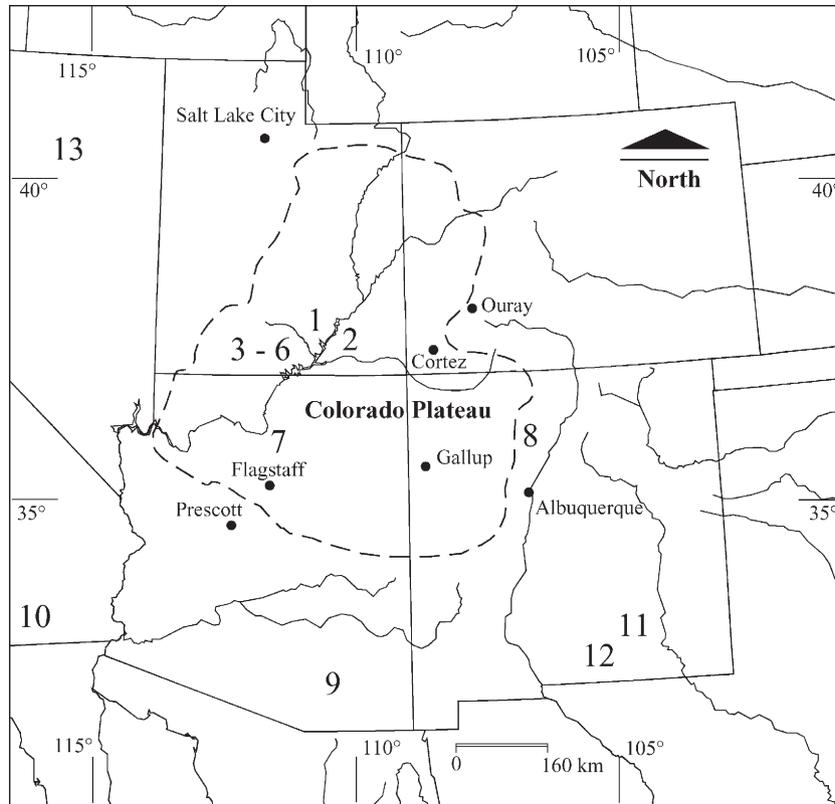


Figure 1. Map of the Colorado Plateau illustrating general locations of *Eucatherium collinum* sites in the Intermountain West. Numbered locations are listed in Table 1.

specimens, comparing dung pellet size and weight, and utilizing dietary information in association with craniodental morphology (Mead and Agenbroad, 1989). The type of graze or browse consumed by herbivores typically determines dung morphology (Mead and Agenbroad, 1989). For instance

*Equus* (horse), *Mammuthus*, and *Nothrotheriops* tend to pass large fragments through their guts, forming large boluses (Fig. 2). Many ruminants such as *Odocoileus* (deer), *Antilocapra* (pronghorn), *Cervus* (elk), *Oreamnos* (mountain goat), *Ovis* (bighorn sheep), and *Ovibos* (musk-ox) tend to produce small

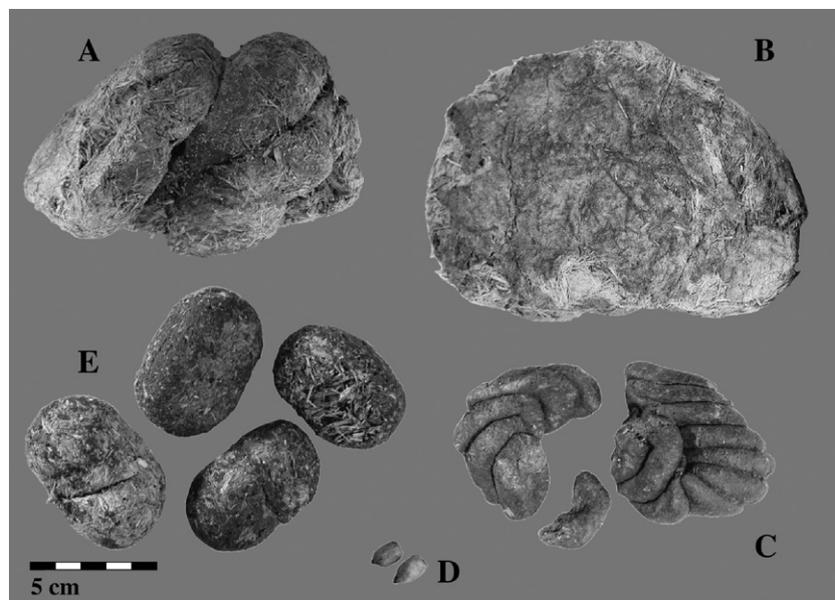


Figure 2. Dung comparison: A, *Nothrotheriops shastensis* (GRCA 59620). B, *Mammuthus* (GLCA 382). C, modern *Bison*, dry diet (NAUQSP 7322). D, modern *Odocoileus* (NAUQSP 6042). E, modern *Equus* (NAUQSP 6057). Photos by Sandra L. Swift.

