

## Demography of late Miocene rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida: linking mortality and sociality in fossil assemblages

Matthew C. Mihlbachler

*Abstract.*—Among polygynous mammals, a heightened risk of mortality is linked to the intensity of intragender competition and life-history stages, such as sexual maturity, where inexperienced individuals are vulnerable to the aggressive behaviors of dominant individuals. In this respect, the age- and sex-specific mortality patterns found in fossil assemblages could be informative of sociality in extinct species. This possibility was explored by comparing the age- and sex-specific demography of attritional rhinoceros assemblages, *Teleoceras proterum* ( $n = 2$ ) and *Aphelops malacorhinus* ( $n = 1$ ), from pond and fluvial sedimentary facies of the late Miocene of Florida, with modern skeletal assemblages of extant rhinos and other large mammals.

Subadult and young adult males (between 15–40% of potential life span) numerically dominate the *Teleoceras* assemblages, indicating a disproportionately high frequency of localized young male mortality. The estimated age-specific mortality rates indicate elevated mortality risks among males at an age equivalent to the years encompassing male physiological and social maturity in modern rhinos, a pattern that suggests a high frequency of socially mediated mortality. Age-specific mortality rate curves of modern black rhino populations are essentially identical. A high frequency of intraspecific fight-related mortality characterizes modern rhinos and strongly suggests that elevated *Teleoceras* mortality was influenced by intragender competition. Although *Teleoceras* is widely believed to have been the analog of extant *Hippopotamus*, mortality rates of young males are not elevated in a modern *Hippopotamus* population. The *Aphelops* assemblage is not significantly male-biased and does not indicate elevated mortality rates of young males, suggesting that aspects of *Aphelops* sociality differed from modern rhinos. Although the nature of *Aphelops* sociality is not clear, aggression toward young males may have been less extreme or less frequent in *Aphelops* populations.

Matthew C. Mihlbachler. Division of Paleontology, American Museum of Natural History, Central Park West at Seventy-ninth Street, New York, New York 10024. E-mail: mihlbach@amnh.org

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### Introduction

The age-specific demographics of fossil assemblages have long been recognized as evidence for the population dynamics of extinct species (Matthew 1924; Kurtén 1953; Voorhies 1969). Adult sex ratios (ASRs) in fossil assemblages, when discernable via a form of sexual dimorphism, add a valuable dimension to paleodemography because they are strongly linked to sociality in extant species (Berger 1986; Byers 1997). Bonebeds containing large quantities of extinct ungulate fossils or other large terrestrial vertebrate material (e.g., dinosaurs) are often presumed to indicate the formation of herds or other types of social groups (e.g., packs) formed by some modern mammals (Turnbull and Martill 1988; Dodson 1996; Currie 1998; Prothero 1998). Berger et al. (2001) found that the ASRs of recent spatially confined catastrophic death assemblages of

ungulates reflect the sex-segregated groups of ruminant artiodactyls and proboscideans, whereas modern horse assemblages (with sex-mixed groups) contained more variable ASRs. Berger et al. (2001: p. 131) proposed that ASRs in mass-death assemblages can be used to “back-cast patterns of sociality in long-extinct species.” Their argument can be directly applied only to catastrophic fossil assemblages where instantaneous and spatially confined mortality events could have frozen an intact portion of the population, allowing one to discern demographic biases in the spatial distribution of the individuals at a single instant in time.

On the other hand, the majority of fossil vertebrate assemblages accumulate over many temporal scales from days to millennia (Kidwell and Behrensmeyer 1993; Martin 1999). Many of the sex-biased Eocene to Holocene

ungulate assemblages examined by Berger et al. (2001) either accumulated gradually or were not spatially confined (due to fluvial transportation), or both (Gingerich 1981; Hulbert 1982, 1984; Barnosky 1985; Straus 1987; Agenbroad 1990; Muhlbachler 1999). By their nature, attritional assemblages cannot preserve "snapshots" of intact social groups and, as such, they cannot be used to directly identify group-forming behaviors in extinct species. Attritional death assemblages are more appropriately thought of as a cumulative record of mortality rather than as localized "snapshots" of populations (Voorhies 1969). Attritional assemblages might still indicate sex-segregated societies, however, if it can be shown that heavily skewed ASRs found in localized records of attritional mortality reflect the sex-specific spatial distributions of adults (e.g., bachelor males wandering outside of the main range of females). But such a conclusion requires that the sex-specific spatial distributions did not greatly fluctuate over the temporal duration during which the mortality occurred.

In addition to ASRs, the age distributions within attritional assemblages should relate to aspects of sociality, because sex-specific social strategies of polygynous mammals regulate age-specific mortality rates in predictable ways (Jarman and Jarman 1973; Dittus 1975, 1977, 1979; Ralls et al. 1980). Polygyny, the dominant mammal reproductive strategy, is a social system in which reproductive success is more variable in males than in females (Trivers 1985; Berger and Cunningham 1994a). By competing with one another for mate monopolization, males kill each other directly in combat or more subtly through the increased energetic demands during periods of intensified competition (e.g., rut) and forced emigration, often to marginal habitat (Ralls et al. 1980). Additionally, males of some species are less responsive to predators and, hence, are more vulnerable to predation (Schaller 1972; Sinclair 1977; Berger and Cunningham 1995). Thus, the male mortality rate in polygynous species tends to exceed that of females. Socially mediated mortality risks also tend to be age specific. Peaks in the age-specific mortality-rate curves of modern mammal popula-

tions correspond to life-history stages, most often young adulthood, when males are especially vulnerable to the aggressive or socially exclusive behaviors of other members of the population (Jarman and Jarman 1973; Dittus 1975, 1977, 1979; Ralls et al. 1980). The degree to which socially mediated mortality may influence the male mortality rate is a result of at least three factors: (1) the effectiveness (or lethality) of weaponlike structures (e.g., tusks, horns) in allowing individuals to physically threaten and injure each other and/or to force subdominant individuals from territories, (2) extrinsic ecological factors that control the distribution and density of females, and (3) the social strategies adopted by adults of both sexes that ultimately determine the degree to which males can monopolize females.

I postulate here that mortality rates, calculated from large attritional fossil assemblages, are potentially informative of two aspects of paleosociality. (1) Differential sex-specific mortality rates, particularly elevated male mortality rates, strongly suggest a highly polygynous form of sociality involving intense competition among males, leading to the deaths of some individuals. Situations where the mortality rates are equal between the sexes indicate situations where the intensity of male competition is not sufficient to influence mortality rates visibly. (2) Second, age-specific peaks in mortality rates will indicate life-history stages (e.g., sexual maturity) associated with increased risks of socially mediated mortality.

*Objectives.*—In this paper, the age- and sex-specific mortality rates of large attritional assemblages of the late Miocene rhinoceroses *Teleoceras proterum* and *Aphelops malacorhinus* from the Love Bone Bed (LBB) and Mixson's Bone Bed (MBB), Alachua County, Florida, are compared with those of large attritional bone collections of extant large ungulates. Rhinoceroses are good cases for exploring the link between mortality and sociality because the three best-studied species, *Ceratotherium simum* (African white rhino), *Diceros bicornis* (African black rhino), and *Rhinoceros unicornis* (Asian greater one-horned rhino), sustain higher frequencies of combat-related wounds

than most other large mammals (Owen-Smith 1988; Dinerstein and Price 1991; Berger 1994). Therefore, as a general prediction, attritional assemblages of rhinos are likely to contain a high proportion of socially mediated deaths. Rhinos possess up to two functional sets of craniomandibular weapons. The keratinous nasal horn is most conspicuous, but rhinos more primitively possess a sexually dimorphic pair of tusklike lower incisors (i2) that hone on a chisel-like set of upper incisors (I1) (Radinsky 1966). *Rhinoceros* males predominantly inflict wounds with the lower incisors (i2) and to a lesser extent with the horn (Dinerstein 1991). Although the living African rhinos have lost their incisors, the horns are elongated and function as the primary weapon (Owen-Smith 1988; Berger 1994). *Teleoceras* possessed the dimorphic pair of honing incisors and a small nasal horn (Mead 2000). If the functions of craniomandibular weapons in *Teleoceras* were similar to those in modern rhinos, *Teleoceras* probably experienced a high frequency of combat-inflicted mortality. In contrast, *Aphelops* is uniquely different from living rhinos because, in addition to lacking a nasal horn, the upper honing incisor was secondarily lost (Prothero et al. 1986; Cerdeño 1995). Consequently the dimorphic tusk is worn to a blunt tip in adults and, from a mechanical standpoint, was probably less effective as a weapon than the sharply honed tusks of other rhinos. It is reasonable to postulate that the loss of the tusk-honing ability in *Aphelops* ancestry corresponded to a form of sociality different from modern rhinos, involving a decrease in the intensity of male competition, and possibly less frequent socially mediated mortality.

