


AN ABSTRACT OF THE THESIS OF

Melinda Elaine Brown for the degree of Master of Science  
in Department of Zoology presented on September 28, 1981

Title: Determination of mode of death of John Day Merycoidodontidae  
(Oreodontidae) by population age structure analysis

**Redacted for privacy**

Abstract approved:



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Dr. John A. Ruben

Volcanic activity during the Tertiary has long been held responsible for the deaths and subsequent fossilization of the vertebrate populations of the John Day region in Oregon. Oreodonts as plains or savannah dwelling ruminant herbivores, were likely to have been subject to potential exposure throughout their lifetime to volcanic debris and gasses. However, statistical comparisons of oreodont and recent ruminant populations indicate that other natural causes (e.g. predation) were more influential factors in the deaths of the oreodonts than cataclysmic volcanic activity. Assumptions that allowed such comparisons to have been made included 1) oreodonts exhibited a similar life style, and had similar age classes and age distributions as extant ruminants thought to occupy generally similar habitats. 2) Fossilization processes at John Day were assumed not to have radically altered the proportions of the various age classes at death although some differential preservation of mature and older individuals may have occurred.

Determination of mode of death  
of John Day Merycoidodontidae (Oreodontidae)  
by population age structure analysis

by

Melinda Elaine Brown

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INTRODUCTION

Tertiary North American volcanic activity was frequent and purportedly caused the death and subsequent fossilization of numerous populations of vertebrates (Merriam, 1901; Osborn, 1909; Peale, 1886; Sinclair, 1906; Voorhies, 1979). The Miocene John Day environment of eastern Oregon was among the more prominent of these volcanically active areas, and it has been proposed that fossilized John Day vertebrates were initially killed by catastrophic igneous activity (Thorpe, 1925, 1937; Williams, 1953). This study presents a means by which the likelihood of such a catastrophic mode of death can be ascertained. This is accomplished by utilizing statistical comparisons of living and fossilized population age structure.

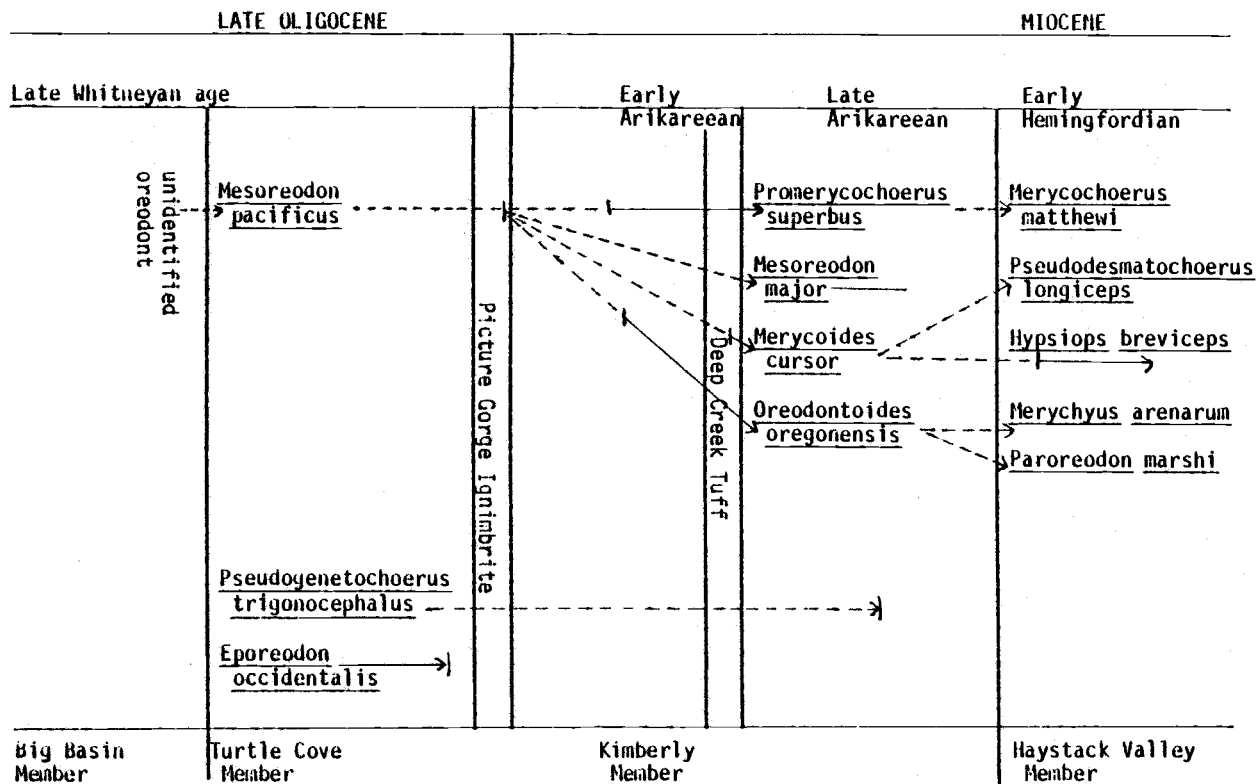
The animals used in these investigations were oreodonts (Ruminantia: Merycoidodontidae), extinct, medium-sized herbivores that were commonly preserved in North American Tertiary sediments. Oreodonts are widely regarded as having been herding, savannah- or plains-dwelling ruminant ungulates, generally similar in habits and appearance to many extant bovids and cervids (Greaves, 1972; Matthew, 1932; Thorpe, 1925, 1937).

Volcanism in Oregon began in mid-Eocene times and increased in magnitude, reaching its peak in the mid-Miocene (Williams, 1953). Deposition of the John Day Formation occurred from the late Oligocene to early Miocene. The formation is composed of water-laid, silicic volcanoclastic rocks, some rhyolite plugs and a few ignimbrite units. Each of the four subdivisions of the formation, Big Basin, Turtle Cove, Kimberly and Haystack Valley, has a characteristic composition (Figure 1). The Big Basin member consists of diagenetically altered fine-to medium-grained air-fall tuff, while the Turtle Cove member is composed of zeolitized tuffs. The Kimberly member consists of unzeolitized, massive tuffs, and the Haystack Valley member consists of unzeolitized, fluvial, lacustrine and air-fall volcanoclastics (Beaulieu, 1972; Fisher and Rensberger, 1972; Merriam, 1901; Robinson, 1976). The boundary between the Turtle Cove and Kimberly members intergrades to a great degree and the faunas present in the lower two-thirds of the Kimberly member are also common to the Turtle Cove member. For those reasons, the two members are treated as a single entity. The Haystack Valley and Kimberly/Turtle Cove Members, in contrast, are separated by an unconformity rendering them as distinct subdivisions.

Topographically, the Kimberly/Turtle Cove region is thought to have been a broad alluvial plain covered with large lakes and surrounded by low standing, ash-mantled hills (Downs, 1956; Matthew, 1901; Thorpe, 1925; Williams, 1953). Interior drainage serviced the lakes, but drainage conditions appear to have changed during the formation of the Turtle Cove member.



Figure 1: Phylogeny and stratigraphic occurrences of John Day oreodonts.



From Fisher and Rensberger (1972) and Lander (personal communication, 1981).

Conditions varied from alternately wet and dry environments allowing for good drainage, to wet environments wherein water-saturated conditions prevailed. The Haystack Valley member was also probably a region of former lakebeds and similar appearance (Fisher and Rensberger, 1972; Marsh, 1875; Merriam, 1901).

The climate during the Oligocene and Miocene was extremely equable, but a general trend towards aridity was evident. Consequently, in central and eastern Oregon, the temperate forests gradually gave way to a savannah or grassland type vegetation (Chaney, 1956) which enabled an extensive adaptive radiation of herbivores to take place (Matthew, 1932; Wanless, 1923; Williams, 1953).

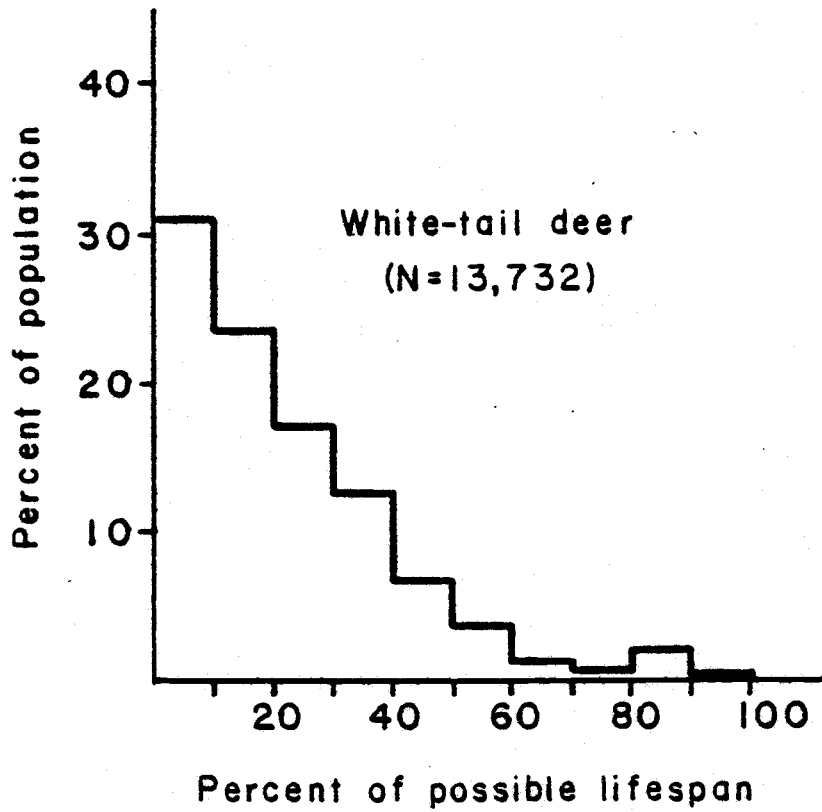
Hypotheses have varied as to the causes behind the deaths of the extensive vertebrate fauna of the John Day beds and have included, besides volcanic activity, predation (Thorpe, 1925), disease (Thorpe, 1925), starvation (Wanless, 1922, 1923) and various stochastic events (Matthew, 1932; Williams, 1953). In view of the highly volcanic nature of the John Day beds, an hypothesis of a volcanic mode of death, at first glance, might seem reasonable. However, in no studies have statistical tests ever been utilized as an investigative means of testing the validity of the proposed hypothesis. The purpose of this study is, therefore, to statistically examine representative fossilized oreodont populations from the John Day region in an attempt to determine some aspects of their mode of death. Specifically, in the event of catastrophic volcanism, random samples of the population of the oreodonts would likely have been killed and subsequently preserved

(Voorhies, personal communication, 1981). Under such circumstances, the fossilized oreodont populations should exhibit an age class distribution generally similar to that of extant, herding plains or savannah-dwelling herbivores (Figure 2). Conversely, if oreodonts died of "natural" causes (i.e., predation, disease, old age) and were subsequently preserved, a high proportion of mature or very old individuals should be represented in such a "death assemblage", as is the case in death assemblages of similar, extant herbivores (Figure 3) as compared to the very low proportions seen in age distributions. Conclusions of this study should presumably be applicable to the majority of vertebrates fossilized in the same regions at John Day.

