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Measuring Late Quaternary Ursid Diminution in the Midwest

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Paleobiologists generally agree that within the past 10,000 yr North American black bears (*Ursus americanus*) have decreased in body and tooth size. Some researchers infer that diminution was gradual and continuous; thus, one might infer that a specimen is old if it is larger than an average-size modern bear. Ursid remains recovered in the 1950s from Lawson Cave, Missouri, that are larger than some modern bears have been reported to date to the late Pleistocene, but association with modern taxa, taphonomic considerations, and a radiocarbon date of 200 yr B.P. indicate that they are modern. Modern specimens from Lawson Cave and other parts of the American Midwest are relatively large compared to modern North American black bears from other areas, suggesting that many supposed late Pleistocene bears from the area might be modern also.

INTRODUCTION

Many paleobiologists believe that through the Holocene various mammal species were represented by progressively smaller individuals. Kurtén and Anderson (1980, p. 184), for example, state that ''In the Holocene, there was a marked decrease in size in [black bears, *Ursus americanus*], a phenomenon also seen in many other species of large mammals,'' and Nagorsen *et al.* (1995, p. 16) indicate that ''the evolutionary trend in *U. americanus* has been a reduction in size, with Pleistocene Black Bears significantly larger than extant forms.'' This relation between size and age is often assumed. Gordon (1986, p. 398), for example, states that body size of western North American black bears continuously and gradually decreased from 10,000 yr ago to the present based on size differences observed in the faunal record, despite the absence of evidence for mid-Holocene bears. Of equal importance is that Gordon's sample of late Pleistocene bears comprises individuals from much of the American Midwest, Texas, and southern California, but none from the Pacific Northwest. On a continent-wide scale, then, bears are assumed to decrease in size through the Holocene because ''the data indicate that the late Pleistocene ancestor was large . . . and that it has become smaller'' (Gordon, 1986, p. 398). Gordon's (1986) assertion that late Pleistocene ursids were, on average, larger than modern ursids was recently tested with fossil evidence from the Pacific Northwest by Nagorsen *et al.* (1995), who found that the proposed relation appears to hold in that region.

Along the same lines, Graham (1991, p. 237), reporting work on late Quaternary black bears in the mid-continent, states that ''[l]ate Pleistocene black bears (*Ursus americanus*) are generally larger than modern black bears from the same geographic area.'' Further, ''[s]ize and morphological attributes have been used to define several fossil species and subspecies of black bears'' (Graham, 1991, p. 237). Graham (1991, p. 244) uses a detailed morphometric analysis of the upper second molar to classify a poorly provenienced black-bear skull and mandibles from Bill Neff Cave, Virginia, as a member of *U. americanus*, ''[b]ecause of its cranial and dental dimensions, which are larger than modern black bears from Virginia and most black bears form other geographic areas, it is quite possible that the Bill Neff skull is from either a latest Pleistocene or earliest Holocene population.'' Graham's (1991) detailed morphometric analysis and comparison with modern specimens from the same region (Virginia) is commendable, given the absence of stratigraphic and radiometric evidence of age.

The general impression one derives from the literature is that size diminution of North American black bears was gradual and continuous throughout the Holocene, and we believe that a tendency exists to consider larger-than-average black-bear-remains relatively old, across the continent (Gordon, 1986, p. 398; Nagorsen *et al.*, 1995, p. 16; Graham, 1991, p. 237, 244). Clearly late Pleistocene black bears were large in certain regions; however, in many areas the fossil record for black bears is poor (including the Midwest and the Pacific Northwest), particularly during the middle Holocene. Did gradual, continuous diminution actually occur across the continent? Or, has that time–space relation simply been inferred? The ease with which gradual diminution is inferred in the Midwest results, in part, from the fact that few ursid remains have been directly dated. Only two cases incorporating directly dated specimens are known to us, and both are from the west coast of North America (Heaton *et al.*, 1996; Nagorsen *et al.*, 1995).