### Materials and Taphonomic Background

*Mixson's Bone Bed*.—Mixson's Bone Bed (MBB), Alachua County, Florida, has been biostratigraphically dated to the early Hemphillian Land Mammal Age (MacFadden and Webb 1982). *Teleoceras* materials used in this study include 43 skulls and associated sets of upper teeth, 130 mandibles and sets of associated lower teeth, and 121 i2s. The minimum number of individuals (MNI) based on left astragali is 117, although the dental material

(based on left mandibles) minimally represents 67 individuals. The sample of *Aphelops* from MBB is not sufficient for this study. Early descriptions of MBB lack explicit detail (Leidy and Lucas 1896; Simpson 1930), but the depositional environment can be described as a large sinkhole that is typical of those found in Florida that represent pondlike environments (S. D. Webb personal communication 1999). The majority of the material shows little evidence of weathering and many of the larger mammals were found partially articulated. MBB appears to contain individuals that died and were buried over a period of several years. It is not known if the collecting methods were biased in a way that would influence this study, but the fact that a large number of heavily crushed and badly damaged specimens were salvaged suggests that the collectors were aiming to collect all of the material regardless of the state of preservation.

*Love Bone Bed*.—The Love Bone Bed (LBB) has been biostratigraphically dated to the latest Clarendonian Land Mammal Age (Webb et al. 1981). The *Teleoceras* material used in this study consists of 43 mandibles, 179 additional isolated premolars, and 78 i2s. The MNI, based on the right dp3 and p3, is 68. The *Aphelops* material used here consists of 34 right and left mandibles, an additional 39 isolated premolars, and 53 i2s. The left p4 indicates the MNI as 28. The LBB is reported to have been part of a fluvial system that experienced a depositional (cut-and-fill) event (Webb et al. 1981). The bones exhibit highly variable states of weathering and water wear, which suggests that some of the material was deposited soon after death whereas other material was buried after longer periods of exposure. Hulbert (1982) considered LBB to be an attritional accumulation. Although the LBB was not excavated in a tightly controlled taphonomic manner, it is reasonable to believe that most of the larger-mammal material encountered was collected except for some of the smallest and most fragile of osteological elements (toe bones, unerupted deciduous teeth), which were routinely encountered in the spoil. *Aphelops* and *Teleoceras* are of similar size (from the standpoint of the sizes and durability of skeletal elements, if not body mass), so it is also

doubtful that there was a collecting bias for either of the rhinos from LBB (R. Hulbert personal communication 2002).

### Methods

Sex can be determined in male and female i2s of *Teleoceras* and *Aphelops* because of the highly significant bimodal distributions of the dimensions of this element (Mead 2000). The i2s were assigned to one of three age categories that were based on eruption and wear patterns similar to those in *Rhinoceros* incisors (Dinerstein 1991): (1) Subadult tusks were unerupted and show no sign of use wear. (2) Erupting tusks and those with mild amounts of use wear on the enamel crown were considered young adults. (3) Tusks showing more extensive wear, with the enamel crown nearly or completely worn away and only the root remaining, were considered intermediate to old adults. The ASRs of the assemblages were approximated with the maximum number of right or left i2s for each sex occurring in each age group.

Unfortunately, the incisors typically fell out of the mandible sometime after death and were mostly found as isolated elements. Therefore, age profiles generated from the cheek-teeth wear stages are not sex specific. Crown height measurements were taken on *in situ* and isolated cheek teeth (p3, p4, m1, m2, m3) in the regions of the protoconid, entocoid, metaconid, and hypoconid. Numerous descriptions of tooth eruption and dental wear in modern rhinos can be used to estimate age in fossil rhinos (Goddard 1970; Hitchins 1978; Hillman-Smith et al. 1986). Only Hitchins's (1978) study on *Diceros* combines empirical age data (counts of annular cementum growth increments) with descriptions of eruption and wear for upper and lower teeth. Hitchins (1978) described 18 dental eruption/wear stages (0–XVII) corresponding to age groups ranging from zero through 37 years. The ages were converted from years to percentage of potential life span, based on the maximum life span of *Diceros* in Hitchins's (1978) study. By converting age into percentage of maximum life span, it is not necessary to assume that the life spans of the extinct rhinos were the same as for *Diceros* when making

age estimations. However, the age estimates are based on the presumption that (1) the schedule of dental eruption was similar to that in *Diceros* with respect to the life span and (2) the maximum stage of dental wear in the oldest age group is about the same as the oldest wear stage in *Diceros*. Both assumptions are reasonable for *Teleoceras* and *Aphelops*. The eruption sequence of the molariform cheek teeth in *Teleoceras* and *Aphelops* (dp3, dp4, m1, p3, m2, p4, m3) was identical to that of living rhinos (Goddard 1970; Hitchins 1978). Likewise the maximum degree of tooth wear of both extinct rhinos are similar in magnitude to the last dental wear stage for *Diceros*. In young mandibles the eruption/wear stages were very similar to those of Hitchins's (1978) on a tooth-by-tooth basis, so juveniles could be assigned to age categories with minimal subjectivity. However, among adults there were more tooth-by-tooth inconsistencies between Hitchins's (1978) wear stages and the fossil specimens so that the age assignments of increasingly older individuals became increasingly subjective. In situations where the tooth-by-tooth wear patterns between the fossil rhinos and Hitchins's (1978) wear stages were inconsistent, the age estimates were based exclusively on the degree of wear in last teeth to erupt (m2, p4, and m3), because these would have been the least affected by variable wear rates.

Hitchins (1978) failed to provide age ranges for the first five of the *Diceros* wear stages. Combined, they account for the first 9% of potential life span. *Diceros* deciduous premolars begin to erupt at or before 0.5 years (Goddard 1970); therefore, wear stage 0 (no erupted cheek teeth) can represent no more than approximately 0–1% of life span. The remaining stages (I–IV) were assigned to equal 2% life span units within the remaining 1–9% life span interval. Minor adjustments were made for the remaining age groups (9–100%). The age ranges of wear stages VII–VIII and X–XII overlapped completely and thus were condensed into single age units. Most wear stages overlapped for small segments of life span (<6% life span) or had small age gaps between them (<8% life span). The boundaries of the age units for these wear stages were ad-

TABLE 1. Eigenvectors from principal components analysis of crown height measurements of dp3's of LBB *Teleoceras*. Abbreviations: P = protoconid, E = entocoid, M = metaconid, and H = hypoconid.

Variable	PC1	PC2	PC3	PC4
P	0.62	-0.07	-0.75	0.24
E	0.51	-0.36	0.22	-0.75
M	0.43	-0.33	0.58	0.61
H	0.42	0.87	0.24	-0.06

justed to meet at the midpoint of the gap or region of overlap. These adjustments were necessary for the life table analysis, described below.

Although the skull and mandible sample sizes at MBB were sufficient for this study, for the LBB assemblages it was necessary to assign isolated lower premolars (dp3, dp4, p3, and p4) to age units. Unworn adult premolars were excluded to avoid replication of individuals that may have already been represented by deciduous premolars. Isolated teeth are less adequate than mandibles for age estimates, and for some wear stages the degree of wear of the p3 and p4 from one wear stage to the next did not change noticeably. In these instances the age units were further combined to minimize the error potential in the LBB age assignments. Finally, adjacent age units that

TABLE 2. Life table for *Teleoceras proterum* assemblage from MBB built from the maximum number of right or left mandibles in each age category. Abbreviations: ob = observed, dx = deaths per age group, lx = number of survivors, qx = mortality rate calculated as the number of mortalities out of a group of 1000 for each percentage of lifespan, ex = life expectancy. Roman numerals correspond to wear stages of Hitchins (1978).

Wear stage	% Life span	ob	dx	lx	qx	ex
0-II	0-5	0	—	—	—	—
III	5-7	2	27	1000	13	29
IV	7-9	4	53	973	27	30
V	9-12	3	40	920	14	31
VI	12-15	4	53	880	20	32
VII-VIII	15-19	15	200	827	60	33
IX	19-25	12	160	627	46	38
X-XII	25-35	21	280	467	57	44
XIII	35-52	3	40	187	13	66
XIV	52-61	3	40	147	30	72
XV	61-86	6	80	107	29	78
XVI	86-96	2	27	27	100	91
XVII	96-100	0	0	0	—	—

TABLE 3. Life table for *Teleoceras proterum* assemblage from LLB built from the most abundant deciduous-adult premolar pair (left dp3-p3). Abbreviations are as in Table 2.