Paleobiological studies of this nature require that many assumptions be made concerning the lifestyle of the animal to be studied. Such assumptions must be supported with as much known data from comparative and functional anatomy of living animals as is possible (Olson, 1980).

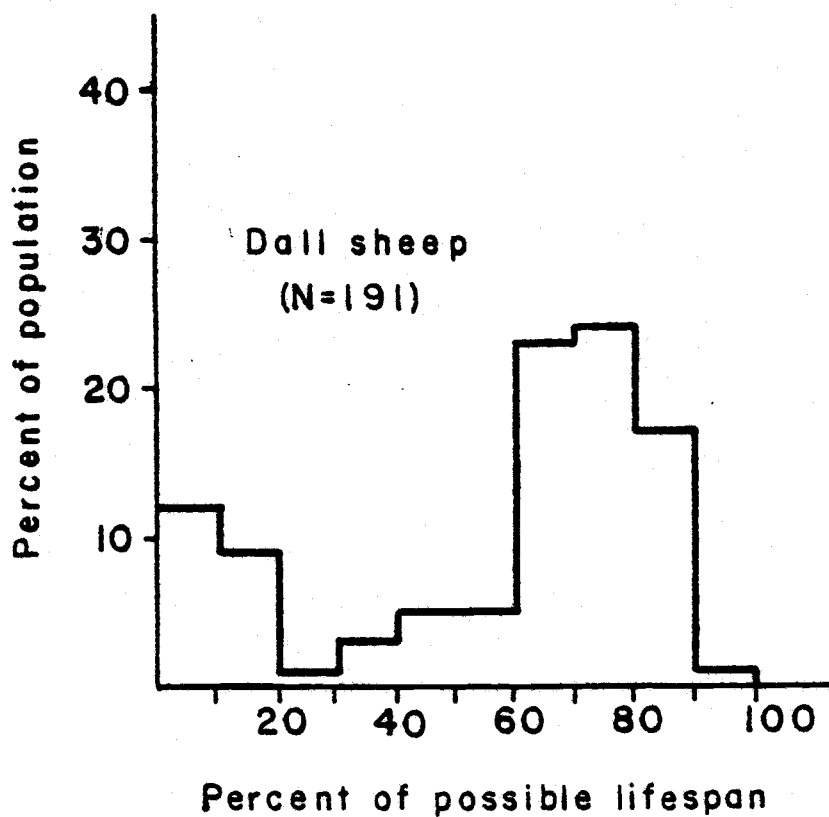
In the case of oreodonts, due to the large numbers of fossils which have been found throughout North America, much is known about their skeletal anatomy. Characteristic primitive ruminant features include brachyodont type, selenodont cheek teeth, four-cusped upper molars and simple molariform premolars. The upper canine was chisel-like in being fairly stout and moderately projecting, but the lower canine had undergone a size reduction and was replaced functionally by the enlarged premolar, similar to the more advanced ruminants (Romer, 1966; Scott, et al., 1941).

Figure 2: Representative extant ruminant population age structure histogram.



Histogram of white-tail deer from Hawkins, et al., 1971; Ozoga, 1972; Severinghouse, 1949; Woolf and Harder, 1979.

Figure 3: Representative predation death assemblage age structure histogram.



Histogram of Dall sheep from Murie, 1944.

Such dental characteristics are unique to the ruminants and thus, they are generally regarded as members of the suborder Ruminantia (Romer, 1966).

As medium-sized herding herbivores (Thorpe, 1925, 1937; Scott 1937) with few morphological peculiarities, they would presumably have been constantly exposed to the elements and to predation throughout their lifetime. Consequently, they were not likely to have frequented caves, dens, or burrows, nor were they likely to have displayed many behavioral adaptations associated with peculiar modes of feeding, shelter-building or reproduction that might have led to a discriminant bias (e.g. escaping catastrophic volcanism) for the preservation of one segment of the population over another in the fossil record (Romer, 1966, Vaughan, 1978). Additionally, oreodonts are ideal for this study because of their relative abundance in the John Day region and specifically in the Turtle Cove, Kimberly and Haystack Valley members (Baldwin, 1976; Cope, 1884; Lander, 1977; Matthew, 1932; Schultz and Falkenbach, 1949, 1968; Thorpe, 1925), (Figure 1). Age structure of the oreodont populations can be determined using degree of tooth wear as is similarly done for living ruminant populations (Morris, 1972; Schultz and Falkenbach, 1968; Thorpe, 1925, 1937). Distinct age classes can be segregated out from the general population and relative frequencies calculated. For example, Medin and Anderson (1970) examined a mule deer (Odocoileus hemionus) population consisting of 29,512 individuals and were able to distinguish 15 separate age classes from 1/2-14 1/2 years of age. Thus, tooth wear data for oreodonts allows statistical comparisons to be made

between the population age structure of fossilized oreodonts and related, extant populations of cervids and bovids which occupy generally similar habitats and which probably exhibit generally similar behavior. It is assumed from the outset of this study that the oreodont populations had age classes similar to those of living ruminants. It is also assumed that the fossilization process itself has not radically altered the proportions of the various age classes of oreodonts at death.

## MATERIALS AND METHODS

The majority of the tooth wear data on the 12 species of John Day oreodonts, Mesoreodon pacificus [Eporeodon (Paraeporeodon) leptacanthus, Schultz and Falkenbach, 1968; E. (P.) longifrons, Ibid; E. (P.) l. perbullatus, Ibid; E. (P.) pacificus, Ibid], Pseudogenetochoerus trigonocephalus [Dayohyus trigonocephalus, Schultz and Falkenbach, 1968; D. wortmanii Ibid; Pseudogenetochoerus condoni, Ibid; P. covensis, Ibid], Eporeodon occidentalis [Eporeodon davisii, Schultz and Falkenbach, 1968; E. occidentalis, Ibid], Promerycochoerus superbus [Desmatochoerus leidyii, Schultz and Falkenbach, 1954; Promerycochoerus latidens, Schultz and Falkenbach, 1949; P. superbus, Ibid; P. s. chelydra, Ibid; P. (Parapromerycochoerus) macrostegus, Ibid; P. (P.) m. furlongi, Ibid; P. (Pseudopromerycochoerus) inflatus, Ibid; P. (P.) montanus, Ibid; Superdesmatochoerus lulli, Schultz and Falkenbach, 1954; S. microcephalus, Ibid], Mesoreodon major [Desmatochoerus curvidens, Schultz and Falkenbach, 1954; Pseudodesmatochoerus wascoensis, Ibid], Merycoides cursor, Oreodontoides oregonensis [Epigenetochoerus parvus, Schultz and Falkenbach, 1968; Oreodontoides oregonensis, Schultz and Falkenbach, 1947], Merycochoerus matthewi, Pseudodesmatochoerus longiceps, Merychyus arenarum, Paroreodon marshi [Oreodontoides (Paroreodon) marshi, Schultz and Falkenbach, 1947; O. (P.) stocki, Ibid] and Hypsiops breviceps [Hypsiops johndayensis, Schultz and Falkenbach, 1950], was obtained from Schultz and Falkenbach (1947, 1949, 1950, 1954 and 1968), (Appendix



1). Additional data were taken from personal measurements made on recently found specimens belonging to the National Park Service and to the Condon Museum, University of Oregon. Schultz and Falkenbach examined specimens in collections from the American Museum of Natural History, California Institute of Technology, University of California at Berkeley, University of Oregon, U. S. National Museum, Woodwardian Museum at Cambridge University and Yale University's Peabody Museum. Their data are reported as relative degree of wear which they have separated into three basic divisions: immature, mature (-M, M, M+), and worn (W, W+, W++, W+++, W++++). Tooth wear data reported for oreodonts corresponded to that obtained by applying the standardized criteria of the age classification schemes of Dow and Wright (1962), Robinette, et al. (1957), and Severinghaus (1949) for living ruminants (Table 1). Specimens at the University of Oregon were personally re-examined utilizing those criteria to verify Schultz and Falkenbach's conclusions and to provide a basis for similarly categorizing the National Park Service specimens.

Overall accuracy of the tooth wear method for specific age determination varies from between 43-100% (Erickson, et al., 1970; Kerwin and Mitchell, 1971; Gilbert and Stolt, 1970; Quimby and Gaab, 1975; Robinette, et al., 1957; Thomas and Brandy, 1975) depending upon the age class being examined and the experience level of the investigator. Such a system permits determination of percentage age class composition. In addition, it has been found that in studies where a large number of specimens are being examined, the errors in age determination will tend to compensate for

Table 1: Tooth eruption and wear in relation to probable age in oreodonts.

OREODONT AGE CLASS (degree of wear)	CORRESPONDING RUNINANT AGE CLASS (in years ±)	DESCRIPTION OF TEETH
I	0-1	I1,I2,I3,C1 deciduous; P1,P2,P3, P4 deciduous; P4 with three cusps. M1,M2 may be erupting, moderate wear on premolars and M1, replacement of lateral incisors.
-M	1-2	I1,I2,I3,C1,P1 permanent; P2,P3, P4 deciduous and badly worn; permanent P2, P3 erupting. M1, M2 erupted and functional with moderate wear, M3 erupting.
M	2-3	All teeth permanent and fully erupted. Lingual crests of M1,M2 sharp and enamel above narrow line of dentine. P1,P2,P3,P4 showing slight wear, crescent design on occusal surface a broad V.
M+	3-4	Lingual crests of M1 blunt; dentine in lingual crests of M1, M2 wider than enamel. Labial side of M1 about 5-7 mm above gum line and occusal surface worn to shallow crescent only. P1 through P3 show increasing degrees of wear.
W	4-5	Lingual crests of M1 almost completely eroded, lingual crests of M2 blunt, M3 sharp, labial side of M1 about 5-6 mm above gum line. M3 posterior crest sloping to labial side and worn, greater degree of wear on premolars, crescent occusal surface pattern shallow on P3,M2,M3, gone on M1.
W+	5-6	Dentine much wider than enamel on all crests. Lingual crests on M1, M2, absent, blunt on M3. M2 5-6 mm above gum line on labial side, some wear on incisors.
W++	6-7	M1 within 3-4 mm of gum line on labial side, M2 within about 4-5 mm on labial side. Slight lingual crest on M3; P1, P2 showing heavy wear, M2, M3 shallow crescent on occusal crescent.
W++	7-9	Premolars showing heavy wear, all molars within about 2-3 mm of gum line on labial side, shallow crescent on occusal surfaces gone.
W++	9+	M1 at gum line (often missing), M1, M2 within about 1-2 mm of gum line on labial side, incisors often missing, dentine wearing.