dung pellets a centimeter or two in diameter (Fig. 3; Guthrie, 1992). Large bovids will produce large pellets or plates of dung (Fig. 2), but with a high water content the dung forms an amorphous mass (patty or cow pie) such as typical for *Bison* (bison) and *Bos* (cattle). The HK pellets from the dry alcoves are large cylindrically shaped pellets with a distinctive ‘Hershey’s Kiss’ type morphology (Fig. 3B). The pellets of *Ovibos moschatus* and *Bootherium* (the extinct helmeted muskoxen) tend to have a similar morphology, but the *Bootherium* pellets (average diameter and length of 18.13 mm and 21.15 mm, respectively) are much larger. *Cervus elaphus* produces a pellet that is generally similar in size to the HK pellets, but more oval-shaped with both ends rounded or tapered to a point. The HK morphology is common in the six alcoves listed in Table 1 from the Colorado Plateau and distinct from other known pellet-producing artiodactyls.

#### Skeletal differences due to diet

All pellet-producing artiodactyls can be separated into three feeding categories: browsers, grazers, and mixed feeders. Species that feed predominantly on tree and shrub foliage ( $\geq 90\%$ ) and eat  $\leq 10\%$  grass are considered browsers. Grazers are defined as those species consuming at least 90% of their diet as grass and  $\leq 10\%$  tree and shrub foliage. Mixed feeders are those species that have between 10 and 90% grass in their diet (Janis and Ehrhardt, 1988; Pérez-Barbería et al., 2001). Using approximate measurements of the skull and dentary from published material and photos taken of *E. collinum* specimens at the Museum of Paleontology, University of California, Berkeley, analysis of the craniodental morphology of *E. collinum* can establish the animals’ feeding category (Janis and Ehrhardt, 1988; Janis, 1995; Solounias et al., 1995; Mendoza et al., 2002).

Solounias et al. (1995) suggest that the best discriminator of diet among extant ruminants is the presence of a prominence or protuberance on the anterior part of the maxillary fossa (Figs. 4 and 5). The robustness of this protuberance varies in bovids due to differences in the biomechanics of mastication. Among grazers the masseter muscle, which originates from the maxillary fossa, is generally larger than in browsers, because

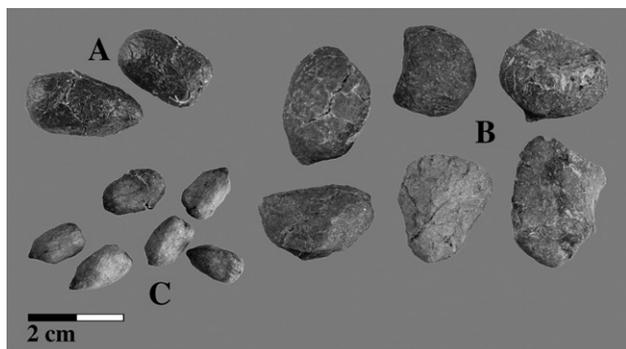


Figure 3. Dung pellet comparison: A, modern *Cervus* (NAUQSP 6146). B, *Euceratherium collinum* (GLCA 2788). C, modern *Odocoileus* (NAUQSP 6042). Photos by Sandra L. Swift.

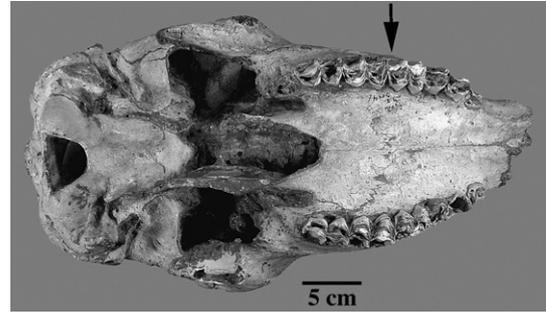


Figure 4. Ventral view of *Euceratherium collinum* skull (Specimen 1009 Museum of Paleontology, University of California). Arrow designates slight protuberance near the maxillary fossa.

of the tougher, more abrasive nature of their diet of grasses. The connection for the larger masseter muscle produces a large protuberance near the maxillary fossa (typically  $>3$  mm; Solounias et al., 1995; Fig. 5), while in browsers the protuberance is small or barely visible (typically  $<1$  mm; Solounias et al., 1995; Fig. 4). In mixed feeders the protuberance is intermediate in size between grazers and browsers. Examination of several maxillae of *E. collinum* indicates the almost imperceptible sign of a protuberance near the maxillary fossa—osteological evidence that *E. collinum* was a browser and not a grazer or mixed feeder.

