Sexual Dimorphism and Mortality Bias in a Small Miocene North American Rhino, *Menoceras arikarense*: Insights into the Coevolution of Sexual Dimorphism and Sociality in Rhinos

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Abstract Rhinos are the only modern perissodactyls that possess cranial weapons similar to the horns, antlers and ossicones of modern ruminants. Yet, unlike ruminants, there is no clear relationship between sexual dimorphism and sociality. It is possible to extend the study of the coevolution of sociality and sexual dimorphism into extinct rhinos by examining the demographic patterns in large fossil assemblages. An assemblage of the North American early Miocene (~22 million years ago) rhino, *Menoceras arikarense*, from Agate Springs National Monument, Nebraska, exhibits dimorphism in incisor size and nasal bone size, but there is no detectible dimorphism in body size. The degree of dimorphism of the nasal horn is greater than the degree of sexual dimorphism of any living rhino and more like that of modern horned ruminants. The greater degree of sexual dimorphism in *Menoceras* horns may relate to its relatively small body size and suggests that the horn had a more sex-specific function. It could be hypothesized that *Menoceras* evolved a more gregarious type of sociality in which a fewer number of males were capable of monopolizing a larger number of females. Demographic patterns in the *Menoceras* assemblage indicate that males suffered from a localized risk of elevated mortality at an age equivalent to the years of early adulthood. This mortality pattern is typical of living rhinos and indicates that young males were susceptible to the aggressive behaviors of dominant individuals in areas conducive to fossilization (e.g., ponds, lakes, rivers). *Menoceras* mortality patterns do not suggest a type of sociality different from modern rhinos although a group forming type of sociality remains possible. Among both living and extinct rhinos, the severity of socially mediated mortality seems unrelated to the degree of sexual dimorphism. Thus, sexual dimorphism in rhinos is not consistent with traditional theories about the co-evolution of sexual dimorphism and sociality.

Keywords *Menoceras* · Mortality · Rhinoceros · Sexual dimorphism · Sociality · Taphonomy

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Introduction

Sexual dimorphism is widely regarded as an evolutionary consequence of intragender competition and/or mate choice among polygynous species that results in highly variable reproductive fitness among males, but more constant fitness among females (Janis 1982; Jarman 1983; Clutton-Brock et al. 1988; Andersson 1994; Berger and Cunningham 1994a; Plavcan 2001). Males commonly possess sex-specific traits such as larger size and/or conspicuous weapons (e.g., horns, tusks, and antlers), and they adopt behavioral strategies (e.g., territoriality) that allow a few males to monopolize many females (e.g. Clutton-Brock et al. 1988). In ruminant artiodactyls (e.g., bovids and cervids), a clade with hundreds of living species, there is a significant relationship between sociality and sexual dimorphism where monogamous species tend to be monomorphic and more gregarious species tend to exhibit conspicuous sexual dimorphism (Alexander et al. 1979; Janis 1982; Jarman 1983; Geist and Bayer 1988; Loison et al. 1999).

However, not all mammal clades show a strong relationship between sociality and sexual dimorphism. For instance, there is no apparent relationship between sociality and sexual dimorphism in the extant members of the Perissodactyla, a formerly diverse clade with a very low level of living diversity. Tapirs (Genus: *Tapirus*) are monomorphic and tend to be solitary (Nowak 1999). Horses and zebras (Genus: *Equus*) are more paradoxical; they are nearly monomorphic in body size although they are the most gregarious living perissodactyls (Berger 1986; Rubenstein 1986). A more recent comprehensive analysis of horse sociality concludes that wild and feral populations of *Equus* form 'bands,' stable associations of mares, their offspring, and one or more stallions who defend and maintain the mare group (Linklater 2000). Horses show moderate dimorphism in canine size (MacFadden 1992) but this secondary sex trait is inconspicuous in comparison to the cranial weapons of ruminants. Rhinoceroses are the only living perissodactyls that possess conspicuous cranial weapons, but unlike horned and antlered ruminants, they are not extremely dimorphic. *Rhinoceros unicornis* (Asian greater one-horned rhino) is dimorphic in incisor (lower second incisor, i2) size and moderately dimorphic in body size and horn size (Dinerstein 1991, 2003). *Diceros bicornis* (African black rhino) is reportedly monomorphic (or so minimally dimorphic that it is not readily detectable with available data) (Owen-Smith 1988; Berger 1994). Yet, its sister species, *Ceratotherium simum* (African white rhino) is clearly sexually dimorphic in body size and horn size (Owen-Smith 1988; Rachlow and Berger 1995). Despite some variability in the degree of sexual dimorphism, all living species are relatively asocial. *Ceratotherium* occasionally forms small ephemeral groups, while other species are less social (Laurie 1982; Owen-Smith 1975, 1988).

In contrast to the high present diversity of ruminant artiodactyls, perissodactyl diversity has greatly diminished over the past several million years. Rather than adhering to a ruminant adaptive paradigm, Berger (1988) and Linklater (2000) have suggested that phylogenetic history and phylogenetic constraints of taxonomically diminished clades such as the Perissodactyla are important considerations for understanding and explaining interspecific variation in spatial and social organization. Extinction itself is an aspect of evolutionary history that may complicate an explaination of sexual dimorphism and sociality in extant perissodactyls. The poor relationship of sexual dimorphism and sociality among extant perissodactyls could be the result of extinction bias, where typical species that conform to a more ruminant-like paradigm are mostly extinct, while the few survivors show patterns of sociality that are historically atypical. Indeed, sexual dimorphism has been identified in numerous extinct perissodactyls including early equids, tapiroids, rhinocerotoids, and other perissodactyl clades that are now extinct, such as the Chalicotheriidae and Brontotheriidae (Radinsky 1963, 1967; Brosuk-Bialynicka 1973; Coombs 1975; Gingerich 1981; Mead 2000; Mihlbachler et al. 2004; Mihlbachler 2005). The frequent occurrence of sexual dimorphism

among extinct perissodactyls suggests that a stronger correlation of sociality and sexual dimorphism might have once existed within this order.

While sexual dimorphism itself may be an evolutionary consequence of sociality, aspects of population demographics relate to sociality in a more proximate sense. Large bone assemblages have long been recognized as a means for studying the demographics of paleopopulations (Matthew 1924; Kurtén 1953, 1983; Van Valen 1964; Voorhies 1969; Clark 1970; Klein 1981; Hulbert 1982, 1984; McDonald 1996). A few have sought to establish links between assemblage demography and sociality (Berger 1983; Voorhies 1985; Barnosky 1985; Benefit 1994, 1999; Berger et al. 2001; Mihlbachler 2003). The demography of mortality is informative of paleosociality because social strategies can predictably regulate age- and sex-specific mortality rates (P. Jarman and M. V. Jarman 1973; Dittus 1975, 1977, 1979; Ralls et al. 1980). Essentially, males of polygynous species kill each other directly in combat, or indirectly through increased energetic demands during periods of intensified competition (e.g., rut) and/or forced emigration to suboptimal habitat. The severity of intragender competition is reflected by male mortality rates, which tend to exceed those of females in highly polygynous species, resulting in sex-skewed populations. Additionally, socially mediated mortality tends to be age specific, revealing life history stages where subdominant males are most vulnerable to the aggressive or socially exclusive behaviors of dominant males (P. Jarman and M. V. Jarman 1973; Dittus 1975, 1977, 1979; Ralls et al. 1980).