Based on black and white-tail deer (Severinghaus, 1949), pronghorn antelope (Dow & Wright, 1962), and male deer (Robinette, *et al.*, 1957) age classifications. (I = immature, M = Mature, W = worn, + and - = degree of wear)

each other, given that the criteria being used to age the animals are truly representative of each age class (Robinette, et al., 1957). Because only two people were involved in collecting the majority of the data, individual variance in aging was kept to a minimum. Those examined from the University of Oregon collection enabled a degree of correlation to exist between Schultz and Falkenbach's data and that collected by the author.

Data could then be transformed for the first time from the system of differing degrees of wear historically used to a system of numerical age classification (Table 1). Such age classification features facilitated meaningful comparisons with ruminants.

Oreodont phylogeny and classification used in this study (Figure 1) was the result of Lander's recent work (1977; personal communication, 1981) with John Day oreodonts. The only other in-depth studies were those undertaken by Schultz and Falkenbach (1940, 1941, 1947, 1949, 1950, 1954, 1956, 1968). Lander's work took into account phenotypic variation within a species, within a growth series and between sexes, as well as variation due to crushing or selective destruction. As a result, he was able to reduce oreodont classification from Schultz and Falkenbach's 11 subfamilies, 46 genera and 179 species to 8 subfamilies, 18 genera and 76 species. Lander's classification seems to fit most easily into the biological species concept, and thus was utilized here.

Data on extant cervid populations of white-tail deer (Odocoileus virginianus) (Hawkins, et al., 1971; Ozoga, 1972; Severing-

haus, 1949; Woolf and Harder, 1979), mule deer (Odocoileus hemionus) (Medin and Anderson, 1979; Robinette, et al., 1957), black-tail deer (Odocoileus hemionus columbianus) (Einarsen, 1946; Longhurst, 1964; Taber and Dasmann, 1957), reindeer (Rangifer tarandus) (Leader-Williams, 1981), elk (Cervus elaphus) (Blood and Lovaas, 1966; Murphy, 1963; Peek, et al., 1967), moose (Alces alces) (Sergeant and Pimlott, 1959) and bovid populations of pronghorn antelope (Antilocapra americana) (Dow, 1952; Kolenosky and Miller, 1962), Dall sheep (Ovis dalli) (Murphy and Whitten, 1976), were obtained for comparison purposes (Appendix 2).

Much age distribution data exists on certain extant bovids and cervids because of their great economic and ecologic importance. Species thought to be of less importance have not been as thoroughly studied and consequently, a truly broad utilization of extant forms for comparative purposes was not possible. Therefore, only those species believed to utilize a similar habitat as oreodonts and whose populations have been extensively studied were chosen for comparison purposes. The majority of those data were also based on tooth eruption and wear. Data collection techniques employed in those studies were variable but generally included long term random sampling by live capture of large populations, total harvesting of restricted, long-term study populations and study of natural mortality casualties. For other comparative purposes, age distribution data from death assemblages of extant ruminants were also obtained (Appendix 3). The most complete studies were those observing the effects of predation on moose (Mech, 1966; Peterson, 1955), Dall sheep (Murie, 1944), elk

and mule deer (Hornocker, 1970).

Age class data within a species were combined and variability minimized by summing across each distinct age class. This yielded a single set of values representative of the average proportion of individuals expected for each age class in a population of a given size. Data from the various studies on each of the living species were combined only if at least six distinct age classes had been identified. No hunter killed data was used .

Three independent methods of approach were utilized in this study. Life tables were constructed for the total oreodont population with separate tables for those oreodonts from either of the two geologic members of the John Day Formation (Figure 1). These groupings enabled analyses to be conducted to determine if variation existed between the populations of the different geologic members as to mode of death. Life tables for extant ruminants were additionally constructed with distinctions made as to the data being from natural death assemblages due to predation or population distribution studies. The stationary age distribution method of Keyfitz (1968) was applied since knowledge of age-specific death rates only was required (Appendix 4). Survivorship curves extracted from the life tables allowed determinations to be made as to whether the oreodont population represented a death assemblage of accumulated natural deaths over a long period of time or an assemblage of catastrophic deaths accumulated over a very short time.

A second method of approach entailed calculation of the mean age of the population. Statistical comparisons utilizing the Student's t-test were then applied. Comparisons of oreodonts as an entire population against extant ruminants both as a natural death assemblage and as a living age distribution were conducted.

Lastly, statistical comparisons between the extant species and the oreodonts were made utilizing chi-square contingency tables (Steel and Torrie, 1980). At all times, the critical chi-square value used corresponded to a P-value of  $\leq 0.05$ . The null hypothesis tested proposed that the probability of a herbivore being in a particular age class was independent of that herbivore being a member of an extant species or an oreodont species. The alternative hypothesis was that such a probability was dependent upon whether the herbivore was an oreodont or not. Comparisons here were made in three ways. The oreodont species were treated as an entire population, then separated into the two major geologic member groups, and finally, as individual species. As an arbitrary limit to prevent small sample size from affecting results in the species comparison, a minimum sample size of 15 was chosen. Six oreodont species, Mesoreodon major, Merycoides cursor, Merycochoerus matthewi, Pseudodesmatochoerus longiceps, Hypsiops breviceps, and Merychyus arenarum were, therefore, excluded from this analysis.

## RESULTS

Tooth-wear based fossilized oreodont and extant ruminant age classifications are given in Table 2 and Figures 4, 5 and 6.

Contingency table chi-square values, representing comparisons of the population age class distributions between the six species of oreodonts and extant herbivores, are given in Table 3. Significant differences existed between population age distributions of the extinct and living species being compared in the great majority of cases (97%). The null hypothesis of independence, therefore, was rejected and the alternative hypothesis of dependence accepted. The only case in which no significant difference existed was in the comparison between Paroreodon marshi and reindeer.

The results of the statistical comparisons made between the species of the Kimberly/Turtle Cove and the extant ruminants and of the Haystack Valley species and the extant ruminants are given in Table 4. Although the population of oreodonts within the Kimberly/Turtle Cove member is significantly different from that of the Haystack Valley member in terms of its age class distribution ( $\chi^2=24.63; 8\chi^2(0.05)=15.5$ ), separate comparisons of each of the two populations with extant species indicated significant differences in all cases.

The Student's t-test values from comparisons between the mean age of the populations of oreodont species and the collective age distribution data and the death assemblage data from the predation studies on the extant ruminants are given in Table 5. At  $p \leq 0.05$ , a significant difference exists between the oreodonts and the

Table 2: Degree of tooth wear and external height of M3 as an indicator of tooth wear of oreodont specimens.

OREODONT SPECIES	CATALOGUE NUMBER	DEGREE OF WEAR	HEIGHT OF M3 (in mm)
<u>Mesoreodon</u> <u>pacificus</u>	F673	M+	14.9
	F697	W+	9.3
	F689	W++	7.8
<u>Pseudogenetochoerus</u> <u>trigonocephalus</u>	NPS	M	11.8
	F677	M+	11.2
	F31298	W+	8.8
	F675	W++	6.4
	F1049	W++	6.0
	F21321	W++	6.1
	F710	W++	3.6
	F29459	W++	4.0
<u>Eporeodon</u> <u>occidentalis</u>	F5267	M	9.6
	F671	M+	10.0
	F772	W	--
	F1050	W	8.8
	F1051	W	7.8
	F681	W+	6.2
	F682	W+	5.3
	F676	W+	6.0
	F187	W++	5.0
<u>Promerycochoerus</u> <u>superbus</u>	F5068	M	--
	F21311	M+	14.5
	F5072	M+	15.3
	F678	W	13.8
	F685	W+	14.5
	F686	W+	13.3
	F692	W+	13.0
	F709	W+	13.7
	F1659	W+	8.3
	F687	W++	10.4
	<u>Oreodontoides</u> <u>oregonensis</u>	F170	W++
<u>Paroreodon</u> <u>marslii</u>	F667	M+	13.1
	NPS	M+	10.2
Unidentified Kimberly/Turtle Cove oreodonts	F31575	I	--
	F31046	I	--
	F31054	M	7.5
	F31055	W	6.2
	F672	W+	5.4
	F4065	W++	6.0
	F31078	W++	4.3

NPS = National Park Service Specimens  
F = Condon Museum, U of O Specimens.



Figure 4: Population age structure histogram of John Day oreodonts.