Wear stage	% Life span	ob	dx	lx	qx	ex
0	0-1	5	74	1000	74	21
I	1-3	2	29	926	16	22
II	3-5	8	118	897	66	23
III	5-7	5	74	779	47	26
IV	7-9	5	74	706	52	28
V-VIII	9-19	5	74	632	12	30
IX	19-25	10	147	559	48	32
X-XII	25-35	22	324	412	75	36
XIII	35-52	3	44	88	30	60
XIV-XV	52-86	2	30	44	19	76
XVI-XVII	86-100	1	15	15	71	93

did not contain fossil specimens were combined into single age units.

The maximum numbers of right or left elements were used to construct the life tables. A life table is a standardized way of analyzing the mortality schedule of a population that chronologically traces the mortality schedule of a theoretical cohort (Deevey 1947; Voorhies 1969). Construction of the life tables (Tables 2, 3, 4) followed the methodology for an attritional assemblage in which the raw data are first converted into the dx column (Voorhies 1969). One adjustment to the qx column (mortality rate) was made:

$$\frac{1000dx}{i(lx)} = qx$$

In this equation, *i* is the duration of the age unit in terms of the percent of life span. Because the age units are not of equal length in the life tables presented here, qx values calculated the standard way (Voorhies 1969) will

TABLE 4. Life table for *Aphelops malacorhinus* assemblage from LBB built from the most abundant deciduous-adult premolar pair (right dp4-p4). Abbreviations are as in Table 2.

Wear stage	% Life span	ob	dx	lx	qx	ex
0-IV	0-9	0	—	—	—	—
V-VIII	9-19	2	71	1000	7	51
IX	19-25	2	71	929	14	54
X-XII	25-35	3	107	857	12	56
XIII	35-52	9	321	750	26	60
XIV-XV	52-86	10	357	429	24	72
XVI-XVII	86-100	2	71	71	71	93

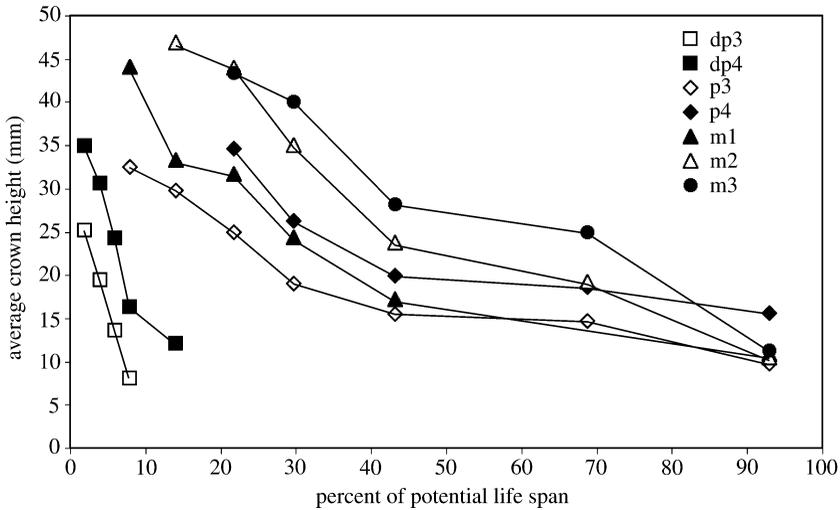


FIGURE 1. Bivariate plot of the average crown heights for lower molariform cheek teeth of *Teleoceras* from the Love Bone Bed against age estimates that are based on dental eruption and wear stages of Hitchins (1978). Average crown height was calculated as the average value of the mean of four crown height measurements taken in the regions of the protoconid, entoconid, metaconid, and hypoconid.

not accurately reflect mortality rates. This alteration of the  $qx$  calculation compensates for unequal age units, so that  $qx$  represents deaths out of 1000 individuals per percent of potential life span. The resulting  $qx$  curves were compared with those calculated from attritional skeletal collections of modern species including *Hippopotamus amphibius* (common African hippo) from Uganda (Laws 1968), *Syncerus caffer* (Cape buffalo) from Serengeti, Tanzania (Sinclair 1977), *Alces alces* (moose) from Isle Royale, Michigan (Van Ballenberghe and Ballard 1997), *Diceros bicornis* from Tsavo, Kenya (Goddard 1970), and *Diceros bicornis* from the Hluhluwe Game Reserve, South Africa (Hitchins 1978). For these modern populations, age was converted to percent of life span, based on the oldest individuals found in each of these assemblages.

## Results

*Crown Height Data versus Wear-Stage Age Estimates.*—The quadratic crown height method (QCHM) is a quantitative method that converts crown height data into age estimates (Klein 1981; Klein and Cruz-Urbe 1983). Although the QCHM seems preferable because of its objectivity, the method was developed for hypsodont ungulates (e.g., horses) whose occlusal surface areas are fairly constant

throughout life and wear at a nearly linear rate. It is less effective among ungulates of moderate crown height (Pike-Tay et al. 2001). Its application to this study is questionable because the occlusal surface area continuously increases with wear in rhino cheek teeth. Therefore, the wear rate of rhino teeth, in terms of crown height, may decrease exponentially with age. The QCHM has not been tested with living rhinos. Nonetheless, it is possible to test the age estimates of the fossil specimens by plotting average crown heights with the age estimates based on dental eruption/wear stages. The curves of the LBB *Teleoceras* adult dentition (Fig. 1) are, for the most part, compatible with the expectation of exponentially slowing rate of wear. However, the rate of wear in the deciduous teeth seems more or less linear, suggesting a systematic error in the age estimates of the juveniles. Plots for MBB *Teleoceras* (not shown) suggest the same pattern. There are too few LBB *Aphelops* juvenile teeth to perform the test.

To explore the juvenile age estimates further, I analyzed the crown height variables of the deciduous dentition with principal components analysis (PCA) to search for discontinuities in the crown height data. Regularly spaced discontinuities in the age distribution of fossil assemblages represent cohorts (yearly

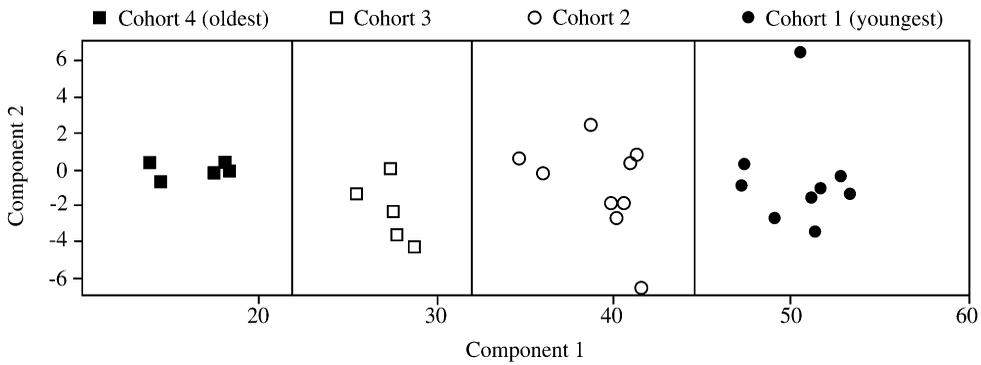


FIGURE 2. Bivariate plot of the first and second principal components of the four crown height variables of the dp3 of *Teleoceras* from the Love Bone Bed. Vertical lines represent areas interpreted as possible cohort boundaries.

groups of individuals born seasonally) (Voorhies 1969). Discrete cohorts, when present, provide another means of determining the ages of individuals in the assemblage and can only exist in a fossil assemblage if (1) births were seasonal or concentrated within a particular time of year and (2) localized deaths occurred instantaneously or at regular (seasonal) intervals (Kurtén 1953; Voorhies 1969). Age clustering did not occur in the MBB data, but cohorts were apparent in the LBB *Teleoceras* data. All variables loaded positively on the first component of the dp3, creating a generalized crown height axis (Table 1), and explained 95% of the variation whereas the remaining three components cumulatively accounted for less than 5%. In the plots of the first and second components, four clusters are definable by discontinuities in the data (Fig. 2). The dp4 data (not shown) yielded a similar pattern with five distinct clusters. Hulbert (1982) located clusters that were interpreted as cohorts in the equid (*Neohipparion*) assemblage from the LBB and discussed why they might exist in this assemblage. The apparent cohorts of the LBB *Teleoceras* assemblage indicate that the dp3 was shed sometime after the fourth year, and the dp4 was shed sometime after the fifth. The additional cohort in the dp4 is not surprising because this tooth is shed later than the dp3. There is no detectable difference between the dental eruption schedules of *Teleoceras* and modern rhinos *Diceros* and *Ceratotherium* (Hitchins 1978; Hillman-Smith et al. 1986). The cohorts are about equally spaced on the "crown height" axis. This also suggests

that the rate of wear in the juvenile teeth was indeed linear and indicates that the age estimates of the juvenile wear stages are accurate. The constant rate of linear wear in juvenile teeth requires a continuously increasing rate of volumetric wear and is probably linked to the continuously increasing metabolic demands during younger growth years. In contrast, the exponentially decreasing rate of crown height wear among the adults requires a more or less constant rate of volumetric wear and is congruent with the less variable metabolic demands of adults.