Most North American black-bear remains assigned to the late Pleistocene have been indirectly dated on the basis of their association with remains of mammalian taxa that became extinct at the end of the Pleistocene, but the *strength*

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of the association is seldom evaluated. This is decidedly the case in the Midwest, where more than a dozen caves have produced the remains of black bears thought—on the basis of their large size—to be late Pleistocene in age (Hawksley, 1986; Tucker, 1984). However, firm, fine-scale radiometric dating is lacking for those remains, and the stratigraphy of the caves is often unclear or unrecorded (Graham, 1991; Hawksley, 1986; Tucker, 1984; Wells, 1959). Further, analysts did not use modern midwestern bear skeletons to establish that prehistoric specimens were large, probably because comparative skeletons are rare; Missouri black bears were extirpated by the early 20th century (Schwartz and Schwartz, 1981). Analysts, therefore, had only size as a measure of age.

In short, there are two interrelated problems in studies of ursid size. First, to argue that a prehistoric specimen dates to the late Pleistocene because it is large assumes all recent bears are small. Second, the inference of continuous and gradual diminution over the Holocene reinforces the first assumption in a self-fulfilling and nonfalsifiable manner. Two things are required to escape this tautological-like trap. First, and most importantly, one must obtain chronometric dates of ursid remains spanning the entire late Quaternary. Second, one must control for geographic variation in ursid size. Nagorsen *et al.* (1995) have met the second requirement fully and the first requirement to a lesser extent in the Northwest, as have Heaton *et al.* (1996). In the remainder of this paper we describe a sample of modern midwestern black bears and directly dated ursid remains recovered from a midwestern cave in order to evaluate the applicability of the continent-wide hypothesis of gradual ursid diminution through the Holocene.

Numerous ursid remains were recovered in the 1950s from Lawson Cave in central Missouri. These remains comprise at least nine individuals (MNI based on right femora) that are nearly as large as purportedly late Pleistocene black-bear remains recovered from other midwestern sites. Indeed, the age of the remains was unknown to the excavator (W. Elder, pers. commun., 1995; Elder, 1959), and this assessment appeared in the literature (Mehl, 1962; Wells, 1959). For example, Wells (1959, p. 13) stated that ''the [black-bear] teeth were strikingly oversized in keeping with other skeletal parts that were proportionally heavy.'' Wells (1959, p. 13) also reported that ''the massive jawbones are more than an inch longer than those of large modern black bears.'' However, in regards to age, Wells (1959, p. 14) expressed uncertainty: ''[a]t the present time it is difficult to say just how old the Boone County [Lawson Cave] bear bones may be . . . Perhaps the bears lived at the time of Daniel Boone himself . . . Probably some of them are very much older, having entered the pit hundreds or even thousands of years ago.''

The age of the Lawson Cave ursids was unclear to Elder (1959) as well. In a letter to John Guilday of the Carnegie Museum, Elder (1959) stated, ''I am frankly envious, for our work to date has only provided bones form animals of historic times.'' Yet, by the end of the letter Elder iterated that ''[s]ome [bones] may be quite old because we found teeth of *Geomys*, which no longer lives within 100 miles of here.'' Elder's concern was misplaced because the modern range of *Geomys* extends well into central Missouri (Schwartz and Schwartz, 1981). We obtained a direct date of one Lawson Cave ursid specimen (CAMS-27141, 170 ± 60 yr B.P.), suggesting a modern age. Detailed taphonomic analysis of the collection (Wolverton, 1996) indicates also that this collection is essentially modern. Comparison of the Lawson Cave ursid remains with a sample of modern bears form Arkansas, Alabama, Missouri, and surrounding states (Table 1) suggests that the hypothesis that remains of large, midwestern black bears are ancient is false.

In this paper we briefly describe Lawson Cave and then discuss the taphonomic history of the faunal remains to establish how the ursid materials were deposited and to evaluate the temporal association of ursid remains with those of other taxa from the cave. This is followed by a review of what is known of late Quaternary ursid taxonomy and morphology and their bearing on the continent-wide diminution hypothesis. We then compare measurements taken on samples of modern black-bear teeth from the Midwest and elsewhere, a sample of purportedly late Pleistocene black-bear remains, and the Lawson Cave materials. These comparisons demonstrate that it is fallacious to assign an age to an ursid fossil based on its size without comparative size data from the geographic area that produced the fossil.