In some instances, data on the sex- and age-specific mortality rates of extinct species may contribute substantially to our understanding of social evolution. For instance, the three best-studied living rhino species, *C. simum*, *D. bicornis*, and *R. unicornis* (Owen-Smith 1988; Dinerstein 2003; Dinerstein and Price 1991; Berger 1994) are found to have some of the highest rates of behaviorally mediated mortality among mammals due to frequent incidences of male mortality resulting from horn and/or incisor (i2) inflicted wounds. Behaviorally mediated mortality has a strong influence on the population demography of modern rhino populations (Dinerstein 1991, 2003; Dinerstein and Price 1991; Berger and Cunningham 1994b; Mihlbachler 2003); however, all modern rhino populations are (or at some point in the recent past have been) highly endangered with diminished and anthropogenically disturbed populations due to poaching, loss of habitat, population bottlenecks, artificial population management, and in some cases phenotypic alteration (horn removal) (Berger 1994, Berger and Cunningham 1994a, b). Such disturbances may have had undocumented consequences on the social dynamics of these species (Berger and Cunningham 1994a), thus rendering it difficult to understand sociality as it might have manifested itself in more pristine conditions.

By using mortality profiles to estimate the intensity of intragender competition, it is possible to examine the coevolutionary relationship of sexual dimorphism and sociality within the Rhinocerotidae using a larger set of species than is currently available in the extant world. Mihlbachler (2003, 2005) examined sexual dimorphism and the mortality dynamics of two extinct rhinos, *Teleoceras* and *Aphelops*, from the late Miocene of Florida and was able to discern aspects of sociality from rhino populations that had not been subjected to anthropogenic disturbances. Among the most notable findings were that *Teleoceras* age- and sex-specific mortality patterns were very similar to those of modern African and Indian rhinos, where young males tend to suffer increased mortality rates due to intramale aggression. The similarity of *Teleoceras* mortality to that of modern rhino populations, with a decided spike in young male mortality, suggests that *Teleoceras* not only shared a highly polygynous form of sociality with modern rhinos, but that this social trait is possibly rooted deeply within the rhino family. On the other hand, *Aphelops* lacked any sign of elevated young male mortality and showed a mortality pattern more closely resembling large artiodactyls, suggesting that at least some rhinos had evolved social systems that were not like living rhinos.

To further examine the coevolutionary relationship of sexual dimorphism and sociality among fossil rhinos, age- and sex-specific mortality patterns and sexual dimorphism in the teeth, skulls, and skeletons are documented in an assemblage of rhinoceros, *Menoceras arikarense* (Fig. 1), from the early Miocene (~22 million years ago) Marsland Formation at Agate Springs National Monument, Nebraska. The *Menoceras* assemblage of Agate Springs is interpreted as a monospecific assemblage (Hunt 1990; Prothero 2005). *Menoceras* is much smaller than any living rhino with a reportedly sexually dimorphic nasal bone (Peterson 1906, 1920; Mead 1998). There are distinctly two 'morphotypes' among the many specimens from the Agate Springs locality. These differences do not appear to be species level differences; rather they are consistent with a generalized pattern of intraspecific sexual dimorphism that is commonly expressed among the numerous radiations of ungulates including living rhinos, and there is little doubt that the 'morphotypes' in the Agate Springs *Menoceras* assemblage represent males and females of a single species. Like the living Asian rhinos and many other species of extinct rhinos, there is clear dimorphism in the size of the tusk-like lower incisor. Additionally, the male skulls of *Menoceras* have a pair of thickened, rugose, rounded, bony knobs that are placed side by side on the distal end of the nasal bone, upon which a pair of laterally positioned horns were situated. The female skulls have much thinner and smoother nasal bones upon which the bony knobs are absent or greatly diminished.

Materials and methods

The collection of *Menoceras* fossil material used in this paper is housed in the vertebrate paleontology collection at the American Museum of Natural History (AMNH), New York. It was mostly collected between the years 1908 and 1920 and is one of several collections excavated in the early part of the twentieth century from a large accumulation of disarticulated bones at Agate Springs National Monument, Nebraska (Peterson 1906; Hunt 1990). The

Fig. 1 a Male (AMNH 22458) and **b** female (AMNH 27866) skulls of *Menoceras arikarense*. Scale bar=15 cm.

American Museum Agate Springs *Menoceras* collection consists of numerous skulls, lower jaws, and postcranial elements. In addition, there is a large partially excavated but essentially intact slab of bone bed on exhibit at the AMNH with at least 20 partially exposed *Menoceras* skulls and hundreds of other bones.

To examine sexual dimorphism, measurements were taken for 66 cranial, mandibular and postcranial variables (Tables 1, 2 and 3). Digital calipers were used for linear measurements. Bone circumference and longer dimensions (over 150 mm) were taken with a measuring tape accurate to a millimeter. Because of the disarticulated nature of the fossil assemblage, sex could not be determined a priori for most of the individual bones. Therefore, it was necessary to look for patterns in the sex combined data either relating to the overall amount of variation or the shapes of the distribution curves that would suggest sexual dimorphism. Mihlbachler (2005) found that sex-combined summary statistics, necessitated by the sex-indeterminate nature of most bones from disarticulated fossil assemblages, were capable of pinpointing strong sexual dimorphism but that they are less successful at locating weak levels of sexual dimorphism. Bearing these limitations in mind, patterns in the data possibly indicating sexual dimorphism were sought out using three statistical metrics. (1) Coefficients of variation for most non-dimorphic traits of mammalian species tend not to greatly exceed a value of ten (e.g., Carrasco 1998; Colbert 2006). On the other hand, sexually dimorphic variables, such as ossicone length in giraffes, tend to yield coefficients of variation that greatly exceed a value of ten (Mihlbachler et al. 2004). (2) Sexually dimorphic characters often have a detectable bimodal distribution. A Shapiro Wilk test for univariate normality was used to locate data that deviated from the

Table 1 Sex specific and sex-combined statistics for skull variables

Variable	Male mean	Female mean	Total mean	SD	Min.	Max.	N	CV	Skew	Kurt	b	P < W
P2–M3	151.2	156.0	153.3	6.6	140	164	29	4.3	−0.06	−0.85	0.47	0.31
P1–P4	77.8	79.6	78.5	3.6	70.2	86.5	24	4.6	0.17	0.62	0.28	0.83
M1–M3	91.0	91.5	91.5	3.8	84.2	97.7	29	4.2	−0.31	−0.99	0.55	0.24
M3–FM	150.7	145.2	147.0	9.2	126.5	162	22	6.2	−0.53	−0.31	0.48	0.55
P2–FM	287.6	293.5	290.9	12.2	264	313	22	4.2	−0.31	0.30	0.33	0.45
OB	128.7	117.9	121.2	12.8	89.5	150.2	29	10.5	−0.24	1.16	0.25	0.32
NC–FM	114.0	111.6	113.5	8.4	99.5	127.0	20	7.4	−0.10	−1.06	0.52	0.54
OW	130.4	116.5	124.1	9.8	104.8	139.9	20	7.9	−0.27	−0.83	0.49	0.60
SL	337.8	331.1	334	16.1	290	358	28	4.8	−1.01	0.73	0.54	0.05
N–NI	82.8	82.7	82.8	11.5	67.0	113.0	25	13.8	1.42	2.26	0.57	0.00
ZW	223.1	183.5	199.9	26.5	155.3	246	27	12.3	−0.07	−1.05	0.52	0.23
NW	75.4	44.3	60.8	17.0	34.3	94.2	34	28.1	0.12	−1.44	0.65	0.01
N–P2	123.4	94.0	108	17.4	72.7	135.9	21	16.1	−0.22	−0.88	0.49	0.47
NT	63.5	19.6	43.5	22.3	15.7	73.8	29	51.3	−0.16	−1.96	0.99	0.00