*Mortality Patterns.*—The age distribution of the skulls and the mandibles for MBB *Teleoceras* (Fig. 3A) indicates that individuals at ages less than 5% of the potential life span were absent. In the LBB *Teleoceras* assemblage (Fig. 3B) all age groups were represented, including the youngest cohort, which was represented by unworn deciduous premolars. An exhaustive survey of all the MBB *Teleoceras* i2s indicates a male bias (Fig. 4A). Males ( $n = 49$ ) are more frequent than females ( $n = 19$ ) and make up 72% of the assemblage. The sex ratio differs significantly from an expectation of parity (Pearson chi-squared:  $p = 0.0003$ ). Males make up 77% of the LBB *Teleoceras* assemblage (male = 36, female = 11) (Fig. 4B) and the bias differs significantly from parity as well (Pearson chi-squared;  $p = 0.003$ ). In both assemblages, according to the tusks, sub-adult and young adult males are numerous, whereas females are more heavily concentrated in the intermediate-to-old adult group. The age estimates based on cheek-tooth wear in-

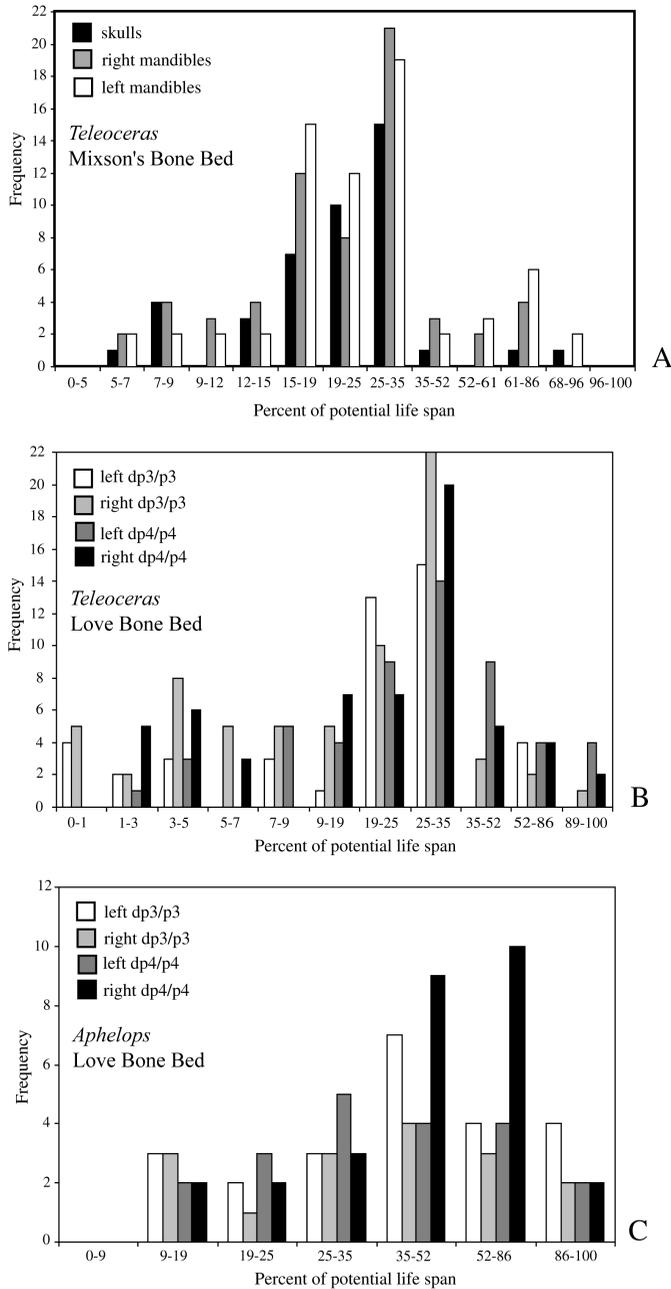


FIGURE 3. Age distributions of Mixson's Bone Bed *Teleoceras* (A), Love Bone Bed *Teleoceras* (B), and Love Bone Bed *Aphelops* (C) based on age estimates from Hitchins' (1978) dental eruption and wear categories.

dicade, for both *Teleoceras* assemblages, that most of the specimens represent individuals between 15% and 35% of potential life span. Judging by the age distribution pattern of the i2s, the vast majority of the individuals in this age range are males.

The age structure of the *Aphelops* assem-

blage (Fig. 3C) was very different from that of *Teleoceras*. The first 10% of the life span is not represented at all. The age distribution of adult premolars suggests either a relatively even distribution throughout the adult age groups or a concentration of individuals within the 35–86% range of life span. Males

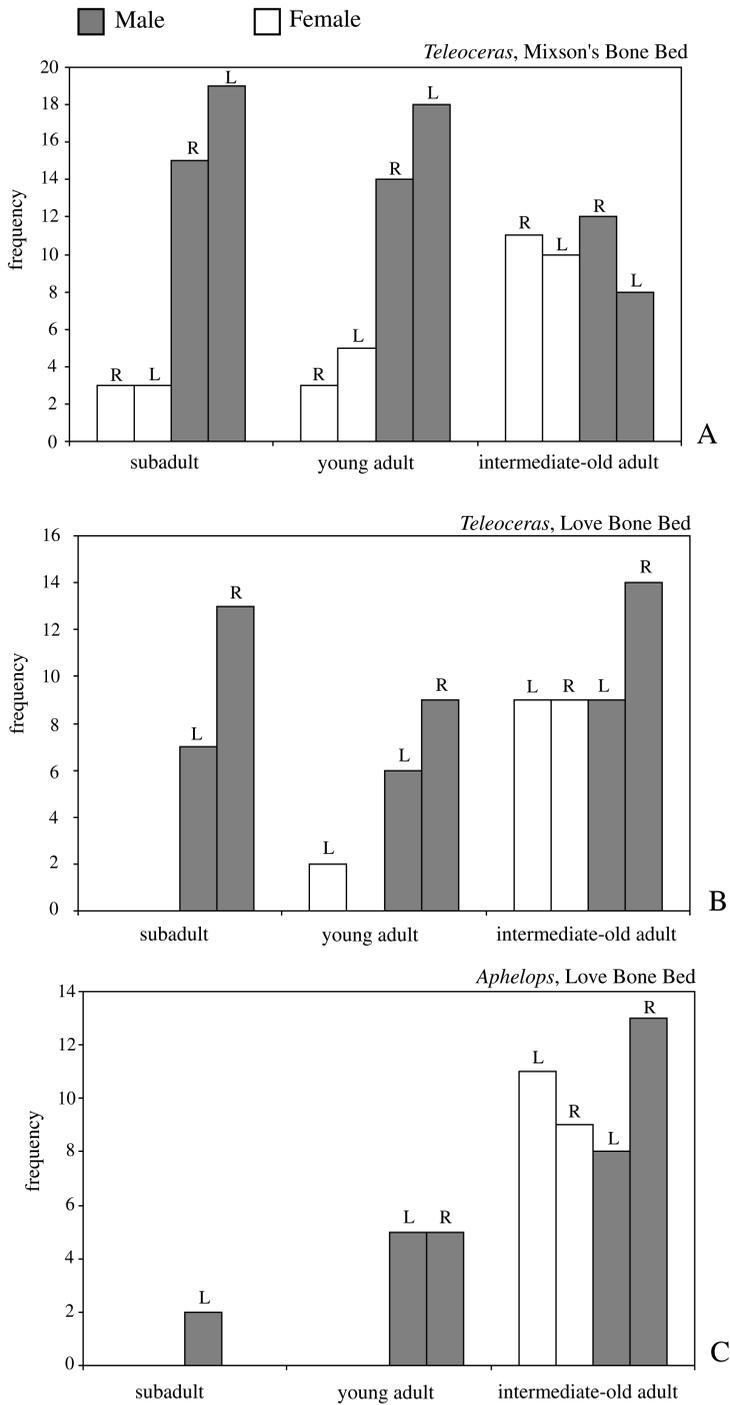


FIGURE 4. Sex-specific age distribution of Mixson's Bone Bed *Teleoceras* (A), Love Bone Bed *Teleoceras* (B), and Love Bone Bed *Aphelops* (C) based on the sexually dimorphic lower incisor (i2). R = right, L = left.

make up 65% of the assemblage (male  $n = 20$ , female  $n = 11$ ); however the male bias is not significantly different from parity (Pearson chi-squared:  $p = 0.11$ ) (Fig. 4c). In contrast to

*Teleoceras*, *Aphelops* males and females are most abundant in the intermediate-to-old adult age group and young males are far less abundant.