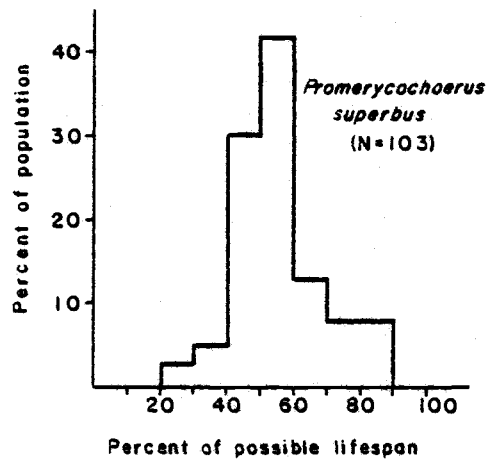
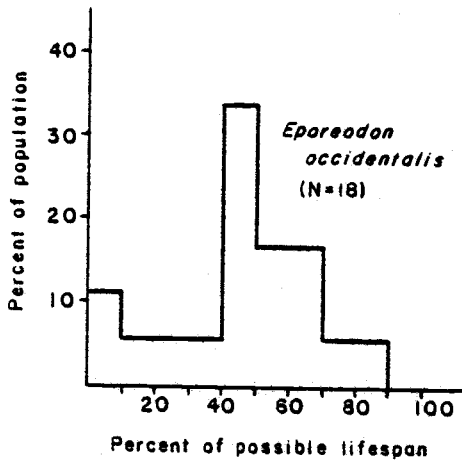
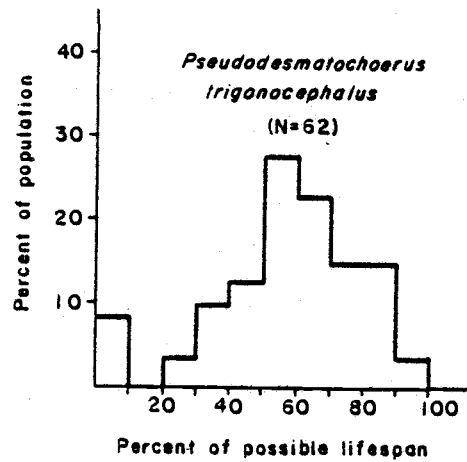
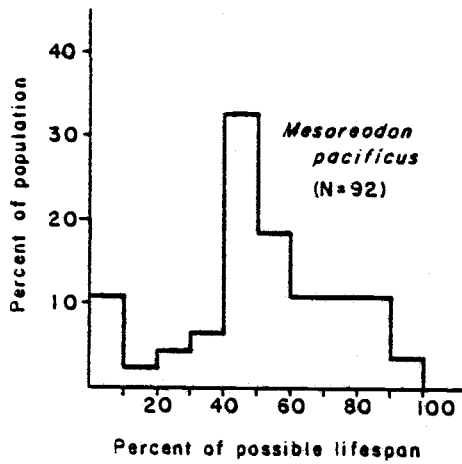
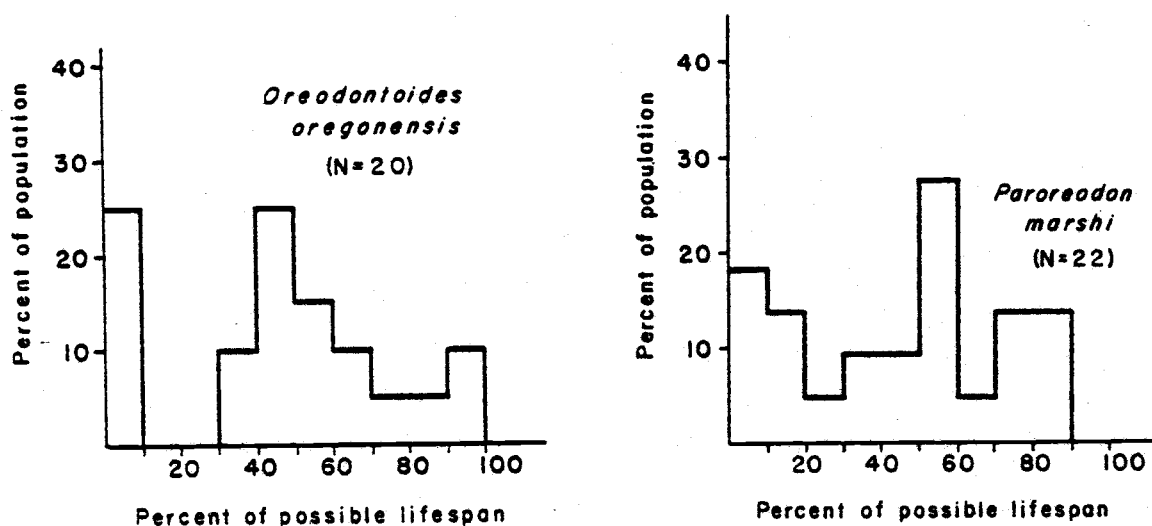


Figure 4: Continued



Data for Mesoreodon pacificus from Schultz and Falkenbach, 1968 and from this study; for Pseudogenetochoerus trigonocephalus from Schultz and Falkenbach, 1968 and from this study; for Eporeodon occidentalis from Schultz and Falkenbach, 1968 and from this study; for Promerycochoerus superbus from Schultz and Falkenbach, 1949, 1954 and from this study; for Oreodontoides oregonensis from Schultz and Falkenbach, 1947, 1968 and from this study; and for Paroreodon marshi from Schultz and Falkenbach, 1947 and from this study.

Figure 5: Population age structure histograms of extant ruminants.

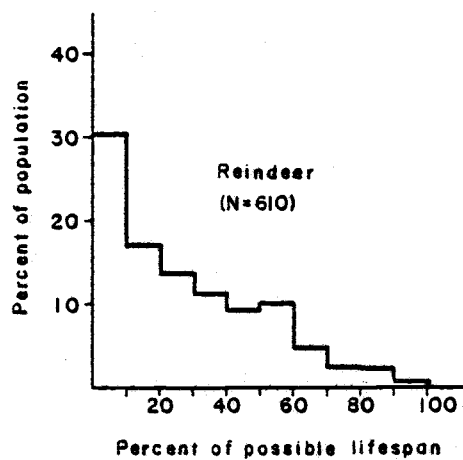
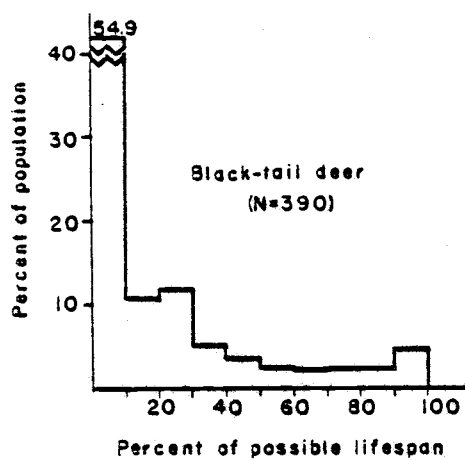
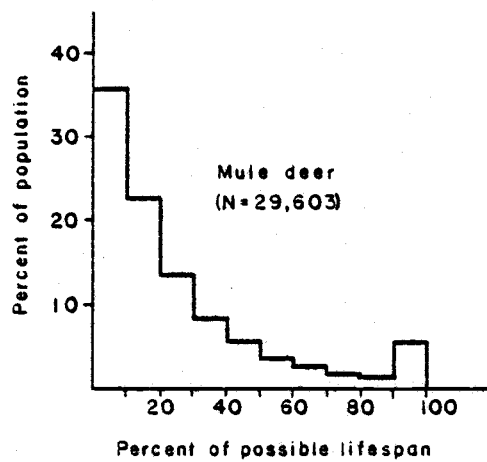
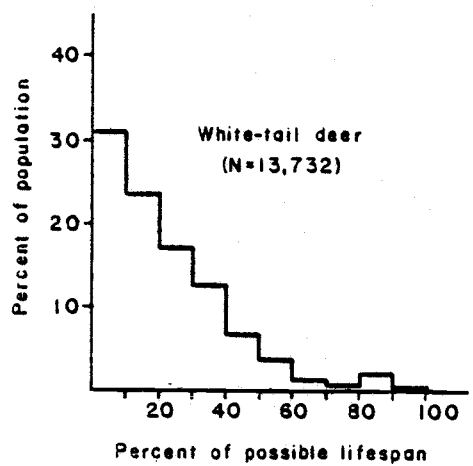
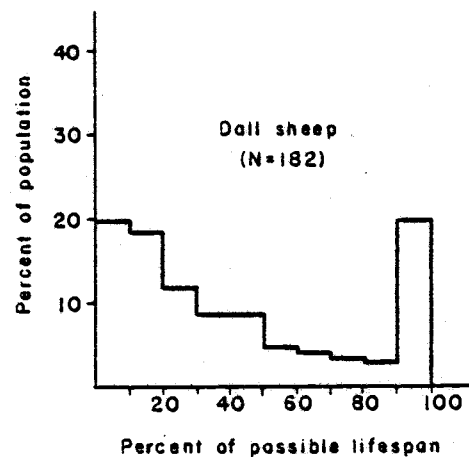
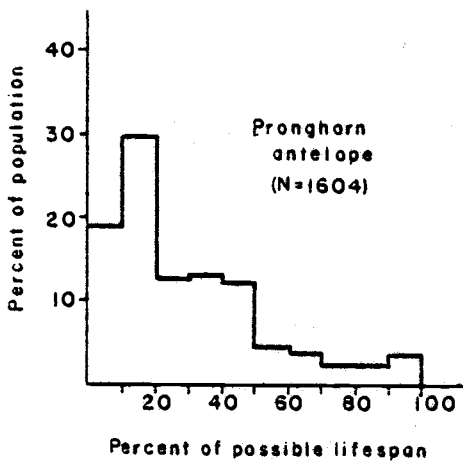
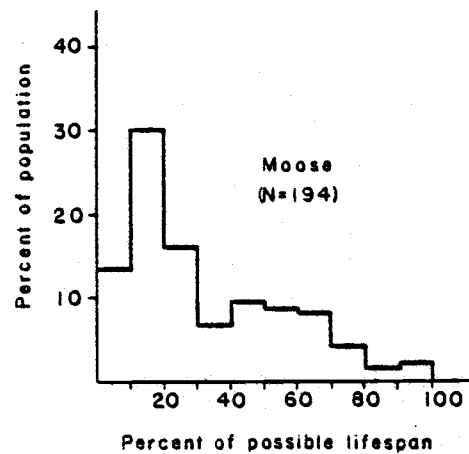
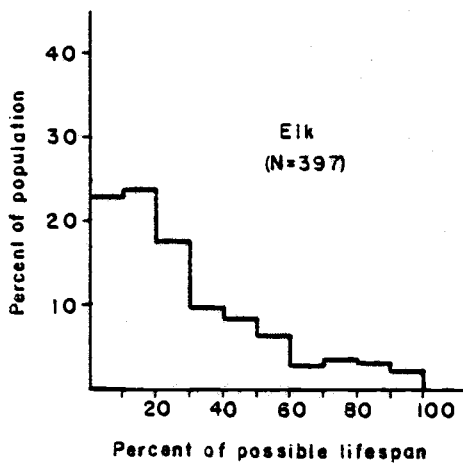


Figure 5: Continued



Data for White-tail deer from Hawkins, *et al.*, 1971; Ozoga, 1972; Severinghaus, 1949; Wolf and Harder, 1979; for mule deer from Medin and Anderson, 1979; Robinette, *et al.*, 1957; for black-tail deer from Einarsen, 1946; Longhurst, 1964; Taver and Dasmann, 1957; for reindeer from Leader-Williams, 1981; for elk from Blood and Lovaas, 1966; Murphy, 1963; Peek *et al.*, 1967; for moose from Sergeant and Pimlott, 1959; for pronghorn antelope from Dow, 1952; Kolenosky and Miller, 1962; for Dall sheep from Murphy and Whitten, 1976.

Figure 6: Population age structure histograms of death assemblages by predation of extant ruminants.