SD (standard deviation), *Min.* minimum, *Max.* Maximum, *N* number of observations, *CV* coefficient of variation, *Skew* skewness, *Kurt* kurtosis, *b* coefficient of bimodality, *P< W* probability value of Shapiro Wilk test of univariate normality, *P2–M3* second premolar to third molar length, *P1-P4* first premolar to fourth premolar length, *M1–M3* first to third molar length, *M3-FM* third molar to foramen magnum length, *P2–FM* second premolar to foramen magnum length, *OB* width of skull at postorbital processes, *NC–FM* length from nuchal crest to foramen magnum, *OW* maximum width of occipital, *SL* skull length, *N–NI* length from anterior tip of nasal to the nasal incision, *ZW* maximum width of zygomatic arches, *NW* maximum nasal width, *N–P2* length from anterior tip of nasal to P2, *NT* maximum thickness of nasal.

Table 2 Sex specific and sex-combined statistics for skull variables

Variable	Male mean	Female mean	Total mean	S.D.	Min.	Max.	N	CV	Skew	Kurt	b	P < W
i2 CW	19.1	15.0	17.2	2.5	10.1	20.6	26	14.4	−0.90	1.08	0.44	0.05
i2 RD	15.7	12.5	14.1	1.8	11.7	17.3	26	12.8	0.27	−1.46	0.70	0.02
i2 CL	33.6	18.9	26.6	11.0	10.5	46.7	25	41.6	0.53	−1.13	0.68	0.02
i2 RL	65.1	44.4	53.6	13.4	40.0	78.7	9	25.0	0.92	−0.27	0.68	0.13
p2–m3	153.0	155.2	154.3	5.0	144.0	165.0	19	3.3	0.18	0.24	0.32	0.96
p2–p4	63.6	63.9	63.8	2.2	59.9	69.4	19	3.5	0.33	1.22	0.26	0.47
m1–m3	89.3	91.1	90.3	3.0	83.6	95.9	21	3.3	−0.32	0.27	0.33	0.90
JD@m1	51.8	51.6	51.7	3.6	46.0	60.5	21	7.0	0.91	0.49	0.52	0.14
JL	315.8	311.7	313.6	7.1	303.0	325.0	13	2.3	−0.31	−1.22	0.62	0.36
m3–MA	113.7	110.1	111.8	7.7	102.4	127.7	13	6.9	0.61	−0.50	0.55	0.28
CH	151.7	147.8	149.6	4.4	138.9	155.0	11	3.0	−0.75	1.23	0.37	0.15
LS	71.1	69.7	70.2	5.1	62.6	79.5	11	7.3	0.25	−0.64	0.45	0.88
SW	46.5	38.5	42.3	5.8	34.9	53.0	17	13.6	0.29	−1.13	0.58	0.27
JD@m3	58.3	58.2	58.2	3.6	53.0	65.8	16	6.3	0.68	−0.03	0.49	0.51

Abbreviations for statistical results are as in Table 1. Abbreviations for osteological variables: *i2CW* transverse width of i2 crown, *i2RD* i2 root diameter, *i2CL* i2 crown length, *i2RL* i2 root length, *p2–m3* second premolar to third molar length, *p2–p4* second premolar to fourth premolar length, *m1–m3* first to third molar length, *JD@m1* depth of jaw below m1, *JL* jaw length, *m3–MA* length from third molar to posterior border of jaw, *CH* length from mandibular condyle to ventral border of ramus, *LS* length of mandibular symphysis, *SW* transverse width of jaw at the symphysis, *JD@m3* jaw depth below m3.

normal distribution curve, possibly relating to bimodalism. The appropriate alpha level for this test is $P<0.1$ (Sall and Lehman 1996). (3) Thirdly, a coefficient of bimodality (b) was calculated as:

$$b = \frac{m_3^2 + 1}{m_4 + 3}$$

where m_3 is skewness and m_4 is kurtosis (Bryant 1991). Values of $b>0.55$ may indicate a bimodal or polymodal distribution (SAS Institute Inc. 1985). However, the nasal bones and lower incisors of *Menoceras* were found to be highly dimorphic with non-overlapping size categories, presumably corresponding to sex. This facilitated a more direct comparison of male and female means for jaw and skull variables via a series of t-tests.

To estimate the age of death of the fossil skulls and jaws, dental wear stages in the modern black rhino (*D. bicornis)* from Hitchins (1978) were used to estimate the ages of 119 jaws and 60 skulls of *Menoceras* following methods that are detailed more fully by Mihlbachler (2003). The lifespan of *Menoceras* is likely to have been shorter than the 30–40 year lifespan of modern rhinos (Owen-Smith 1988) due to its much smaller body size. However, the dental morphology, dental wear patterns, and dental eruption sequence are similar, suggesting that dental eruption and wear rates are nearly equivalent in terms of relative lifespan. The age estimates were normalized by converting years into percentage of potential lifespan (% PL). The maximum potential lifespan (100% PL) was based on the dental wear stage of the oldest individual of *Diceros* (37 years) in Hitchins' (1978) study. Hitchins' (1978) dental wear stages and their approximate meanings in terms of % PL are given in Table 4, along with the life table calculations.

Composite life tables were built from both skulls and jaws (Table 4) using the raw data (OB = number of observations) to first calculate the dx column following the method of Voorhies (1969). Sex was indeterminate in many skulls and jaws because the strongly sexually dimorphic portions (nasal bones and incisors) were not preserved in every specimen. Therefore, it was necessary to construct a sex-combined life table rather than sex-specific life tables. The calculation of mortality rate (qx column) for a standard life table requires that the age intervals (which are based on the dental wear stages) represent equivalent lengths of time (such as a year). However, this was not the case for the *Menoceras* data (nor for the modern rhino data for which the *Menoceras* age estimates are based on). Therefore, one adjustment of the qx column was made:

$$\frac{1,000 \mathrm{d}x}{i(lx)} = qx$$

In this equation, i is an additional variable that represents the duration of the age interval in terms of % PL. This alteration compensates for the unequal age units, so that qx represents deaths out of 1,000 individuals per percentage point of potential lifespan (Mihlbachler 2003). The mortality rate values are now directly comparable between age groups as they would be in a life table where the age intervals are equal time units such as years.