Additional analysis was performed on craniodental variables involving hypsodonty index (the third lower molar tooth height divided by the length of the second lower molar; Janis and Ehrhardt, 1988), relative muzzle width (dividing the premaxillary width by the palatal width; Janis and Ehrhardt,

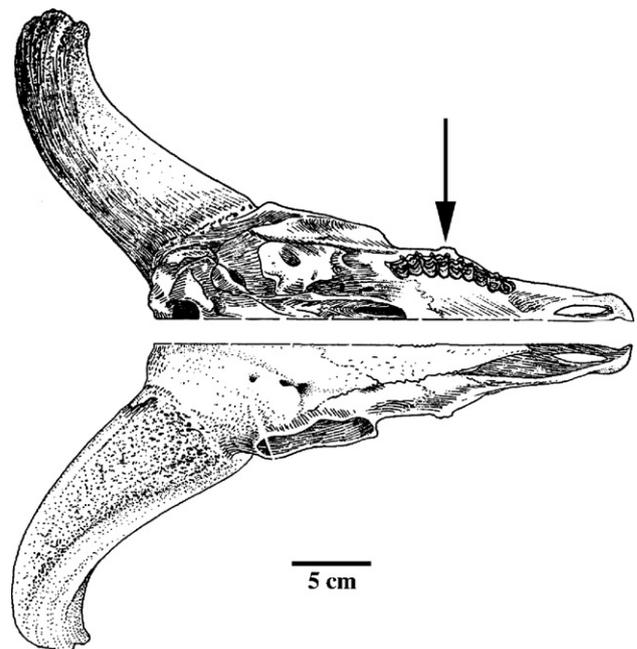


Figure 5. Ventral and Dorsal view of *Ovis canadensis* skull—mixed feeder/grazer (from Olsen, 1973 and modified. Reprinted courtesy of the Peabody Museum of Archaeology and Ethnology, Harvard University). Arrow designates protuberance near the maxillary fossa.

1988), and relative length of the premolar tooth row (length of the lower premolar row compared to the lower molar row; Mendoza et al., 2002). The craniodental variables for bovids appear to have significant overlap between browsers and mixed feeders, but significant distinction occurs between grazers and all other feeding types. For two of the craniodental variables, *E. collinum* falls within the mean for mixed feeders, but for the relative length of the premolar tooth row the *E. collinum* value tended to be closer to browsers. Because of the abrasive nature of grasses, the hypsodonty index for grazers is almost always higher than for browsers or mixed feeders and has always been considered a good indicator of diet, but Janis (1988) states that animal habitat may be more important in determining the degree of hypsodonty than dietary preference. Ungulates preferring open habitats and ground-level vegetation tend to be more hypsodont, because of grit accumulation on plant material. In summary, *E. collinum* shared similarities with browsers and mixed feeders in relative muzzle width and hypsodonty index, but it was more similar to browsers in relative length of the premolar tooth row. *E. collinum* was clearly not a grazer.

#### Dung and diet

Large remains of plants can be easily recognized in the boluses of *Mammuthus* and *Nothrotheriops shastensis*; however, identifying plant macrofossils is much more difficult in pellet-producing ruminants. Ruminants tend to chew all their food into finer components (Mead and Agenbroad, 1989). Therefore, in order to place the HK dung pellets into a definitive dietary classification, a detailed analysis using techniques of microhistology and palynology was utilized to determine diet and paleoenvironment.

Microhistology is the study of microfossil plant remains, consisting of insoluble parts such as phytoliths and cuticles that have traveled through and survived the digestive track of the animal. Research in general has shown that a good relationship exists between the plants consumed and the plant microfossils excreted as dung, but there is potential for error due to some plant species, such as forbs, not surviving digestion (Sparks and Malechek, 1968; Todd and Hansen, 1973; Gardner et al., 1993). Pollen is able to survive most environmental degradation and digestion. Analysis of pollen from dung can help recreate a more regional picture of the paleoenvironment (Bradley, 1999). However, pollen from dung may not be representative of the diet of the animal, because the animal may ingest it directly through the consumption of a flower, or indirectly, if the pollen settled or attached to the leaves of the plants in its diet (Thompson et al., 1980; Mead et al., 1986b; Davis and Anderson, 1987). Few studies of the dung of animals living today have shown a high correlation between the plant species consumed and the pollen present in the dung (Mead et al., 1987). However, pollen can help designate the time of year plants were consumed (Thompson et al., 1980; O'Rourke and Mead, 1985; Mead et al., 1987).