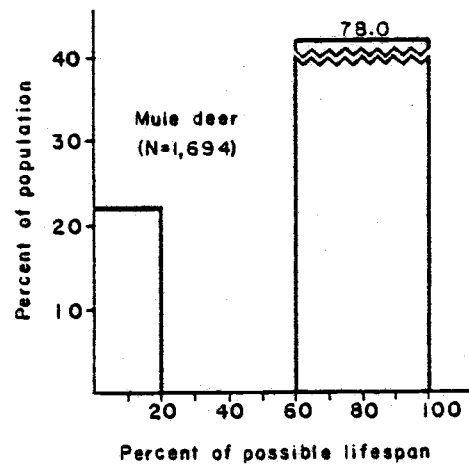
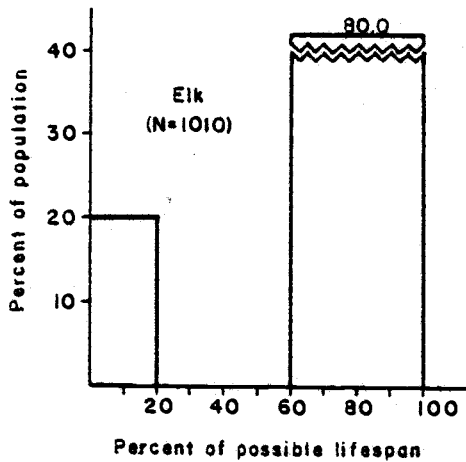
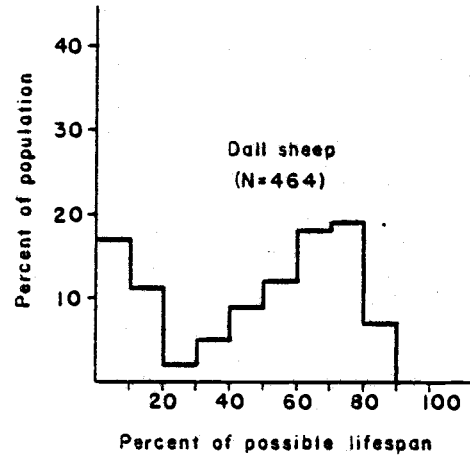
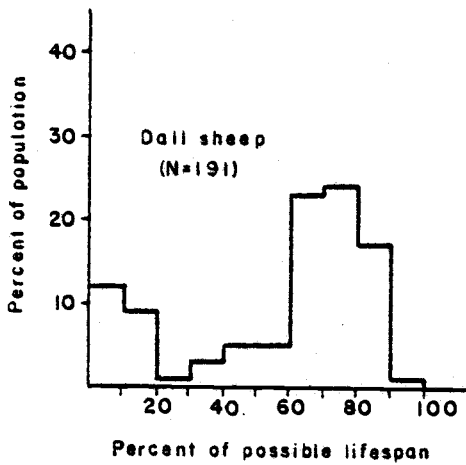
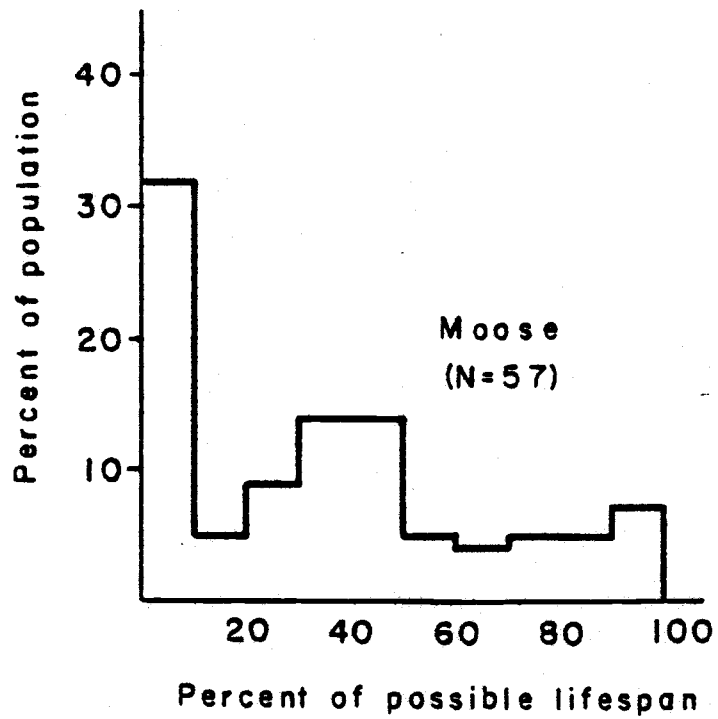


Figure 6: Continued



Data on elk and mule deer from Hornocker, 1970; on moose from Mech, 1966; and Peterson, 1955; and on Dall sheep from Murie, 1944.

Table 3: Chi-square values of contingency table comparisons between oreodonts and extant ruminant species.

	Black-tail deer	Elk	Mule deer	Reindeer	White-tail deer	Pronghorn antelope	Moose	Dall sheep
<u>Mesoreodon pacificus</u>	164.34	98.79	260.13	91.14	242.07	120.61	83.34	74.43
<u>Pseudogenetochoerus trigonocephalus</u>	154.28	97.37	251.57	86.25	234.68	151.75	74.17	61.62
<u>Epreodon occidentalis</u>	61.57	29.31	52.02	33.20	51.52	26.01	32.13	25.93
<u>Promerychoerus superbus</u>	280.43	177.29	630.48	222.23	379.34	318.33	146.14	140.02
<u>Oreodontoides oregonensis</u>	45.82	35.47	37.95	40.81	114.97	29.62	31.50	18.50
<u>Paroreodon marshi</u>	44.03	18.29	47.40	15.13*	51.55	31.09	28.98	18.60
	df=8	df=8	df=8	df=8	df=8	df=7	df=8	df=6
critical $X^2$ (0.05)	15.5	15.5	15.5	15.5	15.5	14.1	15.5	12.6

(\* = non-significant differences)

Table 4: Chi-square values of contingency table comparisons between Kimberly/Turtle Cove and Haystack Valley oreodonts and extant ruminant species.

	Black-tail deer	Elk	Mule Deer	Reindeer	White-tail deer	Pronghorn antelope	Moose	Hall sheep
Kimberly/ Turtle Cove Oreodonts	338.44	239.27	1033.91	237.72	949.28	430.00	186.22	138.16
Haystack Valley Oreodonts	54.79	22.50	51.26	16.44	56.91	33.48	29.60	18.71
	df=8	df=8	df=8	df=8	df=8	df=7	df=8	df=6
Critical $\chi^2$ (0.05)	15.5	15.5	15.5	15.5	15.5	14.1	15.5	12.6



Table 5: Student's t-test comparison between the mean age of the oreodont population at John Day and that of the extant ruminants for both age distribution and death assemblage data.

	Oreodonts	Extant Ruminants (Age Dist.)	Extant Ruminants (Death Assem.)
Sample size (# species)	N=6	N=8	N=3
Mean age of Population	4.80	2.72	4.65
Standard error of mean	±0.13	±0.05	±0.04

Oreodonts vs. extant ruminants (age distribution):

$$t = 7.98 \quad (p \leq 0.01)$$

Oreodonts vs. extant ruminants (death assemblage):

$$t = 0.23 \quad (\text{not sign. } p \leq 0.05)$$

Extant ruminants (age dist.) vs. extant ruminants (death assem)

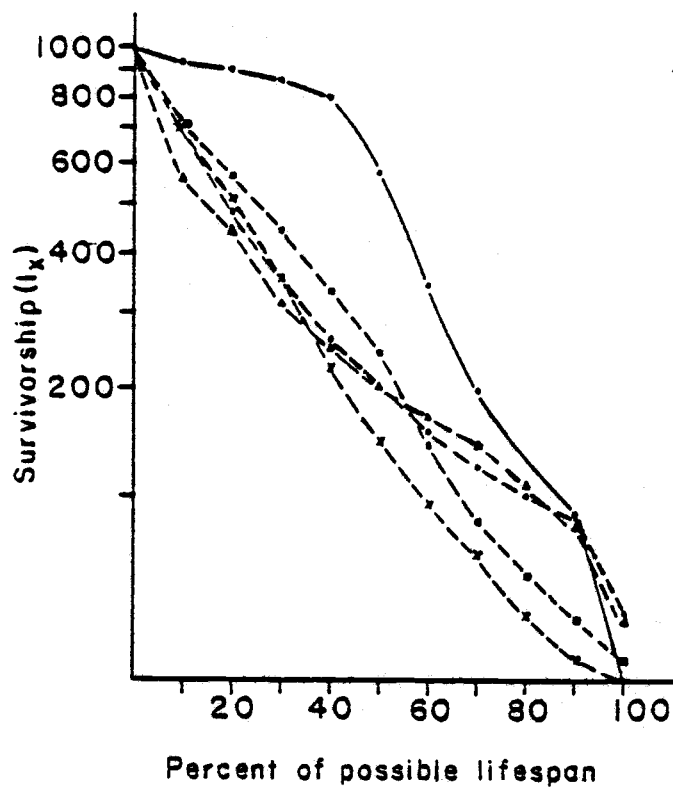
$$t = 3.08 \quad (p \leq 0.05)$$

Extant species and their age distribution and death assemblage data taken from sources listed in "Materials and Methods".

normal age distribution data of the living ruminants, but no difference exists between the oreodonts and the predation data on living ruminants. In addition, a significant difference exists between the age distribution data and the death assemblage data of the extant ruminants.

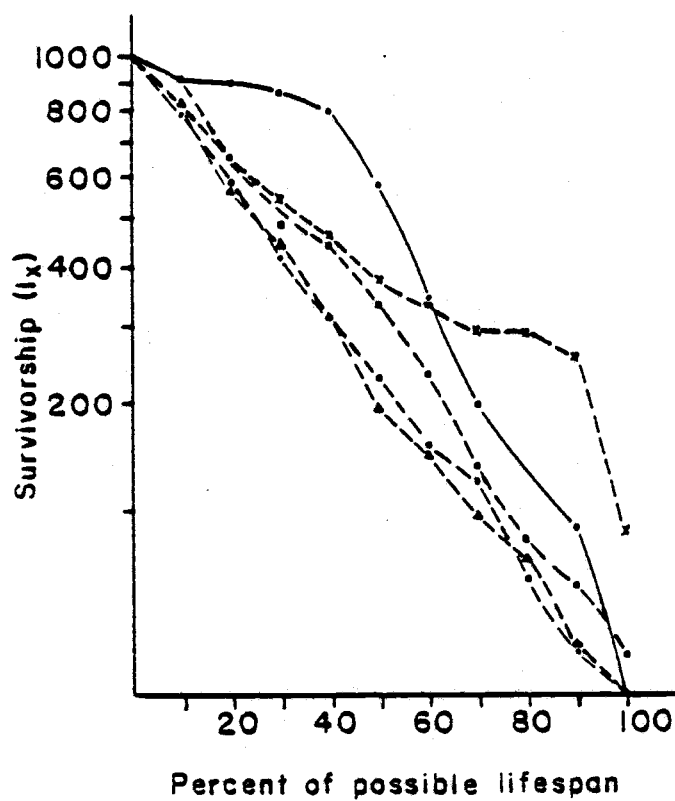
Oreodont survivorship curves as well as those representing the approximate population age distribution of living ruminants and the age distribution normally found in extant ruminant death assemblages due to predation, are shown in Figures 7 and 8. Comparisons between the survivorship curves based on the oreodonts and the death assemblages of the living ruminants indicate the greatest degree of similarity exists with the latter. No differences are observed between the survivorship curves of the oreodont species from either the Kimberly/Turtle cove or the Haystack Valley members (Figure 9).

Figure 7: Survivorship curves for oreodont and extant ruminant age distributions.