## Discussion

*Causes of Attritional Assemblage Biases.*—Clearly the fossil rhino assemblages are age and sex biased to varying degrees. Idealized attritional mortality profiles of stable populations are U-shaped or L-shaped because deaths are expected to occur most frequently among the youngest and oldest members of a population (Voorhies 1969; Lyman 1994). However, the fossil rhino assemblages do not resemble idealized attritional profiles. Preservation biases explain some, but not all, of the deviation from the expected attritional pattern. Juvenile bones are more easily destroyed than adult bones and are typically underrepresented. Actual juvenile mortality rates for large mammals are generally higher than indicated by life tables based on bone assemblages (Laws 1968; Goddard 1970; Sinclair 1977; Van Ballenberghe and Ballard 1997). In the LBB *Teleoceras* assemblage, juveniles (0–9% of life span) constitute about 37% of the sample. Juvenile representation in *Diceros* bone collections is similar (Goddard 1970; Hitchins 1978). The absence of *Aphelops* juveniles (0–9% of life span) at the LBB cannot be completely explained by a taphonomic bias. If *Aphelops* juveniles suffered from mortality rates similar to those of modern large mammals, they must have died near the site less frequently than *Teleoceras* juveniles.

At least three factors explain the sex biases in attritional assemblages. (1) Natal sex ratios are often unbalanced within modern mammal populations (Clutton-Brock and Iason 1986; Owen-Smith 1988). An unbiased sample of the cumulative mortality of a population must ultimately preserve the natal sex ratio. *Diceros* and *Rhinoceros* populations have natal sex ratios that are essentially balanced (Berger and Cunningham 1995; Dinerstein and Price 1991) although *Ceratotherium* births are male biased (up to 65% male) (Owen-Smith 1988). The *Aphelops* bias (65%) is similar and could be explained as a natal birth bias. However, the sex ratios found in the *Teleoceras* assemblages (72–77%) are higher than the known natal male biases of large mammal populations (Owen-Smith, 1988). Although male-biased births may partially explain the sex bias, it seems

likely that *Teleoceras* males are more abundant in the assemblages than their actual natal frequency. (2) The sex ratios of the *Teleoceras* assemblages could have been affected to some degree by differential male and female mortality rates in the first 15% of life span (an age prior to the development of adult tusks, when sex is indeterminate) thus skewing the number of individuals within each sex that reach an age where sex is determinate. (3) Finally, a spatial bias in the distribution of mortality among sex-determinate individuals (~15–100% of life span) would lead to unbalanced ASRs in the assemblages. The disproportionate influxes of subadult and young adult males into these deposits strongly suggest that the third factor is at least partially influential.

*Mortality Rate Curves.*—The *qx* curves of the *Teleoceras* life tables are essentially the same as those of *Diceros* and indicate elevated mortality risks during two life-history intervals (Fig. 5A–D), shortly before or near ten percent of life span, and between 15–40% of life span. The *Aphelops* curve does not contain intervals of heightened mortality rates (Fig. 5E). *Hippopotamus* (Fig. 5F), *Synceras* (Fig. 5G), and *Alces* (Fig. 5H) all lack evidence for such heightened age-specific mortality rates.

Existing data on mortality in modern rhinos offers good evidence for why certain age intervals are associated with increased mortality risks. The younger mortality peak in *Diceros* corresponds to an age before full body size is reached, but after the calf has achieved independence (Owen-Smith 1988). Brain et al. (1999) found that *Diceros* calves between three and five years are susceptible to lion predation, whereas adults are virtually immune to predators. The corresponding spike in LBB *Teleoceras* suggests a similar age of mother-calf separation and resulting susceptibility of the calf to predation. It is not known if the absence of a mortality spike at a similar age at MBB is a taphonomic bias or if it is due to a low frequency of localized juvenile mortality. Other evidence indicates that *Teleoceras* juveniles underwent age-specific periods of increased stress around this age. Mead (1999) found that hypoplasias (interruptions in enamel growth caused by nutritional deficiency) appear fre-

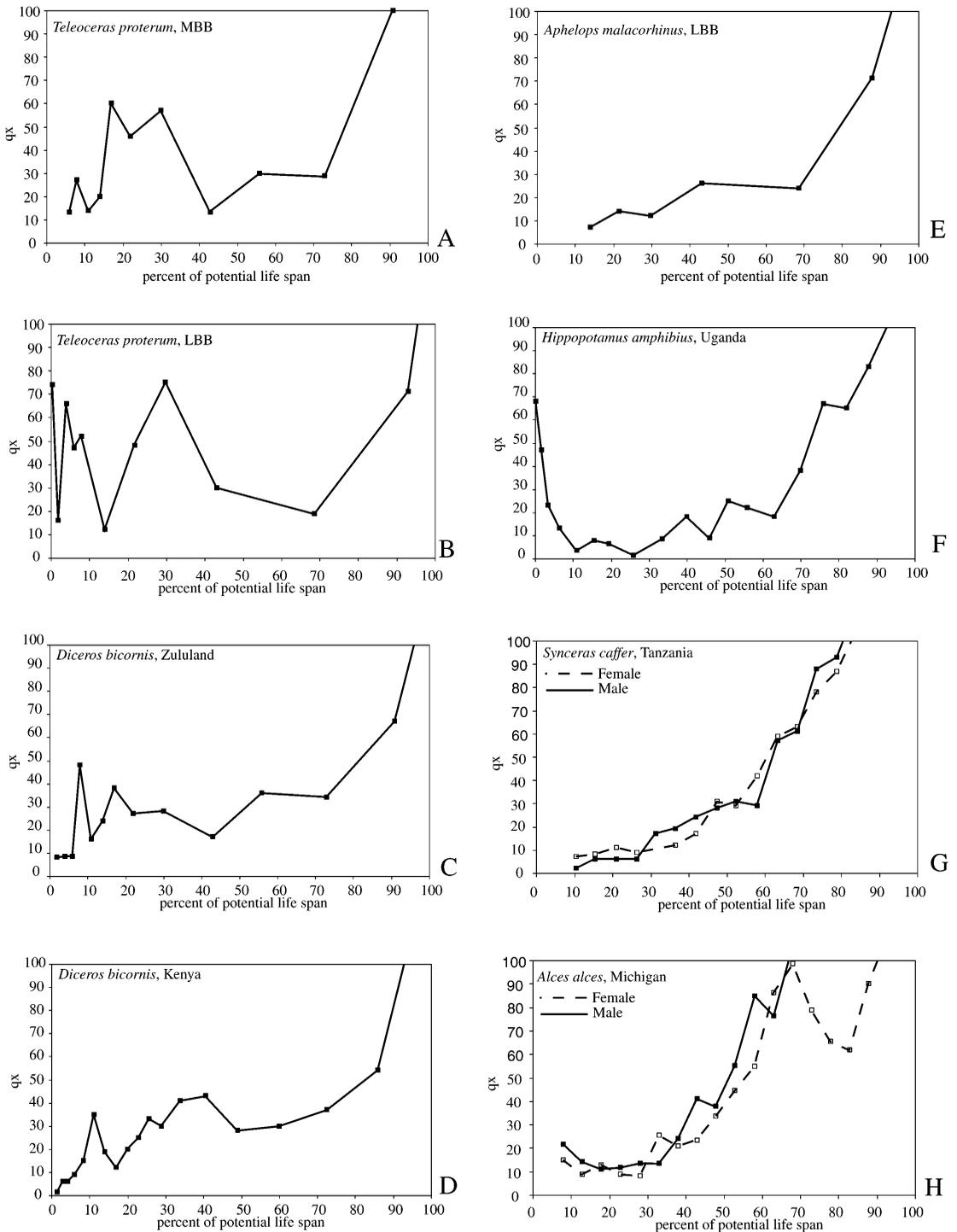


FIGURE 5. Mortality rate curves (qx) calculated from life tables of large mammals. A, Mixson's Bone Bed *Teleoceras proterum*. B, Love Bone Bed *Teleoceras proterum*. C, *Diceros bicornis* (Hitchins 1978). D, *Diceros bicornis* (Goddard 1970). E, Love Bone Bed *Aphelops malacorhinus*. F, *Hippopotamus amphibius* (Laws 1968). G, *Syncerus caffer* (Sinclair 1977). H, *Alces alces* (Van Ballenberghe and Ballard 1997).

quently in quarry samples of *Teleoceras* from Nebraska at specific locations in the enamel of the dp4 (87% frequency) and the p4 (37% frequency). The dp4 hypoplasia represents metabolic disruption occurring at a time near birth. The p4 hypoplasia indicates, according to Mead's (1999) estimates, an age between three and five years. The p4 hypoplasias appear to correspond to the timing of mother-calf separation (Mead 1999). This period corresponds to 8–14% of life span and encompasses the period of the juvenile mortality peak at LBB.