Results

Sexual dimorphism

The distribution of the coefficients of bimodality (b) for the 66 metric variables of *Menoceras* skulls, jaws, and postcrania is seen in Fig. 2. The vast majority of variables yields values of b less than 0.55 and does not appear to be bimodal. Only a small number of variables yielded coefficients of bimodality greater than 0.55, suggesting that some aspects of the skeleton of *Menoceras* are bimodal, but that most are not. Those variables with the highest b values are almost all from the skull and mandible.

A closer look at the skull data (Table 1) reveals which skull variables are sexually dimorphic. Five skull variables showed relatively high coefficients of variation: N–NI, ZW, NW, N–P2, and NT (CV=12.3–51.2) (Table 1). Four skull variables, SL, N–NI, NW, and NT deviate significantly from normality ($P<0.1$). These same four variables and an additional variable, M1–M3, also yield coefficients of bimodality (b) approaching 0.55 or higher. According to their skewness values, two of these variables, N–NI and SL, may deviate from normality because the data are skewed (due to outliers) rather than being clearly bimodal. The above statistics pinpoint the nasal bone as the most sexually dimorphic part of the skulls, with molar row length and zygomatic width also showing possible signs of sexual dimorphism.

Bivariate plots of male and female cranial dimensions are shown in Fig. 3a,b. Plotting NT and NW, the two most significantly bimodal cranial variables, results in two widely separate size clusters. Using these data to assign sexes to the skulls, t-tests comparing male and female means confirmed that six of the cranial variables, orbital breadth (OB; $P=0.02$), occipital width (OW: $P=0.01$), zygomatic width (ZW: $P=0.001$), nasal width (NW: $P=0.01$), nasal-P2 distance (N-P2: $P=0.01$) and nasal thickness (NT: $P=0.01$), were significantly larger in males. To summarize, males are clearly larger in the nasal region and in skull width, but were more similar to females in dental and skull length variables. One interesting result suggested by the t-tests was that females seem to have marginally longer premolar row lengths (P1–P4: $P=0.05$)

Table 3 Sex-combined statistics for postcranial variables

Variable	Mean	SD	Min.	Max.	N	CV	Skew	Kurt	b	P < W
H L	243.9	6.5	231	256	24	2.7	−0.08	−0.35	0.38	0.83
H MC	110.6	3.5	117	102	27	3.2	−0.46	0.33	0.36	0.47
H PW	51.7	2.2	47.9	55.0	24	4.2	−0.15	−1.03	0.52	0.36
H PD	73.3	2.6	68.5	78.0	16	3.5	−0.11	−1.26	0.37	0.96
H DW	72.6	2.1	68.3	76.8	30	2.9	0.11	−0.65	0.43	0.66
H DD	62.6	1.8	59.0	65.2	25	2.8	−0.40	−0.42	0.45	0.39
R L	252.9	6.8	241	270	40	2.7	0.23	−0.07	0.36	0.51
R MC	85.2	3.1	78.0	91.0	43	3.7	−0.20	−0.59	0.43	0.31
R PW	51.3	1.8	47.6	56.5	44	3.6	0.55	0.61	0.36	0.49
R PD	35.2	2.1	29.8	40.5	45	5.9	−0.35	0.74	0.30	0.66
R DW	53.6	2.0	48.8	57.6	41	3.6	−0.45	−0.14	0.42	0.58
R DD	34.9	5.3	30.3	38.4	41	5.3	−0.35	0.08	0.36	0.61
MC3 L	135.6	4.8	127.3	145	25	3.5	0.19	−0.34	0.39	0.55
MC3 PW	29.9	1.7	26.2	32.2	26	5.5	−0.64	−0.45	0.55	0.11
MC3 PD	24.5	1.4	21.1	27	25	5.6	−0.29	0.48	0.31	0.76
MC3 MW	25.8	1.4	22.9	28.7	23	5.3	−0.29	0.41	0.32	0.69
MC3 MD	11.9	0.7	10.4	12.9	24	5.6	−0.037	−0.34	0.43	0.60
MC3 DW	27.3	1.2	25.1	29.5	25	4.2	0.19	−0.66	0.44	0.56
MC3 DD	22.5	0.8	20.8	23.8	24	3.4	−0.22	−0.25	0.38	0.88
F L	327.1	11.0	308	353	26	3.4	0.49	0.19	0.39	0.53
F MC	111.5	5.2	100	120	33	4.7	−0.23	−0.58	0.44	0.47

F PW	100.9	4.4	90.9	108.5	25	4.4	−0.44	−0.31	0.44	0.58
F PD	45.6	1.9	41.3	49.0	29	4.1	−0.20	−0.42	0.40	0.81
F DW	74.9	3.0	69.4	82.4	28	4.0	0.06	0.40	0.30	0.57
F DD	98.4	4.4	86.6	104.6	25	4.5	−1.39	1.62	0.63	0.00
T L	290.1	10.9	273	319	38	3.8	0.40	−0.09	0.40	0.27
T MC	94.5	4.5	87	105	41	4.8	0.24	−0.14	0.37	0.19
T PW	74.0	2.7	66.9	79.5	32	3.7	−0.42	0.26	0.36	0.90
T PD	72.3	3.6	64.4	81.1	31	5.0	−0.16	0.39	0.30	0.76
T DW	51.4	2.3	470	56.0	36	4.4	0.02	−0.81	0.46	0.58
T DD	42.4	2.1	38.5	47.3	38	4.9	−0.08	−0.23	0.36	0.46
MT3 L	128.3	4.1	121.1	139.7	38	3.2	0.78	0.67	0.44	0.15
MT3 PW	27.8	1.2	24.4	30.7	38	4.3	−0.29	0.99	0.27	0.89
MT3 PD	25.7	1.4	22.8	27.9	31	5.6	−0.32	−1.02	0.56	0.18
MT3 MW	22.9	1.2	20.3	26.5	37	5.1	0.28	1.87	0.22	0.39
MT3 MD	14.5	0.8	13.0	15.8	37	5.2	−0.14	−0.83	0.47	0.29
MT3 DW	25.8	1.1	22.5	28.16	37	4.3	−0.31	1.06	0.27	0.64
MT3 DD	22.6	0.8	21.1	24.4	35	3.7	0.42	−0.36	0.45	0.35

Abbreviations for summary statistics are as in Table 1. Abbreviations for osteological variables: *HL* humerus length from proximal to distal articular surfaces, *HMC* humerus minimum circumference, *HPW* width of humerus at proximal articular surface, *HPD* humerus proximal depth, *HDW* humerus distal width, *HDD* humerus distal depth, *RL* radius length, *RMC* radius minimum circumference, *RPW* radius proximal width, *RPD* radius proximal depth, *RDW* radius distal width, *RDD* radius distal depth, *MC3L* third metacarpal length, *MC3PW* third metacarpal proximal width, *MC3PD* third metacarpal proximal depth, *MC3MW* third metacarpal midshaft width, *MC3MD* third metacarpal midshaft depth, *MC3DW* third metacarpal distal width, *MCD3DD* third metacarpal distal depth, *FL* femur length, *FMC* femur minimum circumference, *FPW* femur proximal width, *FPD* depth of femoral head, *FDW* femur distal width, *FDD* femur distal depth, *TL* tibia length, *TMC* tibia minimum circumference, *TPW* tibia proximal width, *TPD* tibia proximal depth, *TDW* tibia distal width, *TDD* tibia distal depth, *MT3L* third metacarpal length, *MT3PW* third metacarpal proximal width, *MT3PD* third metacarpal proximal depth, *MT3MW* third metacarpal midshaft width, *MT3MD* third metacarpal midshaft depth, *MT3DW* third metacarpal distal width, *MT3DD* third metacarpal distal depth.