SETTING AND DESCRIPTION OF LAWSON CAVE

Lawson Cave is a bottle-shaped solution fissure situated in a limestone bluff; dissolution of the limestone caused by percolating rainwater led to the creation of the fissure (Lambert, 1988). The dissolved limestone took the form of a grike (shaft) with a gallery (cavern) at the bottom (Lambert, 1988). The modern entrance to the cave measures 178 by 79 cm and is located near the top of a wooded ridge (long axis oriented east–west); this entrance drops 11.47 m to the cave floor. The entrance cannot be seen from any direction by humans in daylight from any farther away than 5 m. The opening is obscured by trees, bushes, and a ground cover of fallen leaves; thus, it is possible that animals fell into the cave because they came upon the entrance without seeing it.

All indications are that Lawson Cave is a natural trap. Taphonomic analysis suggests that most of the faunal remains underwent a similar accumulation history (Wolverton, 1996). Although we have not examined the entire collection—some of it has been lost—fracture patterns and skeletal-part frequencies indicate that individual animals fell into

TABLE 1
Sample Sizes According to Geographic Distribution

	Alabama	Arkansas	Kansas	Oklahoma	Wyoming	California	Missouri	Lawson Cave (MO)
M^2	8	12	2	2	26	70	8	11
M_3	5	9	0	2	21	61	6	10

the cave. Perhaps the bears fell while attempting to scavage carrion of other victims that fell in accidentally or as scavengers. The accumulation history was relatively short; a modern suite of taxa are represented in the collection (Purdue and Styles, 1987). Particularly abundant are remains of *Sus scrofa* and *Sylvilagus floridanus*; canid specimens (*Canis* sp.), possibly domestic dog, were also recovered. *Sus* and *Ursus* have similar skeletal-part representation in the collection, suggesting that bones of both have been subject to a similar degree of preservational deterioration, i.e., time since deposition (Wolverton, 1996). The similarity of bone condition along with the modern taxa represented suggests that the entire assemblage is young (Wolverton, 1996).

The Lawson Cave ursid sample does not reflect the demography of a living bear population. Most specimens are from full-grown adult and nearly full-grown individuals; a single neonate is represented. Only two bacula were found in the collection; four crania exhibit pronounced sagittal crests, which are characteristic of adult male black bears (Graham, 1991), and one other cranium, which is missing its posterior half, is extremely large. Thus, we estimate that four to five of the nine individuals were male. Recalling that part of the assemblage has been lost, the abundance of black bears relative to other taxa might be an illusion. We analyzed the known collection, excavated from 1954 to 1960. Comparison with faunal remains from other natural traps indicates that the Lawson Cave faunal assemblage is unique only in its high relative abundance of ursid remains (Wolverton, 1996). Given the demography of the ursids represented and the modern entrance, we believe that Lawson Cave was not an ursid den but, rather, a natural trap.

LATE QUATERNARY URSIDS

Leidy (1853) proposed that Pleistocene black bear belonged to *Ursus amplidens* based on tooth measurements form a lower jaw found near Natchez, Mississippi. Over a century later, Kurtén (1963) noted only slight differences in cranial capacity and tooth size among Pleistocene and modern black bears and concluded that Leidy's specimen and several other fossil bears did not warrant designation as distinct species, so he reduced them to the subspecies *U. americanus amplidens.* Tucker (1984) proposed that Missouri black bears—*U. americanus americanus* (modern) and *U. americanus amplidens* (late Pleistocene/early Holocene)—differ in tooth size and shape, particularly the second upper molar. He found that teeth were the best preserved remains and concluded that tooth size is indicative of body size (in contrast to Harlow, 1962; Rausch, 1961).