The second interval of elevated mortality risk in *Diceros* could relate to a high incidence of socially mediated mortality. A mortality peak around this age (young adulthood) occurs among species that sustain a high frequency of mortality from intermale competition (Dittus 1975, 1977, 1979; Ralls et al. 1980). The mortality could be direct (fighting) or indirect (e.g., forced emigration to suboptimal habitat). Alternatively, it is possible that the young-male bias was caused by an increased susceptibility of young males to predation in the area. Although the *Teleoceras* sex biases at MBB and LBB are about equal, large carnivores are far more common at LBB than at MBB. It therefore seems doubtful that intensity of predation influenced the sex ratios.

Direct fighting appears to be the more significant cause of socially mediated deaths among modern rhinos. Recent data on adult *Diceros* mortality indicates that 50% of male deaths and 30% of female deaths are a result of mortal wounds (Hitchins and Anderson 1983; Berger 1994; Berger and Cunningham 1994b). Combat mortality is also frequent among *Ceratotherium* males (Owen-Smith 1988) and *Rhinoceros* males (Dinerstein 1991; Dinerstein and Price 1991). Fight-related incidences of mortality are less frequent among the other modern ungulates examined. *Synceras* intermale confrontations are resolved quickly, with dominance being determined by size or strength, and do not often result in fatalities (Sinclair 1977; Prins 1996). The intensity of male interactions among moose (*Alces*) mostly involves displays and nonlethal fighting (Franzmann 1981). In *Hippopotamus*, territorial bulls are highly tolerant of subordi-

nate males and boundary disputes between territory-holding males are ritualized. Occasionally, fights over a single territory can result in the death of the loser (Klingel 1991; Eltringham 1999), though there is no apparent effect on age-specific mortality rates.

This age of the second mortality peak in *Teleoceras* corresponds to a late stage of eruption and/or early wear stage of the m3 and translates into 6–15 years in *Diceros* (Hitchins 1978). This range encompasses the life-history transition from adolescence to adulthood for males, whose physical and social development is delayed with respect to females. In *Diceros*, physiological sexual maturity varies from 4.5 to 8 years (12–22% of life span), although only males above nine years (24% of life span) mate (Hitchins and Anderson 1983). *Rhinoceros* females first give birth between six and eight years. Males are capable of breeding around five to 7 years but do not usually obtain breeding privileges until 12–15 years (Laurie et al 1983; Dinerstein and Price 1991). *Ceratotherium* females produce their first offspring between 6.5 and seven years but males are not reproductively active until after ten years (Owen-Smith 1988). Mead (2000) found evidence for bimaturism in the epiphyseal fusion of limb bones and skull growth in *Teleoceras*, suggesting that males matured more slowly than females. The majority of individuals in the *Teleoceras* assemblages died during a life-history stage involving the earliest reproductive years of females and during the period of delayed physical and social maturation of males, an age at which individuals are probably vulnerable to the aggressive behaviors of dominant individuals. Individuals in this age category are rare in the *Aphelops* assemblage.

*Teleoceras Mortality and Sociality.*—Prior interpretations of *Teleoceras* sociality are numerous and stem from Cope's (1879) initial observation that the peculiarly shortened limbs of *Teleoceras* were similar to those of *Hippopotamus africanus*. Osborn (1898a,b) believed that *Teleoceras* lived in large herds in rivers and lakes, as do modern hippos. Paleontologists have maintained a belief that its sociality was hippolike rather than rhinolike and large assemblages are typically described as being

congruent with this interpretation (Webb 1977, 1983; Voorhies 1985; Prothero et al. 1989; Prothero 1998; Mead 2000). Female hippos form large schools in water during the day, but at night they come out onto land and graze solitarily. Dominant males are territorial and defend strips of land adjacent to water occupied by the schools. Subdominant males form separate bachelor groups often in isolated ponds or wallows (Klingel 1991; Eltringham 1999). Berger et al. (2001) also concluded from the skewed ASR of the LBB *Teleoceras* assemblage, preliminarily reported by Mhlbachler (1999) but mistakenly attributed to Mead (2000), that *Teleoceras* males formed groups. This general belief that *Teleoceras* formed hippolike groups is of interest because all five extant rhino species are essentially solitary and rarely form small ephemeral groups (two to three individuals) (Laurie 1982; Van Strien 1986; Owen-Smith 1988).

The young male biases in the attritional *Teleoceras* assemblages could represent a gradual accumulation of deaths within territory mainly occupied by bachelor males who ranged apart from the main population, but they give no direct indication of groups because the deaths are attritional. An extant phylogenetic bracket is a phylogenetically constraining framework for developing null hypotheses of unpreserved characters of extinct species, including behaviors (Witmer 1995) from which hypotheses of sociality, generated from assemblage demography or any other means, could be tested. *Teleoceras* and *Aphelops* are phylogenetically positioned outside the clade of living rhinos (Prothero et al. 1986; Cerdeño 1995). Therefore, the bracketing clades are extant members of the Rhinocerotidae and Tapiridae (Janis et al. 1998). Tapirs and rhinos do not form social groups. Though social behaviors are potentially plastic (Byers and Kitchen 1988; Putman 1996; Hirth 2000) there is no a priori reason to infer that extinct rhinos might have formed herdlike groups.

A spatially confined attritional bone assemblage of a modern rhino population would obviously serve as an important link for relating modern rhino behaviors to the demography of fossil rhino assemblages. Such data are not readily available; however, the localized attri-

tional mortality pattern recorded in the *Teleoceras* assemblages are consistent with behaviors and mortality patterns observed in modern rhinos. Observations of a *Rhinoceros* population by Dinerstein (1991) and Dinerstein and Price (1991) in the Royal Chitwan National Park, Nepal, indicate that localized attritional assemblages of modern rhinos would probably contain disproportionate numbers of young males. Dinerstein and Price (1991) found that "the disproportionate number of mortalities among adult males (15 of 18) suggests that competition for mates may be the most important contributor to deaths of males" (Dinerstein and Price 1991: p. 408). Although *Rhinoceros* does not form cohesive social groups, males clearly monopolize mates, because only 48% of adult males mated in that population (Dinerstein and Price 1991). Dominant *Rhinoceros* males were observed to attack young males if they occupied areas where females were concentrated, and male aggression was most likely to occur near rivers where the population density was highest (Dinerstein 1991). Laurie (1982) also reported that *Rhinoceros* individuals temporarily aggregate around water and that dominant males live in the areas of highest female concentration. The clustered distribution of individuals around water is not surprising for mammals that are metabolically obligated to drink standing water, such as rhinos, particularly when standing water is scarce. An inference of sex-segregated bachelor groups is unnecessary to explain the preponderance of young males in the *Teleoceras* assemblages; the observations on *Rhinoceros* indicate that socially mediated deaths from fighting could have led to the disproportionate abundance of males in attritional assemblages from aquatic facies (lakes, ponds, or rivers).

Voorhies (1985) and Mead (2000) examined demographic patterns of *Teleoceras* from the Ashfall Beds, Antelope County, Nebraska. This is a large catastrophic death assemblage, consisting mostly of juveniles and females with conspicuously fewer young adult males, that was buried under volcanic ash along with other large ungulates in a pond or lake environment. It has nearly the inverse sex ratio (28% male) of the attritional Florida assem-

blages (Mead 2000). Both authors interpreted the assemblage as a "snapshot" of a group similar to those of herding artiodactyls or *Hippopotamus*. Bachelor groups were inferred to account for the missing males. Hippo groups generally consist of 10–30 individuals with a single dominant male and two to six subordinate males (Owen-Smith 1988). A culled hippo sample (essentially a catastrophic assemblage) from Uganda demonstrates the sex-biased spatial distribution of hippos, where 42% of the sample from lakeshores ( $n = 1421$ ) were male but in the sample from isolated ponds ( $n = 740$ ) males made up 66% (Owen-Smith 1988). The Ashfall assemblage suggests a similar gender-biased spatial distribution, but the demography of this assemblage can be explained without drawing a hippo analogy. The individuals at Ashfall were clearly subjected to severe environmental stress (suffocating volcanic ash) and it is not immediately surprising that a large number of them would be clumped together near water at the time of death. Notably, rhino mortality, in general, tends to be concentrated near water (Hitchins and Anderson 1983; Dinerstein and Price 1991; Cunningham and Berger 1997). The young males may have been rare at the site simply because aggressive dominant males actively drove them away. Additionally, the rarity of males could partly be explained by a population that was intrinsically female biased owing to an elevated male mortality rate. In the *Rhinoceros* population examined by Dinerstein and Price (1991), sex ratios of calves, young adults, and old adults did not differ from parity, although intermediate-aged females (12–20 years) were significantly more abundant than intermediate-aged males (Dinerstein and Price 1991). This population structure is not fundamentally different from the Ashfall assemblage. The Ashfall assemblage reflects one or both of the following phenomena: (1) a female-biased ASR in the population and (2) avoidance of the site by young males, either because of a localized mortality risk or because they actively formed bachelor herds. The exact social behaviors cannot be identified from the attritional (LBB, MBB) and catastrophic (Ashfall) assemblages; however, either interpretation of the proximate relation-

ship of sociality with the sex-biased mortality patterns (male aggression or sex-segregated groups) suggests an extreme form of polygyny as the ultimate cause of the demographic biases in *Teleoceras* assemblages.