Table 4 Life tables for *Menoceras arikarense* calculated from skulls and jaws

Wear stage[a]	% PL	OB[b]	lx	dx	qx	ex	OB	lx	dx	qx	ex
		skulls	skulls	skulls	skulls	skulls	jaws	jaws	jaws	jaws	jaws
0–III	0–7	0					0				
IV	7–9	4	1,000	67	33	38	5	1,000	74	37	44
V	9–12	1	933	17	6	40	6	926	88	32	46
VI	12–15	4	916	67	24	41	1	838	15	6	50
VII–VIII	15–19	10	850	167	49	43	3	823	44	13	51
IX	19–25	3	683	50	13	49	6	779	88	21	53
X–XII	25–35	19	633	317	48	51	15	691	220	30	57
XIII	35–52	5	317	83	16	73	8	470	118	15	69
XIV	52–61	2	233	33	16	84	4	352	59	19	78
XV	61–86	3	200	50	10	88	11	294	162	22	83
XVI	86–96	6	150	100	67	93	5	132	74	56	94
XVII	96–100	3	50	50	250	98	3	59	59	250	98

[a] Hitchins (1978).

[b] OB—maximum number of observations in each age group.

than males. However, male and female molar row lengths did not differ significantly, despite the fact that the *b* statistic suggested some potential bimodalism in this character. There is weak evidence, at best, that the cheektooth dentitions are sexually dimorphic.

Five jaw variables, four of which relate to the lower incisor (i2CW, i2RD, i2CL, i2RL, and SW), yielded high coefficients of variation (CV>10) (Table 2). The univariate normality test and *b* statistic also indicate that bimodality in the mandible is concentrated in the lower incisor.
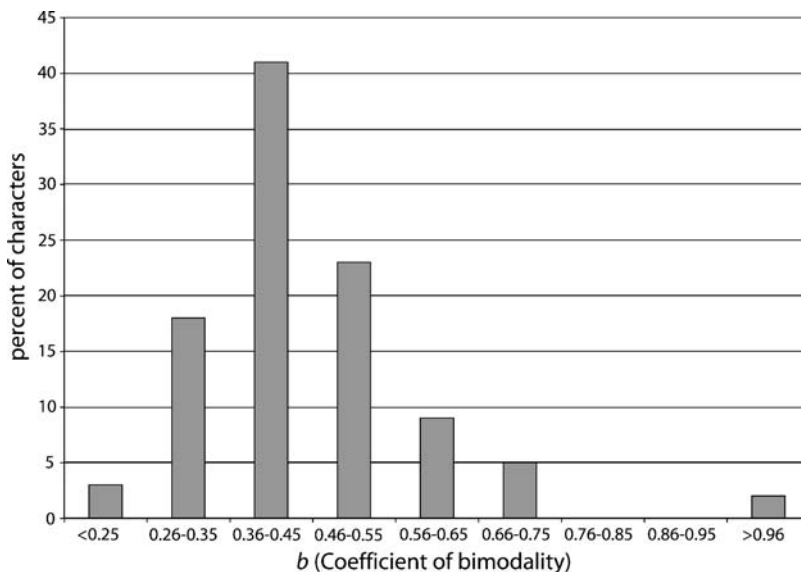
Fig. 2 Histogram depicting the distribution of the coefficients of bimodality (*b*) for cranial, mandibular, and postcranial metric variables of *Menoceras arikarense*.

However, only three variables, all of the lower incisor, deviated significantly from a normal distribution, including i2CW, i2RD, i2CL ($P<0.1$). Three of the lower incisor variables, i2RD, i2CL, and i2RL yielded high bimodality coefficients (b). Other variables, JL, m3-MA, and SW, also produced b values greater than 0.55. Bivariate plots of male and female jaw dimensions are shown in Fig. 3c,d. Plotting CL versus CW of the i2 results in two widely separate size clusters, demonstrating that sex can be determined from this element. Male/female ratios of i2 dimensions found in late Miocene rhinos range from 1.6 to 2.7 in *Teleoceras* and 1.6–2.5 in *Aphelops* (Mihlbachler 2005). Male/female i2 ratios in *Menoceras* (i2CW=1.27, i2RD=1.26, i2CL=1.78, i2RL=1.47) are mostly smaller, indicating that *Menoceras* i2s were somewhat less dimorphic, but nonetheless the i2s form two non-overlapping size categories from which sex can be determined. Using t-tests to compare male and female means in the sex-determinate jaws (those with preserved i2s), males were significantly larger than females in symphysis width (SW) ($P=0.00$) and in all i2 dimensions (*t*-test: $P=0.00$ for i2CW, i2RD and i2CL; $P=0.03$ for i2RL). T-tests did not reveal significant differences between males and females for JL and m3-MA, despite the fact that the b statistic suggests possible bimodalism in these characters.

While the sex-combined statistics pinpointed strongly sexually dimorphic areas in the skulls and jaws, there is no strong evidence for body size dimorphism in the postcrania of *Menoceras* (Table 3). Coefficients of variation are all rather low (CV<10). Three variables produced coefficients of bimodality (b) greater than 0.55, including MC3PW, FDD, and MT3PD. It is possible that any of these three variables are weakly bimodal, although all three of these variables have relatively high skewness values, suggesting that outliers may be contributing to the result rather than strong bimodalism. Only one of these variables, FDD, deviated
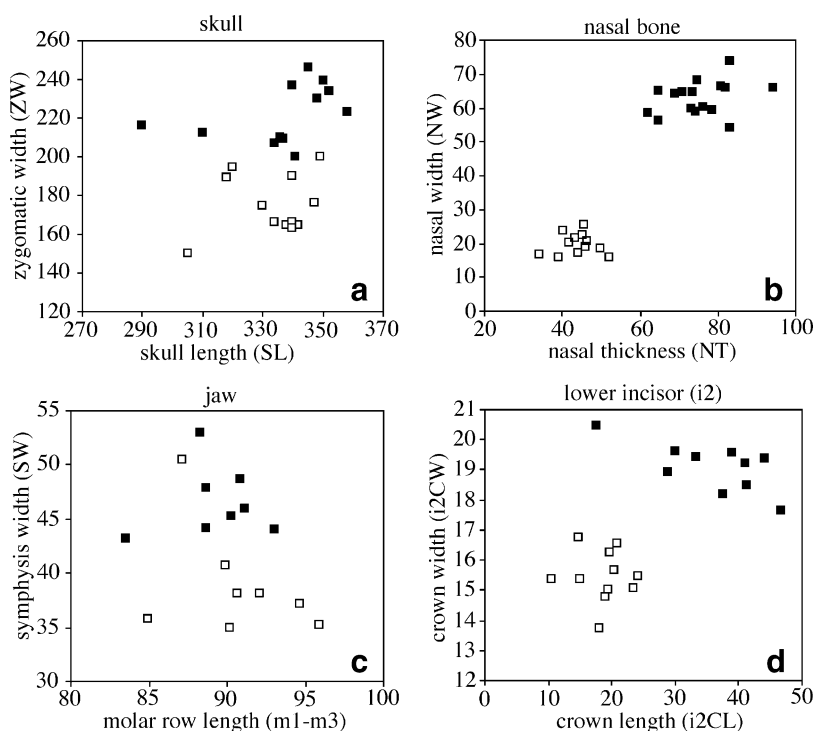