It is immediately apparent from the preliminary results of the microhistology data in Table 2 that the HK pellets are

from a browser, with  $\geq 95\%$  of each pellet consisting of tree or shrub foliage and  $\leq 5\%$  grass. In contrast, the diet of *O. harringtoni* was varied and consisted of grasses, sedges, shrubs, and conifer trees (a mixed feeder), while *Mammuthus* and *Bison* dung consisted predominantly of grasses and sedges (grazers; see Tables 2, 3, and 5 in Mead and Agenbroad, 1989). Could the restrictive dietary results from the HK pellets be a result of food availability? This is unlikely, because we know from analysis of *Mammuthus* and *Bison* dung, in the same stratigraphic unit as *Euceratherium* in Bechan Cave, that grasses and sedges were present and available in the region, yet the producer of the HK pellets did not consume these plants. The diet suggested by the microhistological data indicates a non-grazer, and since *E. collinum* was the only non-grazer whose skeletal remains were found at Bechan Cave, we conclude that the HK pellets were produced by *E. collinum*.

The main dietary components recovered from the *E. collinum* HK pellets included *Artemisia tridentata*, *Acacia* sp., *Oenothera* sp. (evening primrose), *Quercus*, *Rhus* sp. (sumac), and *Chrysothamnus* sp. (Table 2—includes the microhistological results for *E. collinum* HK pellets 1 thru 12 and pollen analysis for pellets 6, 7, and 12). In pellets 6 and 7, *Artemisia* pollen was found in association with plant fragments of *Chrysothamnus* and *Quercus*. As previously mentioned, pollen can designate the time of year plants identified in the pellet were consumed. The presence of abundant *Artemisia* pollen (70% to 87%) in the two pellets suggest the browse plants, *Chrysothamnus* and *Quercus*, were consumed during the fall when *Artemisia* generally blooms. A large percentage of spring pollen (78%) from either *Amelanchier* (serviceberry) or *Quercus* was recovered from pellet 12. It suggests the predominant browse, *Acacia*, was consumed during the spring when *Amelanchier* and *Quercus* typically bloom. Our investigation into the dietary habits of *E. collinum* indicates a change in the dominant browse consumed from spring to fall and suggests *E. collinum* had a year-round presence in the region.

#### Dung morphometrics

In addition to dietary evidence, the sizes, weight, length, and diameter of dung pellets from a variety of extinct and extant artiodactyl species (*Antilocapra americana*, *Cervus elaphus*, *Odocoileus* spp., *Oreamnos americanus*, *Oreamnos harringtoni*, *Ovis canadensis*, *Bootherium*, and *Lama* (llama)), were compared to the HK pellets. The dried fecal material was weighed using a triple beam balance and measured using electronic digital calipers. Length of fecal pellets was measured along a line parallel to the direction the dung was expelled, which is the direction of taper typically exhibited by one end of the pellet. *Alces alces* (moose), *Camelops* (extinct camel), and their ancestors were not included in this analysis, because of their much larger size (Mead et al., 1986c). However, *Lama* was included because of the similarity in fecal pellet size and because several sites containing extinct fossil llama (*Hemiauchenia* and *Palaeolama*) occur in close proximity to the Colorado Plateau (Kurtén and Anderson, 1980; Harris, 1985). All fossil and modern dung samples were curated at the Laboratory of

Table 2  
Percent relative density of plant fragments and pollen for 12 *E. collinum* HK pellets

Alcove	Grobot Grotto						Hooper's Hollow			Bechan Cave					
	1m	2m	3m	4m	5m	6m	6p	7m	8m	7p	9m	10m	11m	12m	12p
Pellet #															
Plants															
Bark	–	2	3	–	–	–	–	–	–	–	2	–	–	–	–
<i>Acacia</i>	–	–	–	1	1	–	–	21	2	–	–	–	–	49	–
<i>Agropyron</i>	–	1	–	–	–	–	–	–	–	–	–	–	2	–	–
cf. <i>Amelanchier</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	78
<i>Ambrosia</i>	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–
<i>Artemisia</i>	–	–	–	–	–	–	70	–	–	87	–	–	–	–	–
<i>Artemisia tridentata</i>	4	95	–	–	24	3	–	–	–	–	97	1	42	21	–
<i>Atriplex</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Betula</i>	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
<i>Chrysothamnus</i>	2	–	–	–	62	94	–	–	–	–	–	–	1	–	–
<i>Descurainia</i>	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
<i>Ephedra</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
<i>Equisetum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
<i>Fraxinus</i>	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
<i>Mimosa</i>	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Oenothera</i>	–	–	–	–	–	–	–	–	–	–	–	23	13	–	–
<i>Phoradendron</i>	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
<i>Picea</i>	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
<i>Pinus</i>	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Poaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
<i>Polemonium</i>	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
<i>Quercus</i>	81	1	97	99	11	2	–	79	98	–	–	74	35	14	–
<i>Ribes</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
<i>Rhus</i>	–	–	–	–	–	–	–	–	–	–	–	–	7	15	–
<i>Sphaeralcea</i>	–	–	–	–	–	–	2	–	–	–	–	–	–	–	13
<i>Sporobolus</i>	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stipa</i>	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–

Microhistological analysis was performed on all 12 dung pellet samples. Pollen analysis was only performed on dung pellets 6, 7, and 12. Abbreviations: m, microhistology sample; p, pollen sample (in shaded columns).