More recently, Graham (1991) studied the relation among many groups of fossil and living North American bears including *U. americanus* (modern black bear), *U. arctos* (modern grizzly), *U. procerus* (fossil grizzly), *U. optimus* (fossil grizzly), and many other specimens that have been classified as distinct species or subspecies. He questioned the validity of the subspecific designation *U. a. amplidens* because the only noticeable difference between Pleistocene and Holocene black bears he found was in terms of size. In fact, some of his modern specimens were statistical outliers as large as average-size late Pleistocene specimens; differences in size alone might not justify the division of late Quaternary black bears into two subspecies. Graham (1991) found that noticeable differences other than size were not evident among ursid fossils after the middle Pleistocene extinction of *U. vitabilis*, the apparent precursor to modern black bears.

Thirty-six genera of mammals became extinct during the late Pleistocene (Grayson, 1987; Martin and Klein, 1984; Kurtén and Anderson, 1980). Individual mammals of many genera, including *Ursus*, were larger on average than their modern counterparts (e.g., Forsten, 1993; Gordon, 1986; Graham, 1991; Harris and Mundel, 1974; King and Saunders, 1984; Seymour, 1993; Wilson, 1978). Some species (e.g., *Bison* spp.) were represented by progressively smaller individuals through the late Pleistocene and Holocene (Wilson, 1978). Other taxa, such as white-tailed deer (*Odocoileus virginianus*), became smaller until the middle Holocene and increased in body size thereafter (Purdue, 1989). The fossil records for white-tailed deer and American bison are relatively complete and tightly controlled chronologically compared to those of most other taxa. The shapes of chronoclines (Koch, 1986) among most other North American taxa (excluding bison and deer) are not known in detail (see Purdue, 1989; Schultz *et al.*, 1972, for exceptions). In contrast, several chronoclines of African and European taxa have been studied in detail (e.g., Avery, 1988; Klein, 1986; Klein and Scott, 1989).

It is difficult to distinguish temporal size change from geographic variability among many species (Dayan *et al.*, 1991; Forsten, 1993). This is particularly true among black bears because of their body-size and tooth-size plasticity.

TABLE 2
Key to Teeth Measurements

Elements measured	Description of measurement	Abbreviation
M^2 and M_3	*Length* denotes antero-posterior length taken at the crown.	Length
	Width denotes medio-lateral width taken at the crown.	Width

Late Pleistocene climatic changes resulted in less nutritious vegetation, such as the replacement of three-carbon cycle plants with four-carbon cycle plants, which might have led to size reductions through time (Graham, 1985). However, climatic and environmental differences also occur over geographic space. For example, Harlow (1962) demonstrated that modern Florida black bears with large heads often do not have correspondingly large bodies; Virginia black bears, in comparison, have relatively smaller heads and larger bodies. In studies of temporal variation, geographic variation must be controlled so that the two are not conflated.

Considerable disagreement exists over the usefulness of measuring ursid teeth to determine ursid body size (Gordon and Morejohn, 1974; Rausch, 1961). In contrast, Gingerich and Schoeninger (1979) demonstrated that tooth size is indicative of body size among other omnivores. Whatever the case, at issue here is tooth size; can midwestern ursid specimens be assigned late Pleistocene age based on large size?

MEASUREMENTS

We measured modern midwestern black bear teeth (Table 1) for direct comparison with those from Lawson Cave and supposed late Pleistocene/early Holocene (P/H) ursids. Modern teeth samples from California and Wyoming are also included for two reasons. First, those samples are directly compared with the midwestern and supposed P/H samples to demonstrate the larger relative size of the latter. Second, we use coefficients of variation to demonstrate range of dispersion (in a relative sense) around the means in samples from known regions (California and Wyoming). The midwestern sample includes bears from a larger region than either state (Table 1). Measurements of P/H teeth were taken