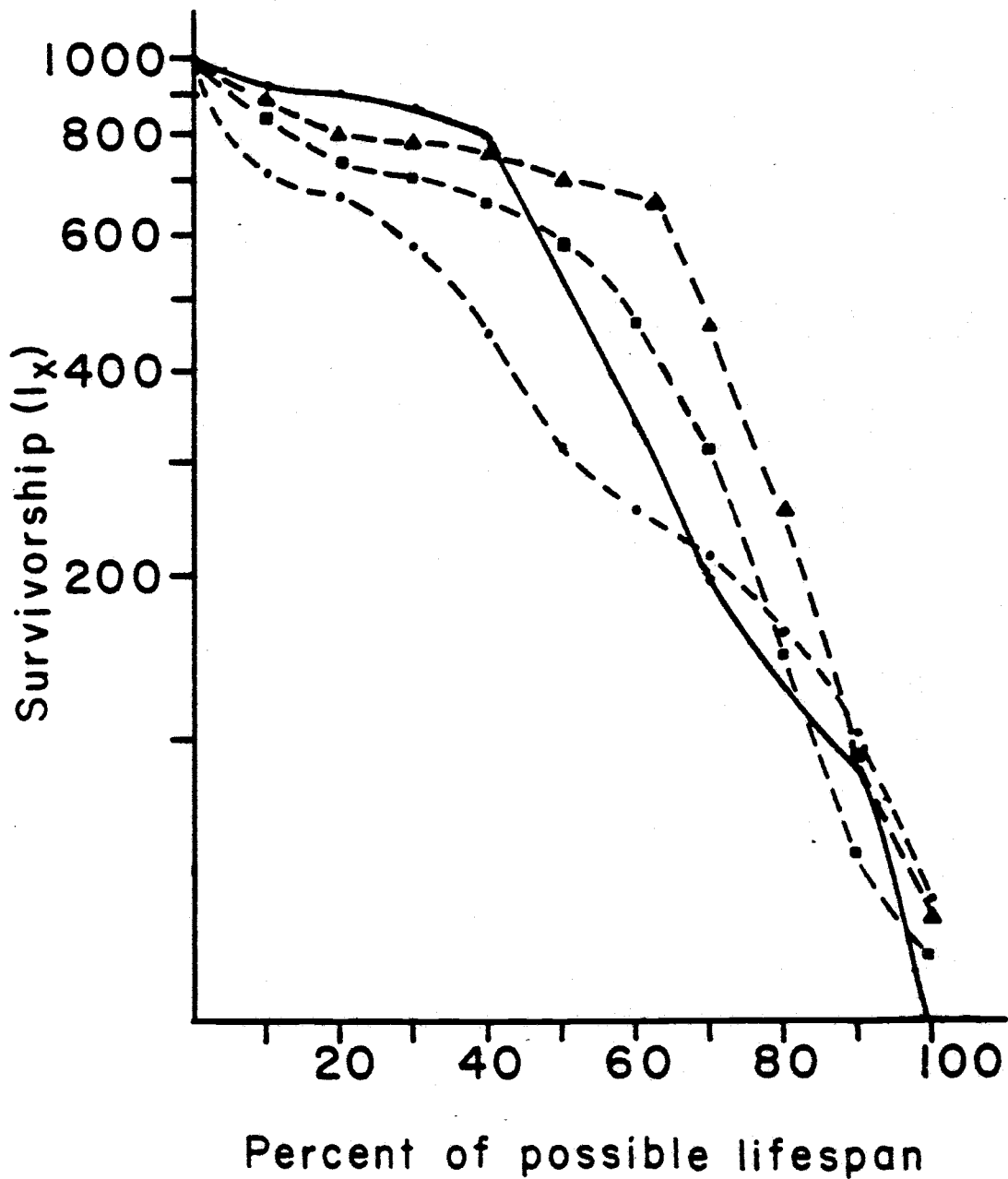
(— = oreodonts, --■-- = reindeer, --●-- = mule deer, --▲-- = black-tail deer, --X-- = white-tail deer)

Figure 7: Continued



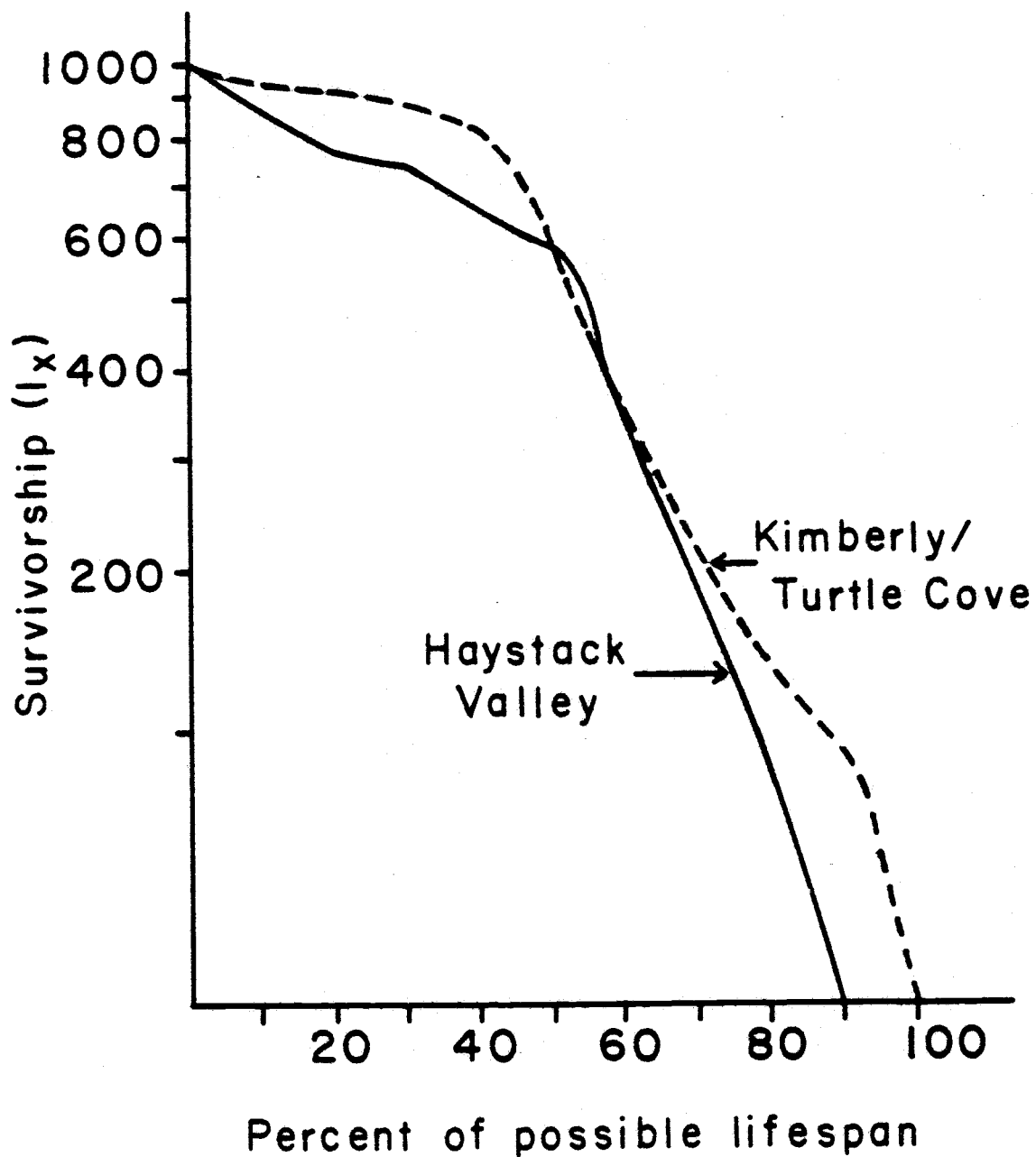
(— = oreodonts, --■-- = moose, --●-- = elk, --▲-- = pronghorn antelope, --X-- = Dall sheep)

Figure 8: Survivorship curves for oreodonts and for predation death assemblages of extant ruminants.



(— = oreodonts, --▲-- = Dall sheep (1937-1941), --■-- = Dall sheep (prior to 1937), --●-- = moose)

Figure 9: Survivorship curves for oreodont species within the Kimberly/Turtle Cove and Haystack Valley members.



Data from Schultz and Falkenbach (1947, 1949, 1954, 1968) and this study.

## DISCUSSION

Statistical analyses indicate that:

(1). The age distribution and survivorship curves of fossilized John Day oreodonts differ from the age distribution and survivorship curves of comparable populations of extant ruminants (i.e., John Day deposits contain a very high percentage of old individuals as compared to the low percentage in extant populations).

(2). The age distribution and survivorship curves of John Day oreodonts closely resemble those of "death assemblages" (via predation) of extant populations of herbivores.

The most parsimonious interpretation of these data is that John Day oreodonts represent a "death assemblage" of individuals that died due to other natural causes (e.g. predation), underwent some taphonomic disruptions and were subsequently fossilized. This sequence of events is consistent with both (1) and (2) above.

Conversely, if the preserved John Day oreodonts had been indiscriminantly killed by catastrophic events as previous authors have hypothesized, and if the fossilization process did not, in fact, substantially alter any age class proportions, then the preserved population would represent a true oreodont age distribution, rather than a "death assemblage". While such a situation is possible, it necessitates oreodonts to have had a population age distribution and survivorship unlike that of most extant ruminant herbivores. Moreover, such an age distribution would have

"mimicked" predator-related "death assemblages" of modern ruminants. Both of the latter interpretations seem unlikely to represent the true case.

Additional support for these conclusions is contributed from another Tertiary paleovolcanic fossil bed which contains animals killed and buried almost instantaneously by volcanic ashfall. Voorhies (1979) has categorized northeastern Nebraska as having been volcanically active in the Miocene and, based on his work on the extinct rhinoceros Teleoceras, has concluded that the majority of individuals preserved in a localized site there were killed by ashfall and preserved in their death poses until recent excavations. Recently, by examination of tooth wear patterns, he has established a population age distribution for the Teleoceras consisting of approximately 50% juveniles and 50% young adults with very few older individuals present (personal communication, 1981). Such a situation is much more consistent with a true extant ruminant population age structure (see Figure 4) than is the case for the John Day oreodonts.

The assumption that the fossilization processes at John Day did not radically alter the age class proportions at death was made at the onset of this study. Although John Day oreodonts probably do represent a death assemblage, when detailed comparisons are made with such assemblages from modern species and even with other assemblages of fossilized oreodonts, some inconsistencies remain. In particular, John Day populations lack a significant component of very young animals, while modern death assemblages contain a fairly significant percentage of such individuals



(Figure 6), as do Miocene oreodont death assemblages from the Great Plains (Voorhies, personal communication, 1981). Such a discrepancy might have resulted from selection against fossilization of very young individuals at John Day.