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Ninety-four complete pellets of the distinctive HK shape were analyzed in our study. Comparative samples of modern *A. americana* and extinct *Bootherium* were fewer in number. The smaller sample of specimens for these mammals does not seriously affect the outcome of this analysis; they were included only to show the wide morphological variability between specimens. Simple statistical analysis was used to determine means and standard deviations between dung weight and size within individual species (Table 3). The results of individual measurements of dung pellets from nine species of artiodactyls are shown in Figures 6 and 7. Some similarities were noted between three artiodactyl species: *Lama*, *Bootherium*, *C. elaphus*, and the HK pellets.

The following results were obtained after testing for significant differences between HK pellets and *Lama*, *Bootherium*, and *C. elaphus* pellets. Diameters and weights of HK pellets were significantly different ( $p < 0.05$ ) from the diameters and weights of *Lama*, *Bootherium*, and *C. elaphus* pellets. HK pellets are significantly different ( $p < 0.05$ ) in length from *Lama* and *Bootherium* pellets; however, *C. elaphus* pellets did not test significantly longer or shorter ( $p > 0.05$ ) in length.

#### Discussion and conclusions: the natural history of *Euceratherium collinum*

Previously confirmed identities of extinct herbivore dung from the dry alcoves and caves of the Colorado Plateau include *Bison*, *Mammuthus*, *Nothrotheriops*, and *Oreamnos harringtoni*.

Table 3  
Dung measurements

	<i>O. americanus</i>			<i>O. canadensis</i>			<i>O. hemionus</i>		
	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.
Mean	8.71	12.16	0.22	8.82	13.86	0.25	9.00	12.84	0.32
Stdev	1.28	2.04	0.06	0.87	1.77	0.06	1.54	2.37	0.17
	<i>C. elaphus</i>			HK pellets			<i>Lama</i>		
	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.
Mean	13.97	19.46	0.70	14.54	19.25	1.06	10.25	17.29	0.41
Stdev	1.72	2.73	0.31	2.01	2.59	0.21	1.21	2.73	0.12
	<i>O. harringtoni</i>			<i>Bootherium</i>			<i>A. americana</i>		
	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.	Dia.	Lt.	Wt.
Mean	11.47	15.59	0.43	18.13	21.15	1.45	9.43	11.56	0.19
Stdev	0.93	1.98	0.09	0.98	1.60	0.20	0.62	2.08	0.03

Dia. = diameter, Lt. = length, Wt. = weight, Stdev = Standard deviation.

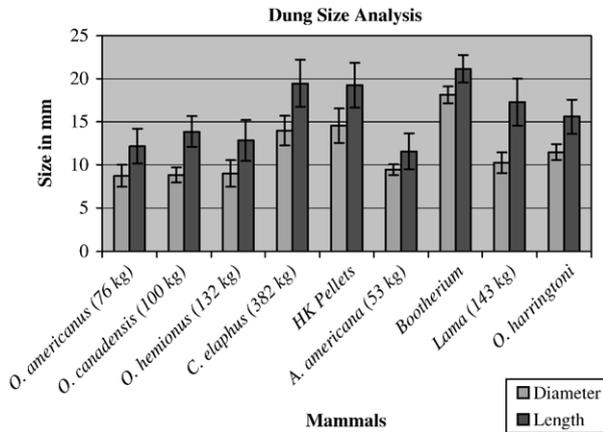


Figure 6. Bar graph comparing diameter and length of dung pellets. Kilograms in parentheses are average body weights of adult male ruminants. Error bars illustrate one standard deviation.

Here we provide evidence confirming the identity of the dung of yet another extinct herbivore, *Euceratherium collinum*, that produced dung pellets with a distinctive morphology that are typically larger in size than pellets of other artiodactyl species presently known from the Colorado Plateau (i.e. *C. elaphus*, *Ovis*, and *Odocoileus*). The HK pellets were also found in association with *E. collinum* skeletal material, the only skeletal remains of a large mammal recovered at Bechan Cave. Analysis of the craniodental morphology and microhistology has provided correlative evidence that *E. collinum* was the most likely producer of the HK dung pellets. The HK dung specimens from Bechan Cave were collected from a late Pleistocene stratigraphic unit dating from 14,700 to 11,000  $^{14}\text{C}$  yr BP (Mead et al., 1986a). There is no confirmed skeletal evidence of *C. elaphus*, *O. americanus*, or llama (various extinct forms) recorded on the Colorado Plateau from the late Pleistocene. *C. elaphus* fossil remains have been found as near as New Mexico, Texas, and Oklahoma, but are more common east and north of Missouri (Kurtén and Anderson, 1980; Thomas and Toweill, 1982; Harris, 1985). Fossil sites containing late Pleistocene remains of *Hemiauchenia* have been located no closer than southeastern Arizona and the Albuquerque Basin (Lindsay, 1978; Morgan and Lucas, 2000). *O. americanus* remains have not been found any farther south than Idaho and northern Wyoming (Mead and Lawler, 1994).