TABLE 3
Descriptive Statistics from M^2 and M_3 Samples

Sample	Measurement	*N*	Mean	Standard deviation	Range	Coefficient of variation (%)
CA/WY Modern	M^2 Width	96	14.55	0.89	12.02–16.61	6.14
	M^2 Length	96	25.50	2.12	21.10–30.95	8.31
	M_3 Width	82	11.60	0.87	9.54–13.50	7.54
	M_3 Length	82	14.42	1.21	12.32–17.06	8.37
Modern Midwest	M^2 Width	32	15.80	1.41	13.49–17.89	8.92
	M^2 Length	32	26.14	2.06	21.08–29.78	7.90
	M_3 Width	22	12.38	1.42	9.52–15.57	11.49
	M_3 Length	22	15.23	1.40	12.02–17.19	9.79
Lawson Cave	M^2 Width	11	16.13	0.84	14.70–17.80	5.77
	M^2 Length	11	28.13	0.93	26.30–29.50	2.97
	M_3 Width	10	12.81	0.70	11.41–13.85	5.46
	M_3 Length	10	16.07	1.11	13.83–17.60	6.91
Modern CA	M^2 Width	70	14.59	0.94	12.02–16.61	6.40
	M^2 Length	70	25.63	2.31	21.10–30.95	9.02
	M_3 Width	61	11.75	0.87	9.54–13.50	7.41
	M_3 Length	61	14.50	1.32	12.32–17.06	9.12
Midwest w/Lawson Cave	M^2 Width	43	15.88	1.33	13.49–17.89	8.36
	M^2 Length	43	26.65	2.03	21.08–29.78	7.60
	M_3 Width	32	12.51	1.26	9.52–15.57	10.06
	M_3 Length	32	15.49	1.37	12.02–17.60	8.86
All Modern	M^2 Width	139	14.96	1.21	12.02–17.89	8.08
	M^2 Length	139	25.86	2.16	21.08–30.95	8.34
	M_3 Width	114	11.85	1.08	9.52–15.57	9.10
	M_3 Length	114	14.72	1.34	12.02–17.60	9.13
Supposed P/H	M^2 Width	20	17.03	0.97	15.20–18.50	5.70
	M^2 Length	20	29.83	1.14	27.30–31.90	3.83
	M_3 Width	12	14.03	1.04	12.30–15.70	7.43
	M_3 Length	12	17.31	1.72	13.40–19.60	9.94

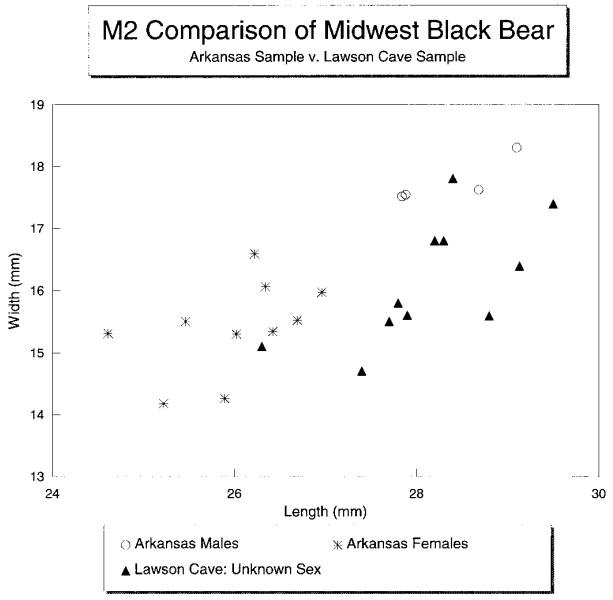

FIG. 1. Scatter plot demonstrating the size relations among M^2s from modern Arkansas (male and female) and Lawson Cave black bears.

from Graham (1991) and from specimens housed at Illinois State Museum (Wolverton, 1996). Table 2 summarizes the measurements taken on each tooth. Descriptive statistics and Student's *t* tests were calculated rather than multivariate analyses because of the simplicity of sample comparisons and because we often measured isolated specimens.

Graham (1991) found the M^2 and M_3 most useful in distinguishing *U. americanus* from *U. arctos.* The upper second molar (M^2) and lower third molar (M_3) provide the clearest distinction among modern, Lawson Cave, and presumed P/H black bears. Those two molars also comprise our largest samples from both modern and prehistoric populations. Other molars, as well as limb bones, were included in a general analysis of the Lawson Cave black-bear remains in which similar graphic and statistical patterns emerged (Wolverton, 1996).