Fig. 3 Bivariate plots of dimorphic cranial dimensions of *Menoceras arikarense*. Solid squares are those interpreted to be males based on non-overlapping size distributions of nasal bones in skulls and the i2 in jaws.

significantly from a normal distribution. This one significant result falls easily within the 10% type 1 error rate expected considering the alpha-level of the test and therefore should be rejected. While weak sexual dimorphism in the postcranial skeleton of *Menoceras* is certainly possible, it is not strong enough to be detected by these sex-combined methods.

Mortality patterns

The age distributions of the skulls and jaws are shown in Fig. 4. No significant differences in the age distributions of the skulls, left jaws, and right jaws were found (Pearson Chi Squared: $P=0.20$). Nonetheless, there are minor discrepancies in the age distributions of the skulls and jaws between 9–19% PL and between 61–86% PL. Regardless of any minor discrepancies, the skulls and jaws agree that the largest number of individuals died between 25–35% PL.

Among the 41 sex determinate skulls (those with preserved nasal bones), males made up 54% ($N=22$) of the adult portion of the sample (19–100% PL). Out of 31 jaws and isolated i2s, males made up 58% ($N=18%$) of the adults. Neither of these sex ratios differs significantly from parity (50% male) (Pearson Chi-Squared: $P=0.64$ for skulls; $P=0.37$ for i2s). Unfortunately, most early fossil collecting expeditions were not explicit about their collecting methods, nor were they interested in demographic aspects of assemblages. The field notes on the collection of the Agate Springs material between 1908 and 1920 gives no clear indication of selectivity in the collecting methods (Albert Thomson, field notes in the vertebrate paleontology archives at the American Museum of Natural History). It is possible that male skulls were preferentially collected. Additionally, the original museum collection was diminished over the years through trades with other museums and it is possible that female
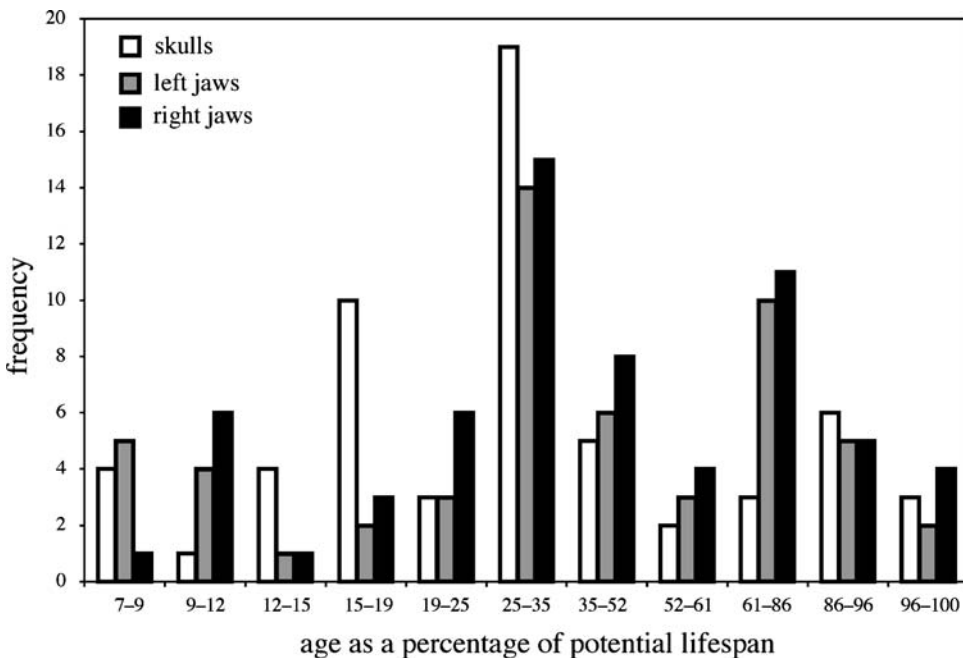
Fig. 4 Frequency distribution of skulls and jaws of *Menoceras* based on dental wear stages of *Diceros bicornis* (black rhino) from Hitchins (1978).
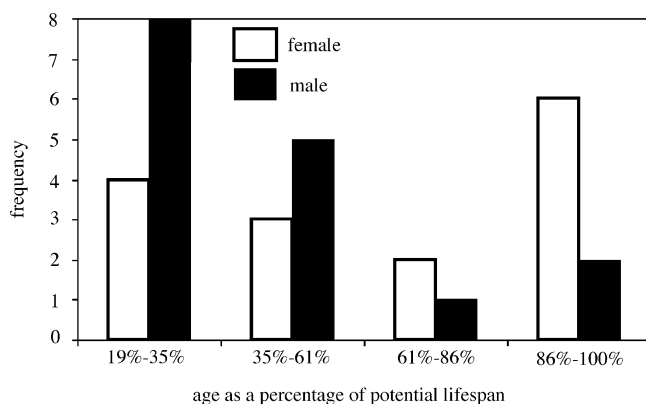
Fig. 5 Sex specific age distribution of *Menoceras arikarense* skulls.

skulls were preferentially removed from the museum collection. Therefore the sex ratio of the collection is suspect. However, these above statistics include only the fully excavated skulls and jaws. In the intact slab of Agate Springs bone bed on exhibit at the AMNH, sex could be identified in 16 partially exposed skulls. Four (25%) of these are male. Lumping all skulls together yields a male/female ratio of 26/31 (46% male), and still does not differ statistically from parity (Pearson-chi squared $P=0.51$). However, the 25% male sex ratio of the 16 skulls in the intact slab does deviate significantly from parity (Pearson Chi-Squared: $P=0.05$). Thus, there seems to be a significant female bias in the intact slab, suggesting that there may have been a female bias in the original assemblage.

While it is possible that a collecting (or specimen trading) bias has effected the overall sex ratio of the sample, other demographic patterns can be found in the sample that were more than likely not to have been effected. Males are most frequently the youngest adults (19–35% PL) (Fig. 5). In contrast, females are most frequently the oldest adults (89–100% PL). The distribution of males and females among young adults (19–61% PL) and old adults (61–100% PL) differs significantly (Pearson Chi-squared: $P=0.044$). Although the sex ratio of the total sample may have been altered due to a collecting bias against females, it is almost inconceivable that there would have been a systematic collecting bias in which young males were preferentially collected over old males, but old females were preferentially collected over young females. Therefore, the differences in the age distributions of males in comparison to females is very likely a genuine reflection of the original assemblage demography regardless of the fact that the actual sex-ratio has been altered by biased collecting or even museum trading.