Ever since Eames' (1930) description of plant macrofossils in dung of extinct *Nothrotheriops shastensis*, the use of Pleistocene dung has been important in recreating the paleoecology of the American Southwest. Previous studies of Pleistocene dung from the Colorado Plateau have provided good data on the diets and paleoenvironments of extinct *N. shastensis*, *Oreamnos harringtoni*, and *Mammuthus*. From the Bechan Cave dung, Mead and Agenbroad (1989) investigated the dietary history of two extinct species, *N. shastensis* and *Mammuthus*. The two dominant dietary components included grasses and sedges, with other plant remains consisting of *Atriplex* (saltbush), *Artemisia tridentata*, *Betula occidentalis* (water birch), *Picea pungens* (blue spruce) and cactus (Mead et al., 1986a; Mead and Agenbroad, 1989).

Although *Artemisia tridentata* and *Quercus* sp. are well represented in the diet of *E. collinum* and as pollen in the dung layer of Bechan Cave, both are now uncommon near the cave. *Quercus* is typically found in cooler microenvironments in canyons where moisture is readily available year round. Withers and Mead (1993) interpret the gradual disappearance of *Quercus gambelii* within Fortymile Canyon as indicating a period of increasingly warmer climate with less precipitation. *Artemisia tridentata* also prefers cooler and more mesic conditions and therefore is not as common today in the canyons.

In summary, *E. collinum* was a year-round browser in the Escalante River Basin where the open, steppe-type paleoenvironment was dominated by grasses, sagebrush, and oaks. Evidence of *Betula occidentalis* and *Picea pungens* at Bechan Cave does suggest that, at minimum, an open boreal forest occurred in close proximity to the canyon habitat of *E. collinum*. However, there is no evidence *E. collinum* browsed these plants, indicating the animal restricted its diet to the steppe-type plants along the edges of the forests. Previous local plant and dietary research, along with data supplied by *E. collinum* HK pellets, indicates cooler and more mesic conditions. However, the environment inhabited by *E. collinum* changed during the Pleistocene/Holocene transition, with warmer and dryer conditions forcing a reorganization of the local plant community. Sub-alpine trees moved to higher elevations, while *Quercus* and *Artemisia* became less common and retreated to cooler habitats with more available moisture within the canyons (Withers and Mead, 1993; Anderson et al., 2000). Even though the local environment underwent significant change during the Holocene, the extinction of *E. collinum* within the Escalante River Basin is puzzling, because appropriate environments containing several of its favorite foods, sagebrush and oaks, are still present within the canyons or in nearby plateaus and mountains. Analysis of the dung contents has yet to address the carrying capacity of local environments. This aspect of changing environments has not been a focus in relation to the late Pleistocene extinction event/process.

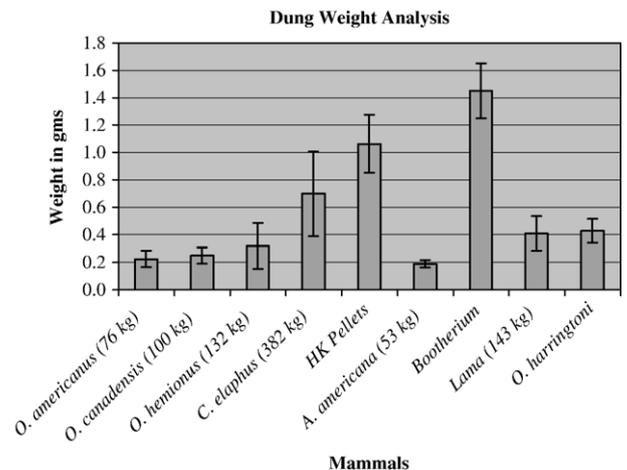


Figure 7. Bar graph comparing weight of dung pellets. Kilograms in parentheses are average body weights of adult male ruminants. Error bars illustrate one standard deviation.