RESULTS

The coefficients of variation (Table 3) demonstrate that the midwestern samples have ranges of dispersion around their means expected for a geographically restricted population (such as those from California and Wyoming). A relatively low coefficient indicates that variation is likely limited (Thomas, 1986); the lowest coefficient occurs on the Lawson Cave M^2 length sample. Given that the cave is a natural trap, geographic variation is restricted to the range (estimated average of 50 km^2) of the resident black bears (Chapman and Feldhamer, 1982, p. 507); however, given that coefficients across all Lawson Cave measurements are relatively low, it is likely that restricted geographic variation and possibly—to a lesser extent—restricted temporal variation play roles in the sample distribution. The last is another line of evidence suggesting a short accumulation history at Lawson Cave if it is assumed that size change occurred among black bears during the late Quaternary; i.e., low coefficients indicate little change or a small sample of temporal variation from the history of ursid evolution.

High coefficients (greater than 10%) suggest either unusually high variation in a species, mixing of species, or mixing of geographically and/or temporally distinct populations (Thomas, 1986). Relatively high coefficients are apparent in the Midwest (Missouri, Arkansas, Alabama, Kansas, and Oklahoma), California, and all-modern (Midwest and California/Wyoming) samples (Table 3). The all-modern samples are geographically mixed. Bimodality should be expected in well sampled regions because of sexual dimorphism, and this might be the case with the California sample (as indicated by large sample size and relatively high coefficients). The Midwest sample is less geographically limited than the California or Wyoming samples (Table 1). Combining the modern Midwest and Lawson Cave samples lowers the coefficients, perhaps suggesting that as sample-size increases for this area less variation due to geographical mixing or fewer sample-size effects exist.

Graphically, the Lawson Cave M^2 and M_3 samples fall between the Arkansas male and female distributions (Figs. 1 and 2). The Lawson Cave M_3 sample closely overlaps the Alabama-male sample (Fig. 2), and midwestern bears, in general, are relatively large in comparison to bears from

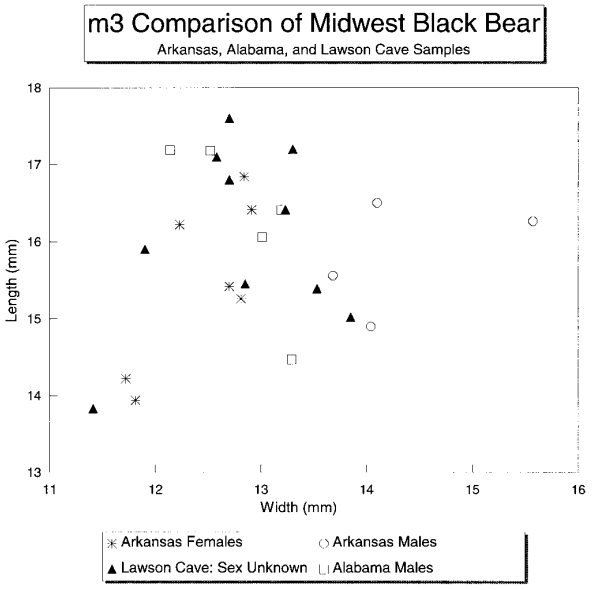

FIG. 2. Scatter plot demonstrating the size relations among M_3s from modern Arkansas (male and female), modern Alabama (male), and Lawson Cave black bears.