John Day oreodonts appear to have been fossilized mainly in air-fall volcanic sediments which had been washed or deposited in the large lakes then prevalent. Those individuals that died nearest the shoreline would have had the greatest chance of fossilization. Proximity to lakes would allow some skeletons to be washed into the water much more readily than others more distant; e.g. those on the plains. Predators have decreasing opportunities to destroy the bones as exposure time is lessened. Crania, mandibles and teeth, as were used in this study, do not appear to have been preferred food items of the majority of Tertiary carnivores (Behrensmeyer and Boaz, 1980; Western, 1980). Few of the John Day oreodont skulls exhibit the characteristic gnawing or chewing markings of the canid or felid predators of that time. There is also less opportunity for microorganisms, weathering and microclimatic conditions to act upon and destroy skeletal elements (Coe, 1980; Hill, 1980). Fluvial transport can additionally cause disarticulation and destruction of skeletons, the degree of which partially depends upon the distance transported (Hanson, 1980). Approximately 98% of the oreodont jaws and skulls excavated from John Day are disarticulated from the rest of the skeleton. In most cases, oreodont teeth from all members of the John Day Formation tend to remain connected to either the mandible or skull, so it is unlikely that they would have been easily displaced. Once

a skeleton reached the lake, little exposure to rapidly moving water should have occurred. At that point, consequently, very few losses due to current transport to the fossil assemblages deposited in the lakes should be exhibited in the fossil record.

The size, age and health of an individual oreodont at the time of death, though, still can potentially introduce an age bias into a thanatocoenosis. Bone size, density and durability are each capable of affecting fossilization. Western (1980) has demonstrated that bones of younger animals are destroyed at a greater rate because they are more completely consumed by predators, scavengers and microorganisms after death and are also more rapidly broken down by weathering processes. In addition, Behrensmeyer (1975), Dodson (1973), and Voorhies (1969) have suggested that selective fossilization may occur due to hydraulic conditions in lakes. For example, the more dense or larger bones are, the greater a chance they may have of sinking to the bottom of a large lake bed and becoming buried in sediments and subsequently fossilized. The lighter and less dense bones of younger animals may tend to remain on the surface which, again, exposes them to scavenging and weathering processes as well as current transport. As a result of these various taphonomic processes, very young animals are often underrepresented in fossil assemblages, as they appear to be in John Day. Consequently, it is probably not possible to infer meaningful survivorship rates from oreodont death assemblages at John Day. Regardless, for the purposes of this study, statistical comparisons were still made utilizing all age classes of oreodonts.

Other factors may have also introduced bias to the age structure of the oreodont populations. Ash probably composed up to 75% of the sediments in the John Day region during the Oligocene and Miocene epochs (Matthew, 1901; Wanless, 1923). The silicic components of ash might possibly have induced an increased ratio of tooth wear not related to age (Franklin, 1950; Robinette, *et al.*, 1957), thus causing inconsistencies to appear within population age structure. However, because the oreodonts were browsing herbivores and not grazers (Greaves, 1972), they would not be exposed to nearly the amount of ash on the bushes as their grazing counterparts would have feeding much closer to the ground. Therefore, I would not expect ash to have significantly altered the natural tooth wear patterns of oreodonts. Examination of numerous oreodont teeth have yielded individuals of all age classes, the great majority of which do not exhibit the extensive wear patterns characteristically caused by ash. Those few which do also show an extreme degree of normal wear leading to their classification as very old individuals (W++++). Consequently, degree of wear can be used in estimating individual ages.

Another major bias which might have entered into this study would be one introduced by the prospecting of a limited number of geographic localities at John Day. It can generally be stated that a great deal more prospecting has been done in those areas that are the least difficult to reach. The actual magnitude of such a bias is unknown, for a systematic exploration of the John Day region has yet to be undertaken. It was, therefore, assumed in

this study that the oreodont specimens which have been found are representative of the Tertiary oreodont populations and were killed in a manner indicative of the mode by which the majority died. In addition, the weathering process proceeds faster in the Kimberly and Haystack Valley members due to the unzeolitized rocks composing them (Western, 1980). In those members the rocks tend to crumble which makes it difficult to find intact specimens. This may account for the smaller numbers of specimens found in those regions. The erosion process in the Turtle Cove region (zeolitized materials) does not proceed as quickly and the oreodonts would, therefore, be better preserved, and consequently more specimens are found intact.

Studies similar to this would be easily applicable to other types of species present in abundance at John Day or other fossiliferous beds, such as those in the Nebraska Great Plains. For example, rodents are known from many specimens at John Day (Fisher and Rensberger, 1972) and similar analyses might be made of their populations.

## BIBLIOGRAPHY

- Baldwin, E.M. 1976. Geology of Oregon. Kendall/Hunt Publishing Company, Dubuque, Iowa, 165p.
- Beaulieu, J.D. 1972. Geologic formations of eastern Oregon. Oregon Dept. Geol. and Min. Ind., Bull. 73:1-45.
- Behrensmeyer, A.K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. Bull. Mus. Comp.Zool. 146(10):473-578.
- Blood, D.A. and A.L. Lovaas. 1966. Measurements and weight relationships in Manitoba elk. J. Wildl. Manage. 30(1):135-141.
- Boaz, N.T. and A.K. Behrensmeyer. 1976. Hominid taphonomy: Transport of human skeletal parts in an artificial fluvial environment. Am. J. Phys. Anth. 45(1):53-60.
- Buechner, H.K. The bighorn sheep in the United States. Its past, present and future. Wildl. Monog. No. 4, 174p.
- Chaney, R.W. 1956. The Ancient Forests of Oregon. Condon Lectures, Oregon State System of Higher Education, U. of Oregon Press, Eugene. 56p.
- Coe, M. 1980. The role of modern ecological studies in the reconstruction of paleo-environments in Sub-Saharan Africa. Chapter 4 in: Fossils in the Making. Vertebrate taphonomy and paleoecology. (A.K. Behrensmeyer and A.P. Hill, eds). U. of Chicago Press, Chicago.
- Cope, E.D. 1884. Synopsis of the species of Oreodontidae. Proc. Amer. Phil. Soc. 21(116):503-512.
- Dodson, P. 1973. The significance of small bones in paleoecological interpretations. U. of Wyoming, Cont to Geol 12:15-19.
- Dow, A.A., Jr. 1952. Antelope aging studies in Montana. Proc Western Assoc. of State Game and Fish Comm. 32:220-224.
- Dow, S. A., Jr. and P. L. Wright. 1962. Changes in mandibular dentition associated with age in pronghorn antelope. J. Wildl. Manage. 26(1):118.
- Downs, T. 1956. The Mascall fauna from the Miocene of Oregon. Univ. Cal., Pub. Geol. Sci. 31:199-354.

- Einarsen, A. S. 1946. Management of blacktailed deer. J. Wildl. Manage. 10(1):54-59.
- Erickson, J. A., A. E. Anderson, J. E. Medin, and D. C. Bowden. 1970. Estimating ages of mule deer, arrival of technical accuracy. J. Wildl. Manage. 34:523-531.
- Fisher, R. V. and J. M. Rensberger. 1972. Physical stratigraphy of the John Day Formation, central Oregon. Univ. Cal., Pub. Geol. Sci. 101:145.
- Franklin, M. C. 1950. The influence of diet on dental development in the sheep. Commonwealth Science and Industry Research Organization. Bull. 252, 34p.
- Gilbert, F. F. and S. L. Stolt. 1970. Variability in aging Maine white-tailed deer by tooth wear characteristics. J. Wildl. Manage. 34(3):532-535.
- Greaves, W. S. 1972. Evolution of the Merycoidodont masticatory apparatus. Evol. 26:659-667.
- Hanson, C. B. 1980. Fluvial taphonomic processes: models and experiments. Chapter 9 in: Fossils in the Making Vertebrate taphonomy and paleoecology. (A.K. Behrensmeyer and A.P. Hill, eds.) Univ. of Chicago Press, Chicago.
- Hawkins, R.E., W.D. Klimstra and D.C. Autry. 1971. Dispersal of deer from Crab Orchard National Wildlife Refuge. J. Wildl. Manage. 35(2):216-220.
- Hill, A.P. 1980. Early postmortem damage to the remains of some contemporary East African mammals. Chapter 8 in: Fossils in the Making. Vertebrate taphonomy and paleoecology. (A.K. Behrensmeyer and A.P. Hill, Eds.) U. of Chicago Press, Chicago.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monogr. No. 21, 39p.
- Kerwin, N. L. and G. T. Mitchell. 1971. The validity of the wearage technique for Alberta pronghorns. J. Wildl. Manage. 35(4):743-747.
- Keyfitz, N. 1968. Introduction to the mathematics of population. Addison-Wesley Publishing Co. Reading, Ms. 450p.
- Kolenosky, G. B. and R. S. Miller. 1962. Growth of the lens of the pronghorn antelope. J. Wildl. Manage. 26(1):112-113.

- Lander, E. B. 1977. A review of the Oreodonta (Mammalia, Artiodactyla) Parts I, II, III. PhD. dissertation. Univ. of California, Berkeley.
- Leader-Williams, N. 1981. Population dynamics and mortality of reindeer introduced into southern Georgia. J. Wildl. Manage. 44(3):640-657.
- Longhurst, W.M. 1964. Evaluation of the eye lens technique for aging Columbian blacktailed deer. J. Wildl. Manage. 28(4): 773-784.
- Marsh, O.C. 1875. Ancient lake basins of the Rocky Mountain Region. Am. J. Sci. (Ser 3) 9:49-52.
- Matthew, W. D. 1901. Fossil mammals of the Tertiary of northeastern Colorado. Mem. Amer. Mus. Nat. Hist. 1(7):355-448.
- Matthew, W. D. 1932. A skeleton of Merycoidodon gracilis and its adaptive significance. Univ. Cal. Pub. Geol. Sci. 22:13-30.
- Mech, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the U.S. Fauna Series 7, Washington, 210 p.
- Medin, D. E. and A. E. Anderson. 1979. Modeling the dynamics of a Colorado mule deer population. Wildl. Monog. no. 68, 77p.
- Merriam, J. C. 1901. A contribution to the geology of the John Day basin. Univ. Cal., Bull. Dept. Geol. 2:12-69.
- Morris, P. 1972. A review of mammalian age determination methods. Mammal Review 2(3):69-104.
- Murie, A. 1944. Dall sheep, Chapter 3 in: Wolves of Mount McKinley, Natl. Parks Service Fauna no. 5, Washington, 238p.
- Murphy, D. A. 1963. A captive elk herd in Missouri. J. Wildl. Manage. 27(3):411-414.
- Murphy, P.A. and S.L. Whitten. 1976. Dall sheep demography in McKinley Park and a re-evaluation of Murie's data. J. Wildl. Manage 40(4):597-609.
- Olson, E. C. 1980. Taphonomy: Its history and role in community evolution. Chapter 1 in: Fossils in the making. Vertebrate taphonomy and paleoecology. (A. K. Behrensmeyer and A. P. Hill, eds.) Univ. of Chicago Press, Chicago.