Discussion

Although a member of the Rhinocerotidae, *Menoceras* is outside of the clade of modern rhinos (Prothero et al. 1986; Cerdeño 1995; Antoine 2002) and is therefore phylogenetically bracketed by modern rhinos and their closest relatives, tapirs. The known behaviors of those species that form the phylogenetic bracket of *Menoceras* are polygynous but do not include large herd-like groups. Social behaviors are plastic in some species and can shift with ecological conditions. Intraspecific behavioral shifts have been reported among ruminant artiodactyl species in association with variation in ecological conditions (Byers and Kitchen 1988; Putman 1996; Hirth 2000). In contrast, horses are reportedly uniform in spatial and

social organization throughout the world within a variety of environmental and demographic contexts (Linklater 2000). The robusticity of horse sociality despite a wide variety of environmental conditions suggests that phylogentic history (Berger 1988) and related biological constraints such as digestive physiology (Janis 1982) are more important factors in determining the sociality of horses and possibly other perissodactyls. Other perissodactyl groups are too poorly studied, cryptic, rare, or geographically confined to derive conclusions about the impact of shifting ecological conditions on social organization. Given what is known about modern perissodactyl sociality, a polygynous but non-herding type of sociality is an appropriate null hypothesis for *Menoceras* or other fossil rhinos, even though behaviors inconsistent with the extant phylogenetic bracket cannot be completely ruled out. It is worth noting that phylogenetic results indicate that the paired horns of *Menoceras* were evolved independently from the horns of living rhinos (Prothero et al. 1986; Cerdeño 1995; Antoine 2002; Prothero 2005). Therefore, some aspects of sociality that may have influenced the evolution of sexually dimorphic *Menoceras* horns, via some form of sexual selection, could have evolved independently from modern rhinos.

It has been suggested from its abundance at Agate Springs that *Menoceras* lived in large herds with unbalanced numbers of males and females (Prothero 1998); however, social groups can only be inferred from catastrophic (instantaneous death) assemblages, which can be thought of as a "snapshot" of the localized population at one moment in time. Most fossils accumulate attritionally. Attritional assemblages cannot be used to directly infer social groups because they accumulated over time and therefore represent a cumulative record of localized mortality events rather than a snapshot of a local aggregation of individuals. Sex and age biases in attritional assemblages indicate differential localized mortality rates within a population over time (Mihlbachler 2003). Sedimentological and taphonomic data suggest that the Agate Springs bone bed represents a drought induced death event that occurred over a period of several months near an ephemeral body of water (Hunt 1990). Though modern rhinos are solitary, or only form small ephemeral social groups, they are water-dependant (Owen-Smith 1988) and rhino mortality tends to be concentrated near water (Hitchins and Anderson 1983; Dinerstein and Price 1991; Cunningham and Berger 1997). The Agate Springs rhino assemblage can be explained as an accumulation of water-dependent animals dying in the proximity of a limited water source during a time of severe drought. Herd behavior remains possible, but the assemblage itself does not indicate herd-behavior.

Sexual dimorphism and sociality

Rhinos possess up to two functional sets of craniomandibular weapons, a keratinous horn and a sexually dimorphic i2 that hones on a chisel-like upper incisor (I1). The strongly dimorphic i2 of *Menoceras* resembles most other rhinos, except modern African rhinos whose incisors are lost. The nasal horns of living rhinos are monomorphic or only moderately dimorphic (Berger 1994; Dinerstein 1991; Rachlow and Berger 1995). On the other hand, the clearly dimorphic nasal bones of *Menoceras* suggest more extreme horn dimorphism, more closely resembling that of ruminants where females sometimes lack horns (or antlers) altogether. Likewise, *Menoceras* females appear to have either lacked a horn or had a greatly diminished horn. The more extreme horn dimorphism of *Menoceras* in comparison to modern rhinos suggests that the horns may have served a more sex-specific function similar to that of ruminants where intrasexual aggression is thought to select for horns in males but horns are less obviously adaptive for females (Jarman 1983, 2000; Kiltie 1985). In ruminants, female horns occur frequently among larger species and are less common among smaller species (Packard 1983; Jarman 2000). *Menoceras* is much smaller than modern rhinos and has been described as

sheep-sized. Its skeletal proportions indicate a body mass well below the 1,000 kg threshold for megaherbivores (*sensu* Owen-Smith 1988).

The absence of extreme horn dimorphism in modern rhinos may indicate that both males and females selectively benefit from horn use. Among Asian rhinos, such as *Rhinoceros*, the size of the i2 is most strongly related to male dominance and the horn is secondary (Dinerstein 1991, 2003). Laurie (1982) suggested the *R. unicornis* females use horns to defend calves from predators, indicating that horns may have greater selective benefits for females. In *Diceros*, the horns are critical for establishing dominance hierarchies in both sexes (Berger 1994; Berger and Cunningham 1998). Moreover, comparisons of artificially de-horned *Diceros* populations with those that have not been dehorned indicate that de-horned females are less capable of defending calves from predators (hyenas and lions) than unaltered rhinos (Berger and Cunningham 1994b), again suggesting that horns are beneficial to females. Due to its smaller size, *Menoceras* females were of a far less appropriate body size to defend calves from large predators regardless of the presence or absence of horns, and predation by large carnivores might have been a more significant threat to *Menoceras* adults. Therefore, females might not have selectively benefited from horn use and may have adopted other unknown behaviors for predator avoidance. This may explain the greater degree of horn dimorphism in *Menoceras*. Large carnivorans contemporaneous with *Menoceras* include canids (e.g., *Osbornodon*) and amphicyonids (e.g., *Daphoenodon*). Additionally, a very large omnivorous enteledont suiform artiodactyl, *Dinohyus*, co-occurs with *Menoceras* at Agate Springs (Hunt 1990).

Taphonomic versus socially mediated assemblage biases

Generally, juveniles are underrepresented in surface collections of skeletons and/or fossil assemblages due to the more fragile nature of their bones (Lyman 1994). At Agate Springs juveniles between 0 and 7% PL are absent, but juveniles between 7 and 19% PL are as well represented as they are in other attritional fossil rhino assemblages (Mihlbachler 2003) and surface collections of modern rhino bones (Goddard 1970; Hitchins 1978). Juvenile skulls are potentially more fragile than jaws; however, the numbers of skulls and jaws present in the 7–19% PL intervals are similar. Given the extraordinary numbers of fossil specimens and the excellent preservation at Agate Springs, it is difficult to completely dismiss the absence of individuals within the 0–7% PL interval as a taphonomic artifact. It is possible that the collectors simply did not bother to collect neonates. At any rate, the absence of neonates in the assemblage does not necessarily indicate that localized neonate mortality did not occur.

To understand the significance of the possible age- and sex-biases among adults, it is helpful to review how demographic biases in localized rhino mortality might reflect aspects of sociality. Observations of rhino behavior and mortality suggest that localized rhino mortality in areas conducive to fossilization (water) is likely to be sex-biased and that the age profiles of males and females may differ. Fighting appears to be the most significant cause of socially mediated deaths in rhinos (Owen-Smith 1988, Dinerstein and Price 1991; Berger 1994; Dinerstein 2003). *Rhinoceros* males are among the most aggressive of ungulates. Intervals of social dominance for males tend to be very short in areas of female abundance. The disproportionate number of mortalities among adult males strongly suggests that competition for mates is the most important contributor to deaths of males. Population density tends to be highest around water and other prime resources. In general rhinos do not form permanent social groups with strong social bonds among adults. Nonetheless, some species are known to concentrate around wallows and *Rhinoceros* males most frequently attack subdominant males that intrude on congregations in wallows or in feeding areas (Laurie 1982; Dinerstein 1991, 2003; Dinerstein and Price 1991).

If fossil rhinos behaved similar to modern ones, males would essentially be at greatest risk from the aggression of dominant individuals in areas conducive to fossil preservation (water), particularly in situations where water is scarce. Therefore, attritional (long term) accumulations of localized rhino deaths in fossil deposits are likely to contain a superabundance of young males (Fig. 6). On the other hand, females are predicted to follow a more standardized attritional profile in which mortality more frequently occurs among old adults (Lyman 1994). Conversely, the opposite pattern is expected in an idealized catastrophic assemblage where instantaneous localized deaths directly reflect the structure of a standing population. In a catastrophic scenario, young females would outnumber old females if the population were stable (Fig. 6). It is also probable that young males would be underrepresented in a catastrophic fossil deposit due to intrinsic sex-biases in the localized population. For instance, in a *Rhinoceros* population, young adult males are less abundant than young adult females due to the elevated male mortality rate (Dinerstein and Price 1991). Likewise, *Ceratotherium* populations tend to be intrinsically female-biased despite a higher rate of male births (Owen-Smith 1988). Additionally, dominant *Rhinoceros* males do not share wallows with subdominant males (Dinerstein 2003). A similar pattern was reported for *Ceratotherium* where males are least abundant in localized populations occurring in areas of prime resources (Owen-Smith 1975). Accordingly, in addition to the possibility of intrinsically female-biased adult populations, subdominant males tend to avoid prime resource areas such as water, due to a localized mortality risk from the aggressive attacks of dominant individuals. Therefore, at any instant young males might be the most underrepresented demographic group in areas conducive to fossil preservation, although over a longer period they may die there more frequently.

Demographically biased assemblages are best documented for the late Miocene rhino, *Teleoceras* (Voorhies 1985; Mead 2000; Mihlbachler 2003). Sex biases in catastrophic and attritional assemblages of *Teleoceras* correspond closely to expectations (Fig. 6) predicted from observed behaviors of modern rhinos. A large group of *Teleoceras* from Ashfall beds of Antelope County, Nebraska that was subjected to a catastrophic burial by volcanic ash in a
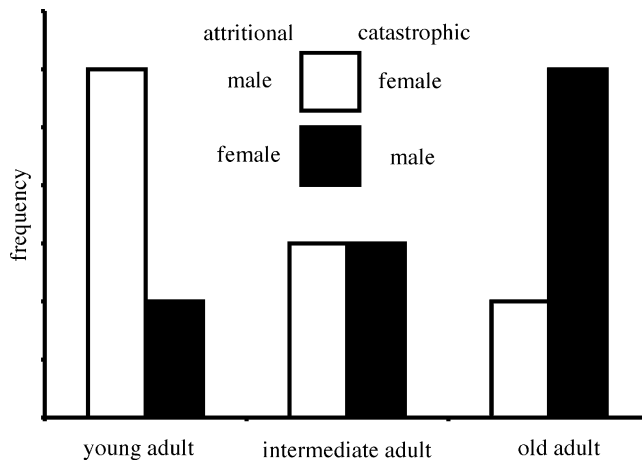
Fig. 6 The expected sex-specific age distributions of adults in idealized attritional and catastrophic assemblages based on a polygynous model of sociality similar to that of extant rhinos where young males experience a heightened risk of socially mediated mortality in areas that are conducive to fossil preservation (e.g., lakes, rivers, ponds).

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pond-like environment was found to contain greater numbers of females. Young males were the most underrepresented demographic group (Voorhies 1985; Mead 2000). In contrast, young adult males were conspicuously superabundant in two attritional assemblages of *Teleoceras* from fluvial and pond-like environments in Florida. In the attritional deposits, female mortality followed the idealized attritional pattern in which localized deaths most frequently occurred among older adults (Mihlbachler 2003).

Hunt (1990) interpreted the Agate Springs assemblage as a localized death event caused by severe seasonal drought around an ephemeral body of water over a period of months. This interpretation suggests that the assemblage is neither an ideal catastrophic nor an ideal attritional assemblage, but may contain aspects of both. Nor is the demography of the assemblage entirely consistent with either a catastrophic or attritional assemblage. The possible female-biased sex ratio suggested by the intact slab resembles a catastrophic scenario for a highly polygynous animal in which localized members of the population were nearly randomly selected for death, thus reflecting a female-biased sex ratio in the localized population. However, the sex-specific mortality patterns are more consistent with an attritional scenario. Localized female mortalities occurred most frequently among old adults. The age distribution of the males is the opposite, with localized mortalities occurring mostly among young males. The demography of the *Menoceras* assemblage is most consistent with the expected attritional pattern for a highly polygynous species in which young males experienced an elevated mortality risk in areas conducive to fossil preservation, but females more frequently die at older ages.

Mortality rate (qx) curves

The female and male mortality rate curves of large polygynous artiodactyls (buffalo, moose, hippo) are undifferentiated and both sexes produce mortality profiles that resemble the more standardized expectation for attritional mortality in which mortality rates are higher among old adults than among young adults (Mihlbachler 2003). However, mortality rate curves of modern (*Diceros*) and fossil (*Teleoceras*) rhinos depart from the idealized expectation by suggesting increased mortality rates at age intervals between 15 and 40% PL (Goddard 1970; Hitchins 1978; Mihlbachler 2003). Both *Teleoceras* and *Diceros* possess potentially lethal cranial weapons, a horn and sharpened i2 in the former and horns in the later. Another Miocene rhino, *Aphelops*, lacks evidence for increased mortality rates in the 15–40% age interval. However, *Aphelops* is uniquely different from modern rhinos in that intermediate and old age adults lack potentially lethal cranial weaponry (Mihlbachler 2003).

The skull-generated (Fig. 7a) and jaw-generated (Fig. 7b) *Menoceras* qx curves are not identical. The skull curve suggests a sharp rises in mortality rate during two life history intervals, one between 15 and 19% PL and another between 25 and 35% PL. In contrast, the age estimates of the jaws suggest steadily rising mortality rates between the 12 and 15% PL interval and the 25–35% PL interval. Inconsistencies in the age estimates of the jaws and skulls may be responsible for this discrepancy. Nevertheless, both elements suggest elevated mortality rates in age intervals between 15 and 35% PL, possibly peaking in the 25–35% PL interval.

Elevated mortality rates within the 15–35% PL interval are consistent with a highly polygynous reproductive system where subdominant individuals are subject to increased risk of death due to intragender competition (Dittus 1975, 1977, 1979; Ralls et al. 1980). The interval of elevated mortality corresponds to approximately 6–15 years in *Diceros* (Hitchins, 1978). Physiological sexual maturity varies from 4.5 to 8 years (12–22% PL) in *