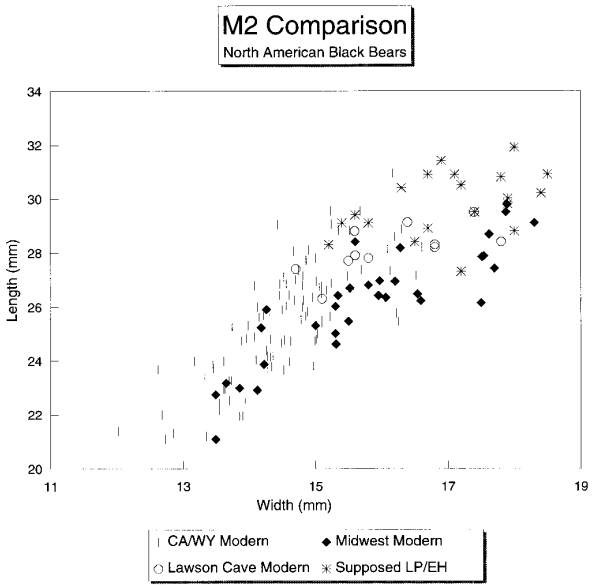

FIG. 3. Scatter plot demonstrating the size relations among M^2s from modern California/Wyoming, modern midwestern, Lawson Cave, and supposed late Pleistocene/early Holocene black bears.

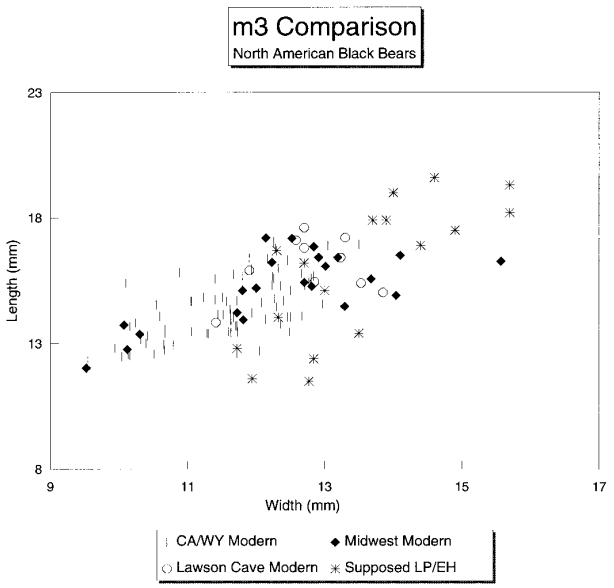

FIG. 4. Scatter plot demonstrating the size relations among M_3s from modern California/Wyoming, modern midwestern, Lawson Cave, and supposed late Pleistocene/early Holocene black bears.

other regions, such as California and Wyoming (Figs. 3 and 4). The Lawson Cave M^2 and M_3 measurements overlap those from the Midwest (Table 3; Figs. 3 and 4). Student *t* tests fail to separate significantly those samples except in the case of M^2 length (Table 4); graphically, the Lawson Cave sample overlaps the middle range of the modern midwestern sample, roughly between the Arkansas females and the Arkansas and Alabama males (Figs. 1 and 2).

The combined measurements from the Lawson Cave and Midwest samples are all significantly different (larger) than their modern California counterparts (Table 4). Although graphically the upper ranges of modern Midwest measurements overlap those of supposed P/H measurements, the teeth samples differ significantly in Student's *t* tests in all cases (Table 4; Figs. 3 and 4).

IMPLICATIONS AND CONCLUSIONS

The Lawson Cave assemblage contains no remains of extinct Pleistocene mammals (Table 5), which suggests a Holocene age. For several other reasons already discussed, the accumulation history of the assemblage appears to be relatively short. The ursid remains seemed large; suggestions specifically concerning the Lawson Cave ursids (Mehl, 1962; Wells, 1959), in conjunction with the general literature on prehistoric midwestern black bears (Hawksley, 1986; Tucker, 1984), and the relatively large size of the remains (compared with modern specimens from other regions) indicated that a middle to early Holocene age was reasonable. As stated earlier, a single AMS date indicates that the assemblage may be no more than 200 yr old.

TABLE 4
Student's *t* Test Comparisons among Samples

	Lawson Cave vs Other Midwest		California vs Midwest (w/Lawson Cave)		Midwest (w/Lawson Cave) vs P/H	
M^2 Width	*t* Statistic	−0.73	*t* Statistic	−5.56	*t* Statistic	−3.42
	P value	0.473	*P* value	<0.0001	*P* value	0.001
M^2 Length	*t* Statistic	−4.38	*t* Statistic	−2.36	*t* Statistic	−7.79
	P value	<0.0001	*P* value	0.020	*P* value	<0.0001
M_3 Width	*t* Statistic	−0.87	*t* Statistic	−3.39	*t* Statistic	−3.65
	P value	0.393	*P* value	0.001	*P* value	0.001
M_3 Length	*t* Statistic	−1.63	*t* Statistic	−3.34	*t* Statistic	−3.56
	P value	0.115	*P* value	0.001	*P* value	0.001

Note. $P < 0.05$ is significant.

TABLE 5
Mammalian Taxa from Lawson Cave Represented by Number of Identified Specimens (NISP)

Taxon	Common Name	NISP
Scalopus aquaticus	Eastern mole	3
Didelphis marsupialis	Opossum	42
Sylvilagus floridanus	Eastern cottontail rabbit	238
Sciurus sp.	Eastern gray squirrel	7
Castor canadensis	Beaver	1
Marmota monax	Woodchuck	66
Peromyscus sp.	White-footed or deer mouse	18
Neotoma sp.	Wood rat	33
Microtus ochrogaster	Prairie vole	19
Geomys bursarius	Plains pocket gopher	1
Canis cf. *familiaris*	Compare to domestic dog	22
Canis sp.	Dogs, coyotes, or wolves	44
Ursus americanus	North American black bear	445
Mephitis mephitis	Striped skunk	12
Procyon lotor	Raccoon	1
Sus scrofa	Domestic pig	170
Odocoileus virginianus	White-tailed deer	5

In most cases (excluding Tucker, 1984), including our own early attempts to gauge the size of Missouri cave specimens, modern comparative samples comprise bears from other regions. Tucker (1984) simply compared fossil and nonfossil remains from Missouri caves and recognized that fossilized specimens were larger, on average; however, he did not determine the temporal variation among the nonfossil bears.

The Lawson Cave black bears do not have uniquely large teeth when compared with measurements from modern Midwest bears. Earlier suggestions that Lawson Cave black bears might be late Pleistocene in age were made without controlling geographic variation in modern comparative samples. Specimens from California or Wyoming are too small, on average, to be of comparative value in studies of temporal variation among midwestern black bears. The hypothesis that larger size suggests older remains is invalid when such geographically separate samples are used. These implications reach beyond the Midwest (e.g., Graham, 1991; Nagorsen *et al.*, 1995).

Most collections of midwestern black-bear remains (e.g., Hawksley, 1986; Tucker, 1984) have not been directly and radiometrically dated; nor have the depositional and formational histories of these collections been studied in detail (see Stiner *et al.*, (1996) and Gargett (1996) for examples of such studies). It is unclear whether midwestern ursid specimens assigned to the late Pleistocene on the basis of associated Pleistocene taxa are in fact of that age. Filling gaps in the temporal record would allow a clearer resolution of chronocline shape for midwestern black bears (for examples of well controlled chronocline and geographic cline studies, see Arnold and Tissot, 1993; Davis, 1981; Dayan *et al.*, 1991; Klein, 1991; Langvatn and Albon, 1986; and Purdue, 1989). More-intimate knowledge of an adaptable, plastic species such as the black bear would provide archaeologists and paleontologists with an opportunity to understand paleoenvironmental and paleoclimatic conditions much like the studies cited above.

The recency of the Lawson Cave ursids and the relatively large size of modern midwestern bear teeth show that it is unwise to infer that prehistoric black-bear remains which are relatively larger than modern black bears from other regions are late Pleistocene/early Holocene in age. Thus, any hypothesized relation between black-bear size and age should be tested via direct dating, particularly in the Midwest where modern comparative samples indicate that modern bears are large. That ursid diminution during the late Quaternary was continuous and gradual cannot be determined without better regional temporal control. We have not disproved the existence of a gradual diminution in black bear size; rather, we have simply stated that at present the data are too limited to discern the Holocene chronocline of black-bear size change. The chronocline will be visible only if specimen age is known and the mid-Holocene record is improved.

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