*Aphelops Mortality and Sociality.*—The LBB *Aphelops* assemblage indicates that *Aphelops* mortality patterns differed demographically from *Teleoceras* patterns. Matthew (1932) reported a sex ratio of 12 females and 7 males for *Aphelops mutilus* from Coffee Ranch, Texas. Dalquest (1983) reported an additional nine male tusks and a dozen female tusks from the site. I examined the material described by Dalquest (1983) and found nine tusks of each sex. Regardless of the discrepancy in the number of female tusks, the total sex ratio of this assemblage (40% male or 43% male) does not differ significantly from parity either (Pearson chi-squared:  $p = 0.2$  or  $p = 0.4$ ). Demographically balanced *Aphelops* assemblages at LBB and Coffee Ranch indicate no causal relationship between sociality and localized mortality patterns. Likewise, there was no apparent link between age-specific mortality risks and sexual maturity at LBB. These results indicate that *Aphelops* sociality was unlike that of *Teleoceras* but further interpretation is difficult. The mortality pattern might indicate a lesser frequency of socially mediated mortality, a non-biased spatial distribution of males and females, or both. It is also plausible that the degree of polygyny was similar to that of *Teleoceras*, but that male competition was manifested in ritualistic displays not known among modern rhinos. Retention of the sexually dimorphic i2 suggests that *Aphelops* had not adopted complete monogamy. In this element, the degree of dimorphism is about that same as in *Teleoceras*. In many ungulates (ruminant artiodactyls), sexual dimorphism correlates with the degree of polygyny (Jarman 1983; Geist and Bayer 1988; Loison et al. 1999). However, the degree of dimorphism in some clades of mammals, including perissodactyls, does not correlate with the degree of polygyny (Berger 1986; Plavcan 2000). It is therefore not feasible to use sexual dimorphism to gauge the relative polygyny of extinct rhinos.

## Conclusion

Modern rhinos are, unfortunately, so rare that fossil assemblages are far more common than modern assemblages. However, the few data available on modern rhino mortality indicate that rhinos experience a high frequency of socially mediated mortality. The extremely disproportionate representation of young males in the *Teleoceras* assemblages could be explained by sex-segregated populations (e.g., bachelor herds), but it is more parsimonious to infer a high frequency of localized male mortality due to intermale competition near the site of fossil preservation. The mortality data do not distinguish which of these proximate factors may have contributed to the sex biases of these fossil assemblages, but the general mortality pattern suggests that *Teleoceras* was highly polygynous. Age-specific mortality rates calculated from the *Teleoceras* assemblages indicate a link between mortality risks and life-history stages that is identical to that of the modern rhino *Diceros*. Although modern rhinos are commonly dismissed as poor models for extinct rhinos, the findings presented here indicate that some extinct rhinos (*Teleoceras*) may have shared some aspects of sociality with modern rhinos. A similar link between mortality risk and life history was not found among modern herd-forming ungulates or *Hippopotamus*, the commonly proposed ecological analog for *Teleoceras*.

*Aphelops* mortality patterns contrast with those of living rhinos and *Teleoceras* because they lack evidence for socially mediated mortality. There is no apparent peak in mortality risk during sexual maturity in *Aphelops*. These findings indicate that *Aphelops* sociality differed from that of *Teleoceras* and modern rhinos. Although the nature of its sociality is unknown these results are consistent with the suggestion that the loss of tusk-honing ability, coupled with the absence of a horn, a condition unlike modern rhinos, corresponded to a lesser intensity of intraspecific competition.

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## Literature Cited

- Agenbroad, L. D. 1990. The mammoth population of the Hot Springs site and associated fauna. Pp. 32–39 in L. D. Agenbroad, J. I. Mead, and L. W. Nelson, eds. *Megafauna and man: the discovery of America's Heartland*. Mammoth Site of Hot Springs, Hot Springs, S.D.
- Barnosky, A. D. 1985. Taphonomy and herd structure of the extinct Irish elk, *Megaloceros giganteus*. *Science* 228:340–344.
- Berger, J. 1986. *Wild horses of the Great Basin: social competition and population size*. University of Chicago Press, Chicago.
- . 1994. Science, conservation and black rhinos. *Journal of Mammalogy* 75:298–308.
- Berger, J., and C. Cunningham. 1994a. *Bison: mating and conservation in small populations*. Columbia University Press, New York.
- . 1994b. Phenotypic alterations, evolutionarily significant structures, and rhino conservation. *Conservation Biology* 8: 833–840.
- . 1995. Predation, sensitivity, and sex: why female black rhinoceroses outlive males. *Behavioral Ecology* 6:57–64.
- Berger, J., S. Dulamtseren, S. Cain, D. Enkkhbileg, P. Lichtman, Z. Namshir, G. Wingard, and R. Reading. 2001. Back-casting sociality in extinct species: new perspectives using mass death assemblages and sex ratios. *Proceedings of the Royal Society of London B* 268:131–139.
- Brain, C., O. Forge, and P. Erb. 1999. Lion predation on black rhinoceros (*Diceros bicornis*) in Etosha National Park. *African Journal of Ecology* 37:107–109.
- Byers, J. A. 1997. *American pronghorn: social adaptations and the ghosts of predators past*. University of Chicago Press, Chicago.
- Byers, J. A., and D. W. Kitchen. 1988. Mating system shifts in a pronghorn population. *Behavioral Ecology and Sociobiology* 22:355–360.
- Cerdeño, E. 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). *American Museum Novitates* 3143:1–25.
- Clutton-Brock, T. H., and G. R. Iason. 1986. Sex ratio variation in mammals. *Quarterly Review of Biology* 61:339–374.
- Cope, E. D. 1879. On the extinct American rhinoceroses and their allies. *American Naturalist* 13:771a–771j.