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## References

- Agenbroad, L.D., Mead, J.I., Mead, E.M., Elder, D., 1989. Archaeology, alluvium, and cave stratigraphy: The record from Bechan Cave, Utah. *Kiva* 54, 335–351.
- Anderson, R.S., Betancourt, J.L., Mead, J.I., Hevly, R.H., Adam, D.P., 2000. Middle- and late-Wisconsin paleobotanic and paleoclimatic records from the southern Colorado Plateau, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155, 31–57.
- Bradley, R.S., 1999. *Paleoclimatology: Reconstructing Climates of the Quaternary*, 2nd edition. Hartcourt/Academic Press, Burlington, MA.
- Davis, O.K., Anderson, R.S., 1987. Pollen in packrat (*Neotoma*) middens: pollen transport and the relationship of pollen to vegetation. *Palynology* 11, 185–198.
- Davis, O.K., Agenbroad, L.D., Martin, P.S., Mead, J.I., 1984. The Pleistocene dung blanket of Bechan Cave, Utah. In: Genoways, H.H., Dawson, M.R. (Eds.), *Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday*. Carnegie Museum of Natural History, Special Publications No. 8. Pittsburgh, pp. 267–282.
- Downs, T., White, J.A., 1968. A vertebrate faunal succession in superposed sediments from late Pleistocene to middle Pleistocene in California. In: Malkovsky, M., Tejkal, J. (Eds.), *Proceeding of XXIII International Geological Congress, Section 10, Tertiary–Quaternary Boundary*. Academic Press, Prague, pp. 41–47.
- Eames, A.J., 1930. Report on ground sloth coprolite from Dona Ana County, New Mexico. *American Journal of Science* 20, 353–356.
- Frick, C., 1937. Horned ruminants of North America. *Bulletin American Museum Natural History* 69, 1–699.
- Furlong, E.L., 1905. Preptoceras, a new ungulate from Samwel Cave California. University of California Publications; Department of Geology 4, 163–169.
- Gardner, C.J., McIvor, J.G., Jansen, A., 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. *Journal of Applied Ecology* 30, 63–74.
- Guthrie, R.D., 1992. New paleoecological and paleoethological information on the extinct helmeted muskoxen from Alaska. *Annales Zoologici Fennici* 28, 175–186.
- Harris, A.H., 1985. *Late Pleistocene vertebrate paleoecology of the West*. University of Texas Press, Austin.
- Janis, C.M., 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: Russell, D.E., Santoro, J.P., Sigogneau-Russell, D. (Eds.), *Teeth revisited: Proceedings of the VIIth International Symposium on Dental Morphology*. Mémoires du Muséum national d'Histoire naturelle du Paris (série C), Paris, pp. 367–387.
- Janis, C.M., 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason, J. (Ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York, pp. 76–98.
- Janis, C.M., Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* 92, 267–284.
- Kropf, M., 2005. The extinct shrub-ox (*Euceratherium collinum*) and its late Quaternary environment on the Colorado Plateau. Unpublished master's thesis, Northern Arizona University, Flagstaff.
- Kurtén, B., Anderson, E., 1980. *Pleistocene Mammals of North America*. Columbia Univ. Press, New York.
- Lindsay, E., 1978. Late Cenozoic vertebrate faunas, southeastern Arizona. *Guidebook—New Mexico Geological Society* 29, 269–275.
- Logan, L.E., 1981. The mammalian fossils of Muskox Cave, Eddy County, New Mexico. *Proceedings of the Eighth International Congress Speleology* 1, 159–160.
- Martin, P.S., Sabels, B.E., Shulter Jr., D., 1961. Rampart Cave coprolite and ecology of the Shasta ground sloth. *American Journal of Science* 259, 102–107.
- Martin, P.S., Wright, H.E., 1967. Bestiary for Pleistocene biologists. In: Martin, P.S., Wright, H.E. (Eds.), *Pleistocene Extinctions; The Search for a Cause*. Yale University Press, New Haven and London, pp. 1–62.
- McGuire, K.R., 1980. Cave sites, faunal analysis, and big-game hunters of the Great Basin: a caution. *Quaternary Research* 14, 263–268.
- Mead, J.I., Agenbroad, L.D., 1989. Pleistocene dung and extinct herbivores of the Colorado Plateau, Southwestern USA. *Cranium* 6, 29–44.
- Mead, J.I., Agenbroad, L.D., 1992. Isotope dating of Pleistocene dung deposits from the Colorado Plateau, Arizona and Utah. *Radiocarbon* 34, 1–19.
- Mead, J.I., Lawler, M.C., 1994. Skull, mandible, and metapodials of the extinct Harrington's mountain goat (*Oreamnos harringtoni*). *Journal of Vertebrate Paleontology* 14, 562–576.
- Mead, J.I., Roth, E.L., Van Devender, T.R., Steadman, D.W., 1984. The Late Wisconsin vertebrate fauna from Deadman Cave, southern Arizona. *Transactions of the San Diego Society of Natural History* 20 (14), 247–276.
- Mead, J.I., Agenbroad, L.D., Davis, O.K., Martin, P.S., 1986a. Dung of *Mammuthus* in the arid Southwest North America. *Quaternary Research* 25, 121–127.
- Mead, J.I., Agenbroad, L.D., Martin, P.S., Euler, R.C., Long, A., Jull, A.J.T., Toolin, L.J., Donahue, D.J., Linick, T.W., 1986b. Extinction of Harrington's mountain goat. *Proceedings of the National Academy of Science* 83, 836–839.
- Mead, J.I., O'Rourke, M.K., Foppe, T.M., 1986c. Dung and diet of the extinct Harrington's Mountain Goat (*Oreamnos harringtoni*). *Journal of Mammalogy* 67, 284–293.
- Mead, J.I., Agenbroad, L.D., Phillips, A.M., Middleton, L.T., 1987. Extinct Mountain Goat (*Oreamnos harringtoni*) in Southeastern Utah. *Quaternary Research* 27, 323–331.
- Mead, J.I., Coats, L.L., Schubert, B.W., 2003. Late Pleistocene faunas from caves in the eastern Grand Canyon, Arizona. In: Schubert, B.W., Mead, J.I., Graham, R.W. (Eds.), *Ice Age Cave Faunas of North America*. Indian University Press, Bloomington and Indianapolis, pp. 64–86.
- Mendoza, M., Janis, C.M., Palmqvist, P., 2002. Characterizing complex craniodental patterns related to feeding behavior in ungulates: a multivariate approach. *Journal of Zoology* 258, 223–246.
- Morgan, G.S., Lucas, S.G., 2000. Pliocene and Pleistocene vertebrate faunas from the Albuquerque Basin, New Mexico. *Bulletin—New Mexico Museum of Natural History and Science* 16, 217–240.
- Nelson, M.E., Neas, J., 1980. Pleistocene musk oxen from Kansas. *Transactions of the Kansas Academy of Science* 83, 215–229.
- Olsen, S.J., 1973. *Mammal remains from archaeological sites, part 1: Southeastern and Southwestern United States*. Papers of the Peabody Museum of Archaeology and Ethnology, vol. 56, no. 1. Harvard University, Cambridge.
- Opdyke, N.D., Lindsay, E.H., Johnson, N.M., Downs, T., 1977. The paleomagnetism and magnetic polarity stratigraphy of the mammal bearing section of Anza Borrego State Park, California. *Quaternary Research* 7, 316–329.
- O'Rourke, M.K., Mead, J.I., 1985. Late Pleistocene and Holocene pollen records from two caves in the Grand Canyon of Arizona, USA. *American*