- Osborn, H.F. 1909. Cenozoic mammal horizons of western North America. Bull. U.S. Geol. Sur. 36:1-120.
- Ozoga, J.J. 1972. Agressive behavior of white-tailed deer at winter cuttings. J. Wildlife Manage. 36(3):861-868.
- Peale, A.C. 1886. Lacustrine deposits of Montana. Science 8(185): 163-164.
- Peek, J.M., A.L. Lovaas and R.A. Rouse. 1967. Population changes within the Gallatin elk herd, 1932-1965. J. Wildlife Manage. 31(2):304-316.
- Peterson, R.L. 1955. North American Moose. Univ. of Toronto Press, Toronto. 280pp.
- Quimby, D.C. and J.E. Gaab. 1957. Mandibular dentition as an age indicator in Rocky Mountain elk. J. Wildlife Manage. 21(4): 435-451.
- Robinette, W.L., D.A. Jones, G. Rodgers and J.S. Gashwiler. 1957. Notes on tooth development and wear for Rocky Mountain mule deer. J. Wildlife Manage. 21(2):134-152.
- Robinson, P.T. 1976. John Day and Columbia River basalt, in: Geologic field trips in northern Oregon and southern Washington. (J.D. Beaulieu, Ed.) Bull. Or. Dept. Geol. and Min. Ind. no. 77, 206p.
- Romer, A.S. 1966. Vertebrate Paleontology. (3rd Ed.) Univ. of Chicago Press, Chicago. 468p.
- Schultz, C.B. and C.H. Falkenbach. 1940. Merycochoerinae, a new subfamily of oreodonts. Bull. Amer. Mus. Nat. Hist., 77:213-306.
- Schultz, C.B. and C.H. Falkenbach. 1941. Ticholeptinae, a new subfamily of oreodonts. Ibid. 79:1-105.
- Schultz, C.B. and C.H. Falkenbach. 1947. Merychyinae, a subfamily of oreodonts. Ibid. 88:157-286.
- Schultz, C.B. and C.H. Falkenbach. 1949. Promerycochoerinae, a new subfamily of oreodonts. Ibid. 93:69-198.
- Schultz, C.B. and C.H. Falkenbach. 1950. Phenacocoelinae, a new subfamily of oreodonts. Ibid. 95:91-149.
- Schultz, C.B. and C.H. Falkenbach. 1954. Desmatochoerinae, a new subfamily of oreodonts. Ibid. 105:143-256.
- Schultz, C.B. and C.H. Falkenbach. 1956. Miniochoerinae and Oreonetinae, two new subfamilies of oreodonts. Ibid. 109:377-382.



- Schultz, C.B. and C.H. Falkenbach. 1968. The phylogeny of the oreodonts. Ibid. 139:1-489.
- Scott, W.B. 1937. History of Land Mammals of the Western Hemisphere. University of Chicago Press, Chicago. 497p.
- Scott, W.B., G.L. Jepson and A.L. Wood. 1941. Artiodactyla, in: The mamalian fauna of the White River Oligocene. Trans. Amer. Phil. Soc., n.s. 28(4):645-733.
- Sergeant, D.E. and D.H. Pimlott. 1959. Age determination on moose from sectioned incisor teeth. J. Wildl. Manage. 23(3):315-321.
- Severinghaus, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildlife Manag. 13(2):195-216.
- Sinclair, W.J. 1906. Volcanic ash in the Bridger beds of Wyoming. Bull. Amer. Mus. Nat. Hist., 22:273-280.
- Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. A biometrical approach. (2nd ed.) McGraw-Hill Book Company, New York. 633p.
- Taber, R. and R.F. Dasmann. 1957. The dynamics of three natural populations of the deer Odocoileus hemionus columbianus. Ecology 38(2):233-246.
- Thomas, D.C. and P.J. Brandy. 1975. Accuracy of dental wear age estimates of black-tailed deer. J. Wildl. Manage. 39(4):674-678.
- Thorpe, M.R. 1925. The geologic history of oreodonts. J. Mamm. 6:69-82.
- Thorpe, M.R. 1937. The Merycoidodontidae, an extinct group of ruminant mammals. Mem. Peabody Mus. Nat. Hist., 3(4):1-428.
- Vaughan, T.A. 1978. Mammology. W.B. Saunders Company, Philadelphia. 522p.
- Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene Vertebrate fauna, Knox County, Nebraska. Cont. Geol. Spec Paper #1:1-69. U. of Wyoming Press.
- Voorhies, M.R. and J.R. Thomasson. 1979. Fossil grass Anthoecia within Miocene rhinoceros skeletons: Diet in an extinct species. Science 206:331-333.
- Wanless, H.R. 1922. Lithology of the White River sediments. Proc. Amer. Phil. Soc. 61(3):184-203.

- Wanless, H.R. 1923. The stratigraphy of the White River beds of South Dakota. Ibid. 62:190-269.
- Western, D. 1980. Linking the ecology of past and present mammal communities. Chapter 3 in: Fossils in the Making. Vertebrate taphonomy and paleoecology. (A.K. Behrensmeyer and A.P. Hill, eds.) University of Chicago Press, Chicago.
- Williams, H. 1953. The ancient volcanoes of Oregon. Oregon State System of Higher Education. Condon Lecture Series, 68p.
- Wolf, A. and J.D. Harder. 1979. Population dynamics of a captive white-tailed deer herd with emphasis on reproduction and mortality. Wildlife Mono. no. 67, 53p.

## APPENDICES

Appendix 1: Population age structure of fossilized John Day oreodont populations.

OREODONT SPECIES	SCHULTZ AND FALKENBACH REFERENCE	I	-II	M	M+	W	W+	W++	W††	W†††	TOTAL
<u>Mesoreodon pacificus</u>	1968	10 (10.4)	2 (2.2)	4 (4.3)	5 (6.5)	30 (32.6)	16 (18.5)	10 (10.9)	10 (10.9)	2 (3.3)	89
<u>Pseudogenetochœrus trigonocephalus</u>	1968	5 (8.1)	0 (0.0)	1 (3.2)	5 (9.7)	7 (11.3)	16 (27.4)	11 (22.6)	7 (14.5)	2 (3.2)	54
<u>Eporeodon occidentalis</u>	1968	2 (11.1)	1 (5.6)	0 (0.0)	0 (0.0)	3 (33.3)	0 (0.0)	2 (16.7)	1 (5.6)	0 (0.0)	9
<u>Præmerycochoerus superbus</u>	1949, 1954	0 (0.0)	0 (0.0)	2 (2.9)	3 (4.9)	30 (30.1)	38 (41.7)	12 (12.6)	8 (7.8)	0 (0.0)	93
<u>Mesoreodon major</u>	1954	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (33.3)	2 (66.7)	0 (0.0)	0 (0.0)	3
<u>Oreodontoides orejoniusis</u>	1947, 1968	5 (25.0)	0 (0.0)	0 (0.0)	2 (10.0)	5 (25.0)	1 (5.0)	3 (15.0)	1 (5.0)	2 (15.0)	19
<u>Paroreodon marshii</u>	1947	4 (18.2)	3 (13.6)	1 (4.5)	0 (0.0)	2 (9.1)	6 (27.3)	1 (4.5)	3 (13.6)	0 (0.0)	20
<u>Hypsipops breviceps</u>	1950	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2 (100.0)	0 (0.0)	0 (0.0)	2

Appendix 2: Population age structure data of extant ruminants.

EXTANT SPECIES	AGE CLASS									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9+
Black-tail deer <u>(Odocoileus hemionus columbianus)</u>	214 (54.9)	42 (10.8)	46 (11.8)	20 (5.1)	14 (3.6)	10 (2.6)	8 (2.1)	9 (2.3)	9 (2.3)	18 (4.6)
Elk <u>(Cervus elaphus)</u>	91 (22.9)	95 (23.9)	69 (17.4)	39 (9.8)	33 (8.3)	25 (6.3)	11 (2.8)	14 (3.5)	12 (3.0)	8 (2.0)
Mule deer <u>(Odocoileus hemionus)</u> (35.6)	10544 (22.7)	6724 (13.4)	3974 (8.2)	2425 (5.4)	1598 (3.6)	1072 (2.5)	752 (1.8)	538 (1.4)	407 (5.3)	1569
Reindeer <u>(Rangifer tarandus)</u>	184 (30.2)	104 (17.0)	82 (13.4)	67 (11.0)	57 (9.3)	61 (10.0)	29 (4.8)	14 (2.3)	7 (1.1)	5 (0.8)
White-tail Deer <u>(Odocoileus virginianus)</u>	4283 (31.2)	3220 (23.4)	2331 (17.0)	1703 (12.4)	942 (6.9)	522 (3.8)	321 (2.3)	196 (1.4)	116 (0.8)	98 (0.7)
Pronghorn antelope <u>(Antilocapra americana)</u>	302 (18.8)	477 (29.7)	202 (12.6)	210 (13.1)	192 (12.0)	66 (4.1)	61 (3.8)	36 (2.2)	58 (3.6)	
Hoose <u>(Alces alces)</u>	26 (13.4)	58 (29.9)	31 (16.0)	13 (6.7)	18 (9.3)	17 (8.8)	16 (8.2)	8 (4.1)	3 (1.5)	4 (2.1)
Dall sheep <u>(Ovis dalli)</u>	59 (32.4)	34 (18.7)	25 (13.7)	12 (6.6)	10 (5.5)	6 (3.3)	34 (18.7)			

From Blood and Lovaas (1966), Dasmann and Mossman (1962), Dow (1952), Einarsen (1946), Hawkins, et al. (1971), Kolenosky and Miller (1962), Leader-Williams (1981), Longhurst (1964), Medin and Anderson (1979), Murphy (1963), Uzoga (1972), Peek, et al. (1967), Robinette, et al. (1957), Sergeant and Pimlott (1959), Severinghaus (1949).

Appendix 3: Death assemblages due to predation on moose (Mech, 1966), Dall sheep (Murie, 1944), elk and mule deer (Hornocker, 1970).

EXTANT SPECIES	N	PERCENTAGE OF POSSIBLE LIFE SPAN									
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
Moose	57	32	5	9	14	14	5	4	5	5	7
Dall sheep prior to 1937	464	17	11	2	5	9	12	18	19	7	0
1937- 1941	191	12	9	1	3	5	5	23	24	17	1
Elk*	1010	80							20		
Mule deer*	1694	78							22		

(\*age classes separated into juveniles and adults only.)

Appendix 4: Method of determining stationary age distribution from age-specific death rate.

$M_x$  = age-specific death rate at age  $x$

$q_x$  = probability of the death of an individual of age  $x$

$$q_x = \frac{M_x}{1 + 0.5M_x}$$

$p_x$  = probability of an individual living through age  $x$

$$p_x = 1 - q_x$$

$l_x$  = probability of an individual living from birth age  $x$

$$l_x = l_0(p_x)$$

From Keyfitz (1968).