- Cunningham, C., and J. Berger. 1997. Horn of darkness: rhinos of the edge. Oxford University Press, New York.
- Currie, P. J. 1998. Possible evidence of gregarious behavior in Tyrannosaurids. *Gaia* 15:271–277.
- Dalquest, W. 1983. Mammals of the Coffee Ranch local fauna, Hemphillian of Texas. Pearce-Sellards Series No. 38. Texas Memorial Museum, University of Texas, Austin.
- Deevey, E. S. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* 22:283–314.
- Dinerstein, E. 1991. Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy* 72:450–457.
- Dinerstein, E., and L. Price. 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. *Journal of Wildlife Management* 55:401–411.
- Dittus, W. P. 1975. Population dynamics of the Toque monkey, *Macaca sinica*. Pp. 125–152 in R. H. Tuttle, ed. *Socioecology and psychology of primates*. Mouton, The Hague.
- . 1977. The social regulation of population density and age-sex distribution in the Toque monkey. *Behaviour* 63:281–322.
- . 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour* 69:266–302.
- Dodson, P. 1996. The horned dinosaurs. Princeton University Press, Princeton, N.J.
- Eltringham, S. K. 1999. The hippos: natural history and conservation. Academic Press, London.
- Franzmann, A. W. 1981. *Alces alces*. *Mammalian Species* 154:1–7.
- Geist, V., and M. Bayer. 1988. Sexual dimorphism in the Cervidae and its relation to habitat. *Journal of Zoology* 214:45–53.
- Gingerich, P. D. 1981. Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). *Paleobiology* 7:443–455.
- Goddard, J. 1970. Age criteria and vital statistics of a black rhinoceros population. *East African Wildlife Journal* 8:105–121.
- Hillman-Smith, A. K. K., N. Owen-Smith, J. L. Anderson, A. J. Hall-Martin, and J. P. Selaladi. 1986. Age estimation of the white rhinoceros (*Ceratotherium simum*). *Journal of Zoology* 210:355–379.
- Hirth, D. H. 2000. Behavioral ecology. Pp. 756–791 in S. Demaris and P. R. Krausman, eds. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, N.J.
- Hitchins, P. M. 1978. Age determination of the black rhinoceros (*Diceros bicornis* Linn.) in Zululand. *South African Journal of Wildlife Research* 8:71–80.
- Hitchins, P. M., and J. L. Anderson. 1983. Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozzi game reserve complex. *South African Journal of Wildlife Research* 13:78–85.
- Hulbert, R. C. 1982. Population dynamics of the three-toed horse *Neohipparion* from the late Miocene of Florida. *Paleobiology* 8:159–167.
- . 1984. Paleoecology and population dynamics of the early Miocene (Hemmingfordian) horse *Parahippus leonensis* from the Thomas Farm site, Florida. *Journal of Vertebrate Paleontology* 4:547–558.
- Janis, C., M. Colbert, M. C. Coombs, W. D. Lambert, B. J. MacFadden, B. J. Mader, D. R. Prothero, R. M. Schoch, J. Shoshani, and W. P. Wall. 1998. Perissodactyla and Proboscidea. Pp. 511–524 in C. Janis, K. M. Scott, and L. L. Jacobs, eds. *Evolution of Tertiary mammals of North America, Vol. I. Terrestrial carnivores, ungulates, and ungulate-like mammals*. Cambridge University Press, Cambridge.
- Jarman, P. 1983. Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews of the Cambridge Philosophical Society* 58:485–520.
- Jarman, P., and M. V. Jarman. 1973. Social behavior, population structure and reproduction potential in impala. *East African Wildlife Journal* 11:329–38.
- Kidwell, S. M., and A. K. Behrensmeier. 1993. Taphonomic approaches to time resolution in fossil assemblages. *Short Courses in Paleontology* No. 6. Paleontological Society, Knoxville, Tenn.
- Klein, R. G. 1981. Ungulate mortality and sedimentary facies in the late Tertiary Varswater formation, Langebaanweg, South Africa. *Annals of the South African Museum* 84:233–254.
- Klein, R. G., and K. Cruz-Urbe. 1983. The computation of ungulate age (mortality) profiles from dental crown heights. *Paleobiology* 9:70–78.
- Klingel, H. 1991. The social organization and behavior of *Hippopotamus amphibius*. Pp. 73–75 in F. I. B. Kayaanja and E. L. Edorama, eds. *African wildlife: research and management*. International Council of Scientific Unions, Paris.
- Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zoologica Fennica* 76:1–121.
- Laurie, A. 1982. Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Zoology* 196:307–341.
- Laurie, A., E. M. Lang, and C. P. Groves. 1983. *Rhinoceros unicornis*. *Mammalian Species* 211:1–6.
- Laws, R. M. 1968. Dentition and aging of the hippopotamus. *East African Wildlife Journal* 6:19–52.
- Leidy, J., and F. A. Lucas. 1896. Fossil vertebrates from the Alachua clays. *Transactions of the Wagner Free Institute of Science of Philadelphia* 4:1–61.
- Loison, A., J.-M. Gaillard, C. Pélabon, and N. G. Yoccoz. 1999. What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research* 1:611–633.
- Lyman, R. L. 1994. *Vertebrate taphonomy*. Cambridge University Press, Cambridge.
- MacFadden, B. J., and S. D. Webb. 1982. The succession of Miocene (Arikareean through Hemphillian) terrestrial mammalian localities and faunas in Florida. Pp. 186–199 in T. Scott and S. B. Upchurch, eds. *Miocene of the Southeastern United States*. Florida Department of Natural Resources, Division of Resource Management, Bureau of Geology, Tallahassee.
- Martin, R. E. 1999. *Taphonomy: a process approach*. Cambridge University Press, New York.
- Matthew, W. D. 1924. Third contribution to the Snake Creek Fauna. *Bulletin of the American Museum of Natural History* 50:59–210.
- . 1932. A review of the rhinoceroses with a description of *Aphelops* material from the Pliocene of Texas. *Bulletin of the University of California Publications in Geological Sciences* 20:411–480.
- Mead, A. J. 1999. Enamel hypoplasias in Miocene rhinoceroses (*Teleoceras*) from Nebraska: evidence of severe physiological stress. *Journal of Vertebrate Paleontology* 19:391–397.
- . 2000. Sexual dimorphism and paleoecology in *Teleoceras*, a North American rhinoceros. *Paleobiology* 26:689–706.
- Mihlbachler, M. C. 1999. Population structure and implications of social behavior in Miocene Florida rhinoceroses. *Journal of Vertebrate Paleontology* 19(Suppl.):64a.
- Osborn, H. F. 1898a. A complete skeleton of *Teleoceras fossiger*: notes upon the growth and sexual characteristics of this species. *Bulletin of the American Museum of Natural History* 10:51–59.
- . 1898b. A complete skeleton of *Teleoceras* the true rhinoceros from the Upper Miocene of Kansas. *Science* 7:554–557.
- Owen-Smith, R. N. 1988. Megaherbivores: the influence of very

- large body size on ecology. Cambridge University Press, Cambridge.
- Pike-Tay, A., C. A. Morcomb, and M. O'Farrell. 2001. Reconsidering the quadratic crown height method of age estimation for *Rangifer* from archaeological sites. *Archaeozoologia* 11:145–174.
- Plavcan, J. M. 2000. Inferring social behavior from sexual dimorphism in the fossil record. *Journal of Human Evolution* 39:327–344.
- Prins, H. H. T. 1996. Ecology and behavior of the African buffalo: social inequality and decision making. Chapman and Hall, New York.
- Prothero, D. R. 1998. Rhinocerotidae. Pp. 595–605 in C. Janis, K. M. Scott, and L. L. Jacobs, eds. *Evolution of Tertiary mammals of North America*, Vol. I. Terrestrial carnivores, ungulates, and ungulate-like mammals. Cambridge University Press, Cambridge.
- Prothero, D. R., E. Manning, and C. B. Hanson. 1986. The phylogeny of the Rhinocerotidae. *Zoological Journal of the Linnean Society* 87:341–366.
- Prothero, D. R., C. Guerin, and E. Manning. 1989. The history of the Rhinocerotidae. Pp. 321–340 in D. R. Prothero and R. M. Schoch, eds. *The evolution of the perissodactyls*. Oxford University Press, New York.
- Putman, R. J. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London.
- Radinsky, L. 1966. The families of Rhinocerotidae (Mammalia, Perissodactyla). *Journal of Mammalogy* 47:631–639.
- Ralls, K., R. L. Brownell Jr., and J. Ballou. 1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. Report of the International Whaling Commission, Special Issue 2:233–243.
- Schaller, G. B. 1972. *The Serengeti lion: a study of predator-prey relationships*. University of Chicago Press, Chicago.
- Simpson, G. G. 1930. Tertiary land mammals of Florida. *Bulletin of the American Museum of Natural History* 59:149–211.
- Sinclair, A. R. E. 1977. *The African Buffalo: a study of resource limitation of populations*. University of Chicago Press, Chicago.
- Straus, L. G. 1987. Upper Paleolithic ibex hunting in southwest Europe. *Journal of Archaeological Science* 14:163–178.
- Trivers, R. 1985. *Social evolution*. Benjamin/Cummings, San Francisco.
- Turnbull, W. D., and D. M. Martill. 1988. Taphonomy and preservation of a monospecific titanotheres assemblage from the Washakie formation (Late Eocene), Southern Wyoming: an ecological accident in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:91–108.
- Van Ballenberghe, V., and W. B. Ballard. 1997. Population dynamics. Pp. 223–245 in A. W. Franzmann, C. C. Schwartz, and R. E. McCabe, eds. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington, D.C.
- Van Strien, N. J. 1986. The Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814) in the Gunung Leuser National Park Sumatra, Indonesia. Paul Parey, Berlin.
- Voorhies, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *Contributions to Geology*, University of Wyoming, Special Paper 1:1–69.
- . 1985. A Miocene rhinoceros herd buried in volcanic ash. *Research Reports of the National Geographic Society* 19:671–688.
- Webb, S. D. 1977. A history of savanna vertebrates in the New World, Part I. North America. *Annual Review of Ecology and Systematics* 8:355–380.
- . 1983. The rise and fall of the late Miocene ungulate fauna in North America. Pp. 267–306 in M. Nitecki, ed. *Coevolution*. University of Chicago Press, Chicago.
- Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. *American Journal of Science* 281:513–544.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. Pp. 19–33 in J. J. Thomason, ed. *Functional morphology in vertebrate paleontology*. Cambridge University Press, New York.