- Association of Stratigraphic Palynologists Contributions Series 16, 169–186.
- Pérez-Barbería, F.J., Gordan, I.J., Nores, C., 2001. Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research* 3, 221–230.
- Schultz, C.B., Howard, E.B., 1935. The fauna of Burnet Cave, Guadalupe Mountains, New Mexico. *Proceedings of The Academy of Natural Sciences of Philadelphia* 87, 273–298.
- Scott, W.B., 1962. *A History of Land Mammals in the Western Hemisphere*. Hafner Publishing Company, New York.
- Simpson, G.G., 1963. A new record of *Euceratherium* or *Preptoceras* (extinct Bovidae) in New Mexico. *Journal of Mammalogy* 44, 583–584.
- Sinclair, W.J., 1905. New mammalia from the Quaternary caves of California. University of California Publications; *Bulletin of the Department of Geology* 4, 145–161.
- Sinclair, W.J., Furlong, E.L., 1904. *Euceratherium*, a new ungulate from the Quaternary caves of California. University of California Publications; *Bulletin of the Department of Geology* 3, 411–418.
- Solounias, N., Moelleken, S.M.C., Plavcan, J.M., 1995. Predicting the diet of extinct bovids using masseteric morphology. *Journal of Vertebrate Paleontology* 15 (4), 795–805.
- Sparks, D.R., Malechek, J.C., 1968. Estimating percentage dry weight in diets using a microscopic technique. *Journal of Range Management* 21, 264–265.
- Thomas, J.W., Toweill, D.E., 1982. *Elk of North America: Ecology and management*. Stackpole Books, Harrisburg, PA.
- Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., Long, A., 1980. Shasta Ground Sloth (*Nothrotheriops shastensis* Hoffstetter) at Shelter Cave, New Mexico: environment, diet, and extinction. *Quaternary Research* 14, 360–376.
- Todd, J.W., Hansen, R.M., 1973. Plant fragments in the feces of bighorns as indicators of food habits. *Journal of Wildlife Management* 37, 363–365.
- Withers, K., Mead, J.I., 1993. Late Quaternary vegetation and climate in the Escalante River Basin on the central Colorado Plateau. *Great Basin Naturalist* 53, 145–161.