Paleoethological Reconstruction and Taphonomy of *Equus lambei* from the Bluefish Caves, Yukon Territory, Canada

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ABSTRACT. The Bluefish Caves, northern Yukon, Canada, have yielded evidence of pre-Holocene human occupation of eastern Beringia. The three caves at Bluefish contain a large and complex late Pleistocene fauna in situ. Our research on the mortality patterns and the paleoethology of *Equus lambei* (an extinct species of horse), a dominant component of the Bluefish assemblages, was based on the dental remains. Mortality profiles for *Equus lambei* indicate that predators were the likely primary agents of bone accumulation at Cave I, while Caves II and III appear to have accumulated bones through accidental or natural deaths, probably regularly monitored by humans and other predator/scavengers. Paleoethological reconstruction for *E. lambei* supports the suggestion that the Bluefish Basin was not a polar desert during the late Pleistocene. Finally, the use of tooth height/age tables to establish age profiles of fossil equid populations is demonstrated to be limited to establishing broad, relative age categories.

Key words: *Equus lambei*, Bluefish Caves, full/late glacial, eastern Beringia, paleoethology, incremental analysis, tooth height/ age tables

RÉSUMÉ. Les grottes du Poisson Bleu situées dans le nord du Yukon au Canada ont fourni la preuve d'une occupation humaine de la Béringie orientale précédant l'Holocène. Les trois grottes contiennent une faune nombreuse et diverse, découverte *in situ*, datant du Pléistocène tardif. Nos recherches sur les schémas de mortalité et la paléoéthologie de *Equus lambei* (une expèce de cheval disparue), qui est l'une des composantes principales des communautés de ces grottes, sont fondées sur des restes dentaires. Les profils de mortalité pour *Equus lambei* indiquent que l'accumulation des os trouvés dans la grotte I serait surtout l'oeuvre de prédateurs, tandis que ceux des grottes II et III proviennent de morts accidentelles ou naturelles, ces deux grottes ayant probablement été fréquentées sur une base régulière par des humains et d'autres prédateurs/chasseurs. La reconstruction paléoéthologique de *E. lambei* étaye l'hypothèse que le bassin du Poisson Bleu n'était pas un désert polaire durant le Pléistocène tardif. Enfin, l'utilité des tables de hauteur de la couronne dentaire en vue d'établir les profils d'âge des populations d'équidés fossiles se limite à la détermination de larges catégories d'âge relatif.

Mots clés: *Equus lambei*, grottes du Poisson Bleu, Pléniglaciaire/tardiglaciaire, Béringie orientale, paléoéthologie, skeletochronologie, tables de la hauteur/de l'âge des dents

INTRODUCTION

A continuous paleoenvironmental record for the last glacial period, the Wisconsinan, is preserved in deposits in the northern Yukon, the Northwest Territories, and Alaska (Harington, 1978; Morlan, 1980; Hughes et al., 1981). These deposits have been the focus of several multidisciplinary projects, such as the Yukon Research Programme, the Yukon Refugium Project, and the long-term study of Pleistocene vertebrate fossils undertaken by the Canadian Museum of Nature.

Archaeological discoveries at the Bluefish Caves, Bluefish Basin, in eastern Beringia (Fig. 1) indicate that unglaciated lowland areas, including the Bonnet Plume, Old Crow, Bluefish, and Bell Basins, may have played a part in the history of human habitation in the New World, particularly during the maximum expansion of the Cordilleran and Laurentide ice sheets. For this reason, we seek a better understanding of Late Pleistocene environments in the Bluefish Basin.

The floral and faunal communities of Pleistocene eastern Beringia appear to have differed fundamentally from present-day tundra communities (Harington, 1978; Guthrie, 1980, 1982, 1985; Matthews, 1982). A better understanding of Pleistocene faunal communities in eastern Beringia has been hampered by the lack of in situ fossil assemblages that are representative of past biocenoses (Matthews, 1982; Guthrie, 1985). Thus, the abundant faunal and palynological remains found in situ in the three caves that make up the Bluefish Caves complex (Fig. 2) make this an invaluable assemblage for furthering our knowledge of animal communities and their environment in eastern Beringia.

Horses (*Equus lambei)* have been discovered in the Bluefish Caves in a stratigraphic context that spans the last 15 000

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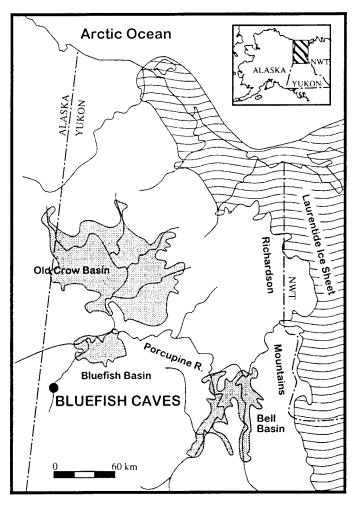
FIG. 1. Location of the Bluefish Caves, Northwest Territories.

years of the Late Pleistocene. Equid specimens from Bluefish have been radiocarbon-dated from 22 680 B.P. to 12 290 B.P. at the latest (see below). Cut marks on equid bones reveal contemporary human presence (C.R. Harington, pers. comm. 1996). This paper examines the taphonomy of the equid component of the Bluefish fauna by reconstructing patterns of mortality and seasonality on the basis of dental remains. A more complete taphonomic study of all of the faunal components at Bluefish is being prepared by C.R. Harington (pers. comm. 1997).

Dating of Equus lambei *Remains in Eastern Beringia*

Equus lambei was the dominant equid form in the steppe-like terrain of eastern Beringia during the late Wisconsinan (Harington and Clulow, 1973:724). *Equus lambei* appears in pre-late Wisconsinan deposits in Dawson, Old Crow, and Alaska and in Middle Pleistocene deposits in Alaska as well as in several other Beringian sites (Péwé and Hopkins, 1967). The type specimen, from Gold Run Creek, Alaska, was first described by Hay (1917). At Bluefish Caves, *Equus lambei* specimens have been radio-carbon-dated between 12 900 ± 100 B.P. (GSC 28881, *E. lambei* femur, Cave I) and 17 440 ± 220 B.P. (RIDDL

278, *E. lambei* metatarsal, Cave I). Two additional bone fragments, also identified as equid, have been dated to 12 290 ± 440 (NMC 1236, Cave III) and 22 680 ± 530 (NMC 1237, Cave II) respectively.

Originally described as a member of the genus *Asinus*, *Equus lambei* is now assigned to the caballine group on the basis of physical traits described by Harington (1989) and Forsten (1988) and multivariate analyses carried out by Eisenmann (1980, 1986; Burke and Cinq-Mars, 1996). *Equus lambei*, the Yukon horse, was "the easternmost representative of a circumpolar species of small, caballoid, horse of which Przewalski's horse and the tarpan were the last wild Eurasian survivors" (Forsten, 1988:163). Close similarities exist between *Equus lambei*, Late Pleistocene horses in Siberia (Harington, 1977; Eisenmann, 1986), *Equus przewalskii* and modern Arabian breeds (Eisenmann, 1986; Burke and Cinq-Mars, 1996).

The Bluefish Caves Fauna

The three Bluefish caves contain palimpsest deposits, the result of multiple re-occupations by different agents (Morlan and Cinq-Mars, 1982; Cinq-Mars, 1990). In all three caves, the bones of predators such as the wolf, bear, and lion have been identified. Tooth marks are attested, and cut marks on bone, as well as cultural material, indicate a human presence (Morlan and Cinq-Mars, 1982; Cinq-Mars, 1990). The faunal assemblages from the Bluefish Caves are probably the result of random sampling of regional populations over a relatively long (10 000 year) period during the Late Pleistocene. Given the numerous potential agents of bone accumulation, and the length of the probable period of bone deposition, as well as the relatively small sample sizes, any interpretation of the age and seasonality profiles of the Bluefish fauna must be undertaken with care.

Archaeologists have investigated numerous Late Paleolithic sites in karstic environments in southern France whose composition is similar to the Bluefish Caves deposits. The taphonomy of these sites may provide us with a useful guide towards understanding the formation of the bone deposits at Bluefish, and will be discussed below.

METHODS

The Archaeological Sample

The Bluefish caves have yielded a total of 524 horse cheek teeth: 306 maxillary and 218 mandibular teeth. Isolated teeth were sorted by anatomical position, right from left, where possible, using a combination of criteria. In both upper and lower teeth, the first molar (M1) appears more square than the second molar (M2), and the roots of the second molar are relatively more curved. In the premolars (P), P^3 is more square than P^4; viewed lingually, their occlusal surfaces are angled in opposite directions. Similarly, the occlusal surface of P_3 is angled mesially, whereas that of P_4 is angled distally. The
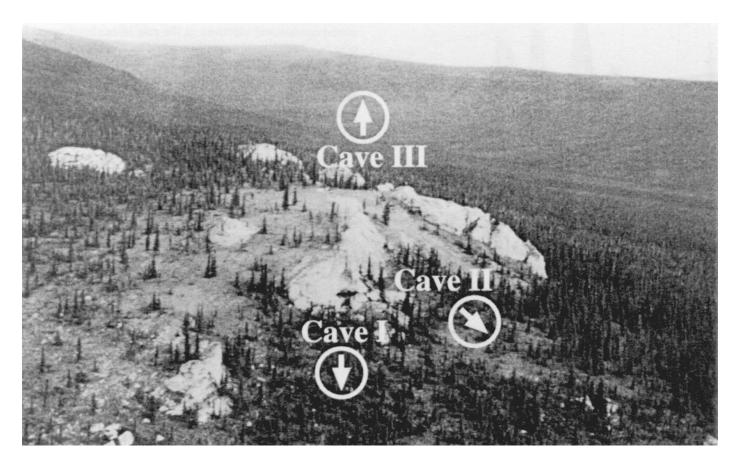
FIG. 2. Relative position of the three Bluefish Caves: the arrows indicate the rough orientation of the rock shelters.

occlusal surface of P_4 has a more wedge-shaped appearance than that of P_3. Isolated teeth which could not be assigned to a given anatomical position with confidence were not used in this study. A relatively large number of teeth, for which exact find-location had been noted, could be refitted into complete or partial tooth rows, using enamel patterning, relative tooth height, and the pattern of interstitial wear.

A total count of teeth from each dental anatomical position was obtained using both sorted, isolated teeth and teeth from partial and complete tooth rows. This count was used to calculate dental MNI (minimum number of individuals). The maximum dental MNI, based on cheek teeth, is 51 individuals: 25 individuals from Cave I, 13 from Cave II, and 13 from Cave III.

Full results of a metrical analysis of *Equus lambei* teeth from Bluefish Caves are published elsewhere (Burke and Cinq-Mars, 1996). For the present research, tooth height measurements were taken following Levine (1982). The condition of preservation of the tooth rows allowed us to measure crown height on most teeth, since they were exposed in their alveoli on either the buccal or the lingual sides, or both.

Age (mortality) profiles for horses (Figs. 3 and 4) were calculated for each cave using a combination of tooth height/age calculations (based on tables generated by Levine [1982] for adult dentition) and eruption/wear patterns of deciduous teeth. Tooth height of M^1 was used to generate age profiles (Fig. 3), since it is the first adult tooth to erupt and is well represented in the Bluefish assemblage. Deciduous tooth rows (with unerupted or erupting first molars) were aged using Levine's (1982) eruption tables (Table 1) and added to the age profiles (Fig. 4).

A representative sample of teeth (equal to dental MNI *minus* poorly preserved and deciduous teeth), taken from each cave, was thin-sectioned to determine season of death. Forty-two samples were available for thin-sectioning: 18 from Cave I, 7 from Cave II, and 17 from Cave III. The teeth were set in resin blocks and thin-sectioned using established methodology (Burke, 1995; Burke and Castanet, 1995). The resulting thin-sections were viewed under transmitted, polarized light, and season of death was determined by observing the nature of the final cementum growth ring (Table 2).

Tooth Height/Age Tables

Mortality profiles give archaeozoologists a better understanding of the taphonomic processes affecting a faunal assemblage and allow them to identify patterns of predation. Dental remains provide several ways of estimating an animal's age at death. The techniques most commonly used by archaeozoologists are 1) tooth height/age tables (e.g., Spinage, 1976; Klein, 1981; Levine, 1979, 1982, 1983, 1990); 2) eruption data (supra); and 3) occlusal wear patterns (see discussions in Welsh, 1975; Levine, 1979, 1982, 1983).

The usefulness of eruption sequences and occlusal wear stages as estimators of an animal's age at death is limited by
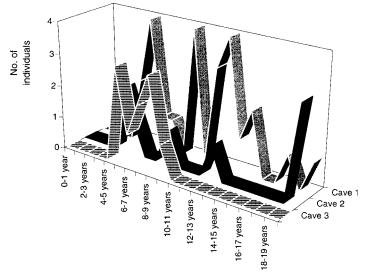
FIG. 3. Mortality profiles for equids based on upper M1 and deciduous eruption/wear patterns.
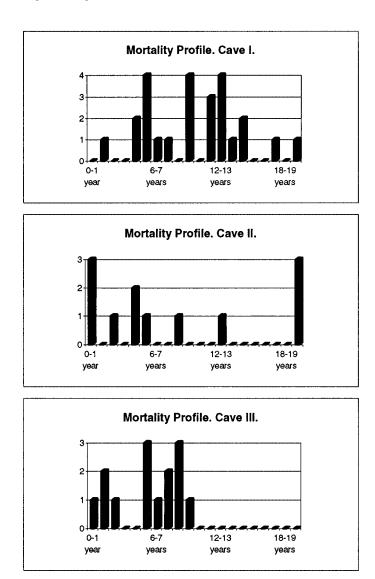

FIG. 4. Mortality profiles for equids based on tooth height.

the age at which adult dentition is complete, and by inter- and intra-populational variation in the rate of occlusal wear. In equids, all adult teeth are fully erupted by c. 4–6 years of age, and occlusal surfaces wear flat by about 6 years of age (Welsh, 1975; Levine, 1982). Furthermore, individual and inter-populational differences in tooth hardness and feeding patterns interfere with the application of wear tables as a means of ageing older animals (Welsh, 1975; Levine, 1982; Coy et al., 1982; Stallinbrass, 1982).

The use of tooth height to calculate age offers the possibility of ageing the entire adult population. This method has been criticized as a means of establishing absolute age at death, on the basis of allometric differences within and between populations of a same species (Hall-Martin, 1976; Stallinbrass, 1982). The assumptions required for claiming a relationship between age and tooth height (i.e., rate of wear) have also been criticized, notably the assumption of 0 mm crown height at death and of a constant (though curvilinear) relationship between crown height and age (Klein, 1981; Levine, 1982). Nevertheless, ageing based on tooth height remains a frequently used tool in archaeozoology.

Levine (1982) has developed tooth height/age tables for the study of late Pleistocene European equids. We tested the applicability of these tables on a non-European fossil equid, using the Bluefish horse assemblage. Sixteen upper and fifteen lower cheek-tooth rows (complete or partial) were used for the test. We used only tooth rows recovered as such, as opposed to reconstructed series.

First, we established that tooth size in the Bluefish sample is comparable to the mean size of the fossil teeth used in Levine's (1982) tables, eliminating the possibility that allometric differences are affecting the data (Table 3). Following the methodology suggested by Levine, we compared the mesio-distal diameter of the Bluefish teeth with the mean tooth sizes that she recorded (Levine, 1982: Table 1) for teeth of comparable height. Sample sizes are large enough in six of seven height categories to establish that the mean size of the Bluefish teeth is within three standard deviations of the values recorded by Levine (1982: Table 3). In theory, this means that the tooth height/age tables should be applicable to the Bluefish sample.

Having established that the Bluefish and European fossil samples are of roughly comparable size, we used Levine's tables to age the Bluefish samples. Internal comparisons of attributed ages were made within each tooth row (Tables 4 and 5). Results indicate that the tables over- or underestimate the ages of adjacent teeth by at least two age categories in 47% of the cases for mandibular series (Table 4) and 72% of cases for maxillary series (Table 5). In the case of mandibular series, the only recorded regularity is the consistently "younger" (by one age category) age for P_4 when compared with P_3 and/or M_1. This result may be a function of the small sample sizes and their presumably random distribution within the confidence intervals fitted around Levine's original graphs.

Our research confirms that tooth height may be used only to establish the relative ages of animals within a population, in order to establish the shape of the mortality profile for that

TABLE 1. Age in months of deciduous teeth estimated using eruption/wear patterns.

Cave	Individual	Catalogue	Mand/Max	Tooth	Probable Age	Maximum Age	Wear data
I	dI	I7-4-6, I7-6-9	R Max	dP3, dP4	4–15	36	M1 unerupted
I	dII	J8-1-88, J8-1-52, J8-1-51	L Mand	dP2-dP4	4–18	36	M1 unerupted
II	dIII	D5-F-10	L Mand	dP2-M1	4–9	9	M1 erupting
II	dIII	D5-F-40	R Mand	dP2-M1	4–9	9	M1 erupting
II	dIV	E6-9-12	L Mand	dP2-M1	4–9	9	M1 unerupted
II	dIV	E6-G-11	R Mand	dP2-M1	4–9	9	M1 unerupted
II	dV	B3-3-15	L Max	dP2-M1	9–36	36	M1 in wear, dP2 worn
II	dV	C2-1-2, B4(N)-10-5	R Max	dP2, dP3-M1	9–36	36	M1 in wear, dP2 worn
II	match?	D3-7-1	R Mand	dP2		36	very worn
II	match?	D3-6-3	L Mand	dP2		36	very worn
II	n/a	J6-8-3	L Mand	dP4		54	very worn
II	n/a	B4(N)-10-5	R Mand	dP3		48	very worn
II	n/a	E6-G-12	L Mand	M1	< 9	9	unerupted
II	n/a	I6-6-4	L Max	dP2	24 – 36	36	dP2 very worn
II	n/a	G7-B-12	L Max	dP4	30 – 42	42	dP4 very worn
III	dVI	S-3-69	L Mand	dP2-M2	16 – 24	24	M1 in wear, M2 erupting
III	dVI	M-9-97	R Mand	dP2		36	in wear
III	dVII	M-12-28	R Mand	dP3-M1	4 – 9	9	M1 unerupted
III	dVIII	A-12-8	R Max	dP2-dP4	9 – 15	24	dP4 worn
III	dVIII	T.P.1-F-44	R Max	M1		15	M1 in wear
III	dVIII?	T.P.2-C-3	L Mand	dP2-dP4	9 – 15	24	M1 erupted (wear on dP4)
III	dIX	T.P.1-F-51, T.P.1-F-41	R Mand	dP2-dP3	4 – 36	36	worn
III	dIX	85-89, T.P.1-F-66	L Mand	dP2-dP3	4 – 36	36	worn
III	dX	85-62	L/R Max	dP2-M3	24 – 36	36	
III	dXI	85-46	Mand	dP2-M2	16 – 24	24	M2 erupting
III	n/a	85-20	L Max	dP4	16 – 24	24	worn
III	n/a	C-6-8	L Max	dP2		24	very worn
III	n/a	S-3-47d	L Mand	Tooth buds		n/a	unerupted
III	n/a	S-3-4	R Mand	dP4		48	worn/very worn
III	n/a	T.P.1-E-34	R Mand	M3	> 24		unerupted

population. Age categories are assigned to the *y* axes in Figures 3 and 4 to make them more readable; they are intended only as rough guides. The use of age determinations based on tooth height tables is restricted "to predicting the mean ages of samples of a population rather than of individuals" (Spinage, 1976:276; see also Klein, 1981).

RESULTS

Mortality Patterns

Mortality profiles were produced for the animals in each cave using M[1] tooth heights, combined with eruption/wear data for subadult individuals (Figs. 3 and 4). Results for Cave I (N = 25) show a pattern typical of human predation (Fig. 4), i.e., prime-aged adults are best represented. Cave II shows an attritional pattern of mortality, but the number of individuals aged is small (N = 13). Cave III shows a more limited age distribution, featuring only subadult and prime-aged animals up to approximatively nine years of age, and underrepresenting older adults. Again, the total number of samples aged is low (N = 14).

Seasonal Profiles

Season of death determinations for horses using incremental analysis are at present limited to two broad categories, or "seasons": winter (December to March) and summer (April to November, which can be subdivided tentatively into early spring/summer/fall) (Burke, 1995; Burke and Castanet, 1995). The season of death of 30 individuals (N = 30 teeth) could be estimated from thin-sectioned teeth (Table 2). Preservation factors and damage to the tooth's surface prevented the remaining teeth from producing legible slides. Incremental analysis shows the presence of horses during both "winter" and "summer" at all three of the Bluefish Caves (Fig. 5).

Horses in the wild are observed to give birth in mid to late spring (Waring, 1983). Eruption data can therefore be used as a seasonal indicator for certain restricted age categories. Seasonal information derived from eruption/wear patterns of a small number of individuals within these age categories at the Bluefish Caves shows the multiseasonal presence of horses (Table 6, Fig. 6).

Distribution of the Sexes at Bluefish Caves

Social ratios for horses are affected by the presence of two distinct social groupings: family herds and bachelor herds. Family herds consist of a group of four to ten mares with their foals and an adult stallion. The bachelor herd is a more socially unstable group of two to four adult males (Waring, 1983; MacFadden, 1992) that are either too young, too infirm, or too old to maintain a harem.

At the Bluefish Caves, the presence of yearlings in Caves II and III (Fig. 4) indicates the probable contribution of family herds to the mortality profiles. In Cave III in particular, the

indications are that one or more family herds may have contributed to the mortality profiles.

Canine teeth, which generally occur only in males, are considered one of the few means of distinguishing the sexes in *Equus caballus* (MacFadden, 1992). The taphonomy of the Bluefish Caves does not preclude random sampling of both bachelor and family herds. The prevalence of canine teeth in Cave III (and in the other caves) contradicts the expectation, generated by the age distributions, that family herds are represented. Where it could be observed, the ratio of mandibles with and without canine teeth is 11:12 in Cave III, 3:5 in Cave II and 1:1 in Cave I. The possibility that canines are retained in both sexes of *Equus lambei* is discussed elsewhere (Burke and Cinq-Mars, 1996).

DISCUSSION

Mortality patterns for horse in Caves II and III (Fig. 4) reflect a random sampling of the local populations, comprising both bachelor and family herds. These caves may have operated as both a focus point of natural deaths and a focus for the activities of several different carnivore and scavenger species over a relatively long period of time. The age pattern observed in Cave III, in particular, may represent catastrophic events involving family herds. Alternatively, the most vulnerable members of family herds, the inexperienced yearlings, died or were preyed upon, as were isolated and socially vulnerable bachelor males. Cave II appears to be a random sample of a natural mortality curve for equids, with similar seasonal indicators to Cave III, but sampling more age categories.

The pattern of horse mortality in Cave I (Fig. 4) probably reflects greater predator activity in the vicinity of this cave than at either of the other caves. Mortality profiles and seasonal data indicate that the Cave I assemblage is not just the result of natural and accidental deaths and scavenging activities, but that predators (potentially including humans) were also actively hunting and using the cave throughout the year.

A number of late Pleistocene sites discovered in karstic environments in southern France (Brugal and Jaubert, 1991) offer a useful analogy to the Bluefish Caves assemblage. Of three basic taphonomic patterns observed by Brugal and Jaubert (1991) in southern France, one in particular is compelling. These sites, which contain large, diverse faunas associated with relatively small archaeological components, apparently operated as natural traps and as loci for scavenging by humans and other predators. The sites (often karstic pitfalls) contain mixed faunal assemblages, and the mortality patterns are affected by seasonal, sometimes catastrophic, deaths (related to active erosion and surface flooding) and the seasonally random trapping of individual animals.

At Bluefish, erosion of the karst system which formed the three caves occurred well before the formation of the bone deposits. As a result, the Bluefish caves were not karstic pitfalls. However, the shallow caves could have provided

TABLE 2. Season-of-death estimates based on incremental study of dental cementum.

Catalogue	Tooth	Cave	Season
85-MISC-29	LM1	III	Summer
H6-3-9d	LM1	II	Winter
85-89	LM1	III	Summer
I6-MISC-1a	LM1	II	Spring
85-96	LM1	III	Indeterminate
E6-G-11	LM1	II	Indeterminate
85-90	LM1	III	Fall/Winter
F6-C-4	UM1/P4	I	Winter
85-109	LM1	III	Summer
G6-4-9	UM1	I	Fall/Winter
S-3-89	LM1	III	Summer
G6-5-1	UM1	I	Winter
MISC-87-39	LM1	III	Summer
G6-7-2	UM1	I	Indeterminate
D5-90	LM1	III	Summer
G7(E1/2)-17-4	UM1	I	Winter
85-109A	LM1	III	Spring
H7(E)-13-7	UM1	I	Summer
85-MISC-98	LM1	III	Winter
I7-1-47	UM1	I	Indeterminate
S-3-69	LM1	III	Winter
I7-2-13	UM1	I	Summer
85-76B	LM1	III	Winter
18(N)-8-6	UM1	I	Winter (late)
T.P.I.-D-22	LM1	III	Winter
J7-1-31	UM1	I	Indeterminate
85-64	LM1	III	Summer (early?)
J7-1-45	UM1	I	Winter
A-13-19	LM1	III	Indeterminate
J8-1-97	UM1	I	Spring?
M-9-83	LM1	III	Summer
K6-1-15	UM1	I	Summer
85-46	LM1	III	Indeterminate
K8-1-12	UM1	I	Summer
C3(E)-3-2A	LM1	II	Spring/Summer
SW-174	UM1	I	Indeterminate
G7-B-7	LM1	II	Summer
H7(E)-18-6	UM1/2	I	Winter
C3(E)-3-2	LM1	II	Summer
G6-7-3	UM2	I	Summer
J7-8-17	LM1	II	Spring/Summer
L8(S)-13-7	UM1	I	Summer
M-12-28[1]		III	Fall/Winter

[1] Season of death based on age/eruption and wear patterning; age = 4–9 months

limited shelter, or the promise of shelter, to a variety of animals including horses (cf. d'Andrea and Gotthardt, 1984). Sheltering animals dying in or near the caves during seasonally bad weather would leave the same taphonomic signature as animals falling into pitfalls or caught in seasonally active natural traps. In light of the model discussed by Brugal and Jaubert (1991), the taphonomy of the assemblages at Bluefish Caves II and III could be a result of natural deaths, both catastrophic and individual, combined with the effects of regular monitoring of the caves by a variety of scavengers and predators, such as humans, looking for windfalls.

Paleoethology and Environmental Reconstructions at Bluefish Caves

Seasonality estimates for horses indicate that this species was found near the Bluefish Caves in both summer

TABLE 3. A comparison of tooth size differences between *E. lambei* and European Upper Pleistocene horses reported in Levine (1982:232).

Tooth element	Height (mm)	*E. lambei* sample			Levine sample		Z score
		Mean Ole[1] (mm)	Standard deviation	N	N	Mean OLe [1] (mm)	
P^2	35–40	37.6	1.64	N = 5	N = 14	37.4	– 0.09
P^3	35–40	29.8	4.32	N = 6	N = 9	29.9	0.02
	45–50	27.5	NS[2]	N = 2	N = 17	30.2	NS
	65–70	29.4	NS	N = 2	N = 10	31.4	NS
P^4	45–50	25.8	NS	N = 1	N = 12	28.7	NS
	75–80	28.7	NS	N = 1	N = 10	29.8	NS
M^1	35–40	24.0	0.99	N = 6	N = 7	25.8	1.82
	40–45	24.2	NS	N = 3	N = 16	25.7	NS
	65–70	25.6	0.69	N = 5	N = 16	27.4	2.61
	70–75	26.8	0.65	N = 3	N = 5	28.3	NS
M^2	45–50	24.6	NS	N = 1	N = 5	27.7	NS
	70–75	26.1	0.12	N = 3	N = 9	26.9	NS
	75–80	26.8	0.47	N = 4	N = 3	28.4	3.36
M^3	25–30	29.0	NS	N = 1	N = 5	27.6	NS
	40–45	26.1	NS	N = 2	N = 1	25.7	NS
P_2	25–30	32.2	NS	N = 2	N = 1	30.1	NS
	30–35	34.2	NS	N = 1	N = 5	31.1	NS
	45–50	32.8	2.26	N = 5	N = 9	31.7	– 0.49
	50–55	33.2	NS	N = 2	N = 3	31.8	NS
P_3	30–35	27.7	NS	N = 3	N = 1	25.0	NS
	65–70	28.8	NS	N = 3	N = 3	29.0	NS
P_4	35–40	27.7	NS	N = 1	N = 5	26.5	NS
	40–45	26.8	NS	N = 2	N = 1	24.1	NS
	75–80	28.6	NS	N = 2	N = 9	27.0	NS
M_1	35–40	24.2	NS	N = 2	N = 1	23.2	NS
	65–70	26.9	0.73	N = 4	N = 9	27.0	0.14
M_2	40–45	24.9	NS	N = 2	N = 1	23.8	NS
	75–80	30.8	NS	N = 2	N = 9	27.7	NS
M_3	35–40	33.6	NS	N = 1	N = 5	32.0	NS
	45–50	31.06	NS	N = 1	N = 1	27.9	NS

[1] Size parameter used is occlusal length (Ole).

[2] NS = insufficient sample size.

and winter months (Fig. 5). To understand the seasonal movements of horse populations in the Bluefish Basin during the Late Pleistocene and their implications for a taphonomic study of the Bluefish Caves, paleoethological reconstructions are necessary. Paleoenvironmental data and modern ethological data for *Equus caballus* were used. Although *Equus przewalski* is arguably more closely related to *Equus lambei* than is feral *Equus caballus*, Przewalski horses have been observed only in captivity or in steppe environments, where remnant populations still lived at the turn of the century (e.g., the Dzungarian Gobi). Holocene open-steppe regions probably are not useful analogies to the Bluefish Basin during the last Glacial, either topographically or in terms of vegetation cover. If Guthrie (1985) is right, the Wisconsinan steppe-tundra was a vegetation mosaic, rather than a true steppe.

Metrical and morphological study of horse teeth from Bluefish confirms the close similarity between *Equus lambei* and wild and domestic horses alive today (Burke and Cinq-Mars, 1996). Horses generally inhabit steppe-like or savannah-like regions and are nonselective grazers, capable of enduring a wide variety of climatic conditions. They form small, stable bands of four to ten individuals and make small adjustments to their seasonal ranges within territories of varying size (Berger, 1986).

Paleoenvironmental reconstructions for the Bluefish Basin (Morlan, 1980; Hopkins, 1982; Ritchie et al., 1982) suggest a Late Pleistocene environment characterized by cold winters and cool summers, low annual precipitation (190–375 mm) with dry summers, and continuous permafrost. The Bluefish Caves were situated on a slope approximately 200 m above the valley floor, in a herbaceous tundra zone. During

TABLE 4. Age attributions for mandibular teeth using tooth height.

Catalogue No.	N[1]	Age categories, years[2]	N[3]
85-109	4	P2 = 10-11, P3 = 10-11, M1 = 10-11, M2 = 10-11	1
85-76	2	P3 = 3-4, M1 = 5-6	3
85-89	5	P2 = 7-8, P3 = 6-7, P4 = 5-6, M1 = 5-6, M2 = 8-9	4
85-90	6	P2 = 10-11, P3 = 11-12, P4 = 10-11, M1 = 10-11, M2 = 10-11, M3 = 12-13(11-12)	3 (2)
85-90	4	P2 = 5-6, P3 = 5-6, P4 = 4-5, M1 = 5-6	2
85-95	6	P2 = 6-7, P3 = 6-7, P4 = 5-6, M1 = 6-7, M2 = 6-7, M3 = 5-6	2
B3-3-23	4	P2 = 6-7, P3 = 6-7, P4 = 4-5, M3 = 5-6	3
C3(E)-2-37	2	P3 = 5-6, P4 = 4-5	2
C3(E)-3-2	6	P2 = 5-6, P3 = 5-6, P4 = 4-5, M1 = 6-7, M2 = 5-6, M3 = 5-6	3
C3(E)-3-2A	3	P2 = 5-6, P3 = 4-5, P4 = 3-4	3
H6-3-8	3	M1 = 5-6, M2 = 5-6, M3 = 5-6	1
H6-3-9	5	P2 = 6-7, P3 = 6-7, P4 = 4-5, M1 = 5-6, M2 = 5-6	3
I7-3-12	2	P2 = 4-5, M1 = 4-5	1
I7-3-27	4	P2 = 4-5, P4 = 4-5, M1 = 4-5, M3 = 5-6	2
J7-8-19	5	P3 = 12-13(11-12), P4 = 10-11, M1 = 11-12, M2 = 11-12, M3 = 9-10	3 (4)

[1] Number of teeth in series from which crown heights were available.
[2] After Levine, 1982.
[3] Number of age categories (Levine, 1982) spanned by series.

TABLE 5. Age attributions for maxillary teeth using tooth height.

Catalogue #	N[1]	Age in years	N[2]
85-115	4	P2 = 5-6, P3 = 8-9, M2 = 7-8, M3 = 7-8	4
85-120	2	P2 = 13-14, M2 = 12-13	2
85-41	4	P2 = 11-12, M1 = 9-10, M2-9-10, P4 = 9-10	3
85-MISC-2.1	2	P2 = 8-9, M2 = 7-8	2
85-MISC-1	5	P3 = 11-12, P4 = 9-10, M1 = 9-10, M2 = 8-9, M3 = 8-9	4
E3-4-3	3	M1 = 5-6, M2 = 6-7, M3 = 5-6	2
H5-3-23	2	P2 = 6-7, P3 = 6-7	1
M-9-112 (left)	2	P2 = 7-8, M3 = 5-6	3
M-9-112 (right)	4	P2 = 11-12, P3 = 11-12, P4 = 8-9, M3 = 7-8	5
MISC-52	4	P4 = 9-10, M1 = 9-10, M2 = 12-13, M3 = 9-10	4
S-3-79	6	P2 = 7-8, P3 = 6-7, P4 = 5-6, M1 = 5-6, M2 = 6-7, M3 = 5-6	3
T.P.1-E-46 (l)	4	P2 = 8-9, M1 = 5-6, M2 = 6-7, M3 = 5-6	4
T.P.1-E-46 (r)	3	P2 = 8-9, M2 = 6-7, M3 = 5-6	4
T.P.1-F-35	2	P2 = 10-11, P3 = 11-12	2
M-9-94	2	M1 = 7-8, M2 = 8-9	3
M-9-94A	4	P2 = 11-12, P3 = 11-12, P4 = 8-9, M3 = 7-8	5

[1] Number of teeth in row from which tooth height could be measured.
[2] Levine, 1982.
[3] Number of age categories (Levine, 1982) spanned by series.

the Late Pleistocene, the valley bottom consisted of sedge and grass marsh with stands of willow (Ritchie et al., 1982). Upland plateaux above the caves were covered with herbaceous tundra during the Late Glacial. Climatic conditions would have been harsher during the Full Glacial, when the
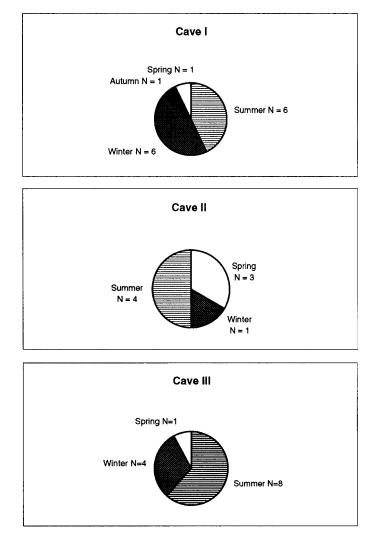

FIG. 5. Seasonal mortality of equids based on analysis of cementum increments.

high plateaux may have been inhospitable for animals such as the horse (Ritchie et al., 1982). This interpretation of the pollen data as indicative of polar desert conditions in the uplands is contested, however (Guthrie, 1985).

The hypothetical desertification of the highland regions during the Full Glacial period would have resulted in compression of the home ranges of horses in the Bluefish Basin, with abandonment of the high summer ranges. This information allows us to propose two possible models of range use for horses in the Bluefish Basin during the Late Pleistocene:

1. The mid-slope region around the Bluefish Caves may have been used as a "compressed" summer range, the valley bottom as a spring/winter/fall range. However, incremental data indicate the presence of horses during the winter months at Bluefish Caves, which is inconsistent with this reconstruction.

2. The Bluefish Basin became a refugium of sorts, where horse populations were forced into a single, annual range. This model fits the seasonal data. However, use of a single, annual range is not consistent with the ethology of modern

TABLE 6. Season of death of juveniles estimated using probable age at death.[1]

Cave	Individual (Cat.)	Age (months)	Probable Season
I	dI	4 – 15	Indeterminate
I	dII	4 – 18	Indeterminate
II	dIII	4 – 9	September-January
II	dIV	4 – 9	September-January
II	n/a (E6-G-12)	< 9	May-January
II	dV	9 – 36	Indeteterminate
III	dVI	16 – 24	Indeteterminate
III	dVII	4 – 9	September-January
III	dVIII	9 – 15	January-August
III	dIX	4 – 36	Indeterminate
III	dX	24 – 36	Indeterminate
III	dXI	16 – 24	September-April

[1] Table includes all deciduous rows ("individuals") and isolated teeth with seasonality data.

FIG. 6. Seasonal mortality of equids based on analysis of cementum increments and eruption data. Data available for Cave II (Fig. 6A) and Cave III (Fig. 6B).

feral horse populations, which are observed to make seasonally differentiated use of their annual territories (Welsh, 1975; Berger, 1986).

The presence of horses at the Bluefish Caves during both summer (April-November) and winter (December-March) months during the Late Pleistocene could also indicate a third pattern of range use. In the Granite Ranges, a rugged, seasonal habitat in the Great Basin region of the United States (Berger, 1986), horses move between valley bottoms, which shelter them in winter, and upland plateaux, accessible only in summer. Valleys and upslope regions are part of a fall/winter/spring range, and upland plateaux are summer ranges.

By analogy, the slopes on which the Bluefish Caves are situated could have constituted part of the fall/winter/spring ranges during the Late and Full Glacial, with herds ranging onto the upland plateaux above the caves during the peak of summer.

Summer (April-November) deaths near the Bluefish Caves would therefore represent early or late seasonal movements between plateaux and valley ranges that are entirely consistent with what we know of the behaviour and feeding habits of *Equus caballus* in the wild. During the winter months, the horses may have descended into the valley to seek shelter among the shrubs and willow stands (as reconstructed by Ritchie et al., 1982). Alternatively, the slopes around the caves, and the caves themselves, may have provided protection from sudden storms (d'Andrea and Gotthardt, 1984). The lowland marshes would have been avoided in the spring and fall because they harboured biting insects, especially during the relatively warmer Late Glacial.

CONCLUSION

The age profiles for the Bluefish Caves show that horse deaths in Cave I may reflect greater predator activity in the vicinity of this cave. The equid mortality patterns for Caves II and III probably reflect the fact that bone accumulation at these caves was the result of both natural deaths and the activities of several different predators over a long period of time. The model of a site where accidental and natural deaths frequently occurred, that was regularly monitored and visited by various predators and scavengers, including humans, is proposed for Caves II and III. This model remains to be tested using the remainder of the Bluefish assemblage.

The pattern of seasonal mortalities for horses at the three Bluefish Caves shows that horses were present in the vicinity of the caves during most of the year. When the ethology of *Equus lambei* is considered along with the behaviour of horses living under cold, seasonal conditions elsewhere, the pattern of mortalities at Bluefish could indicate a pattern of herd movements similar to that observed among horses in the wild today.

The area surrounding the Bluefish Caves can therefore be considered within the known ecological tolerances of horses. This conclusion presents us with an alternative to the palynological reconstructions of an upland polar desert during the Full Glacial around the Bluefish Basin. It also supports the proposal that the Bluefish Basin was not a marginal habitat, or glacial refugium, but rather an area inhabited by a diverse fauna during both Full and Late Glacial periods.

Finally, age tables based on tooth height, derived from European caballoids, do not appear to be directly translatable to *Equus lambei*. It would be necessary to recalibrate the tables proposed by Levine (1982) before they could be used to determine precise ages from tooth height for fossil North American horses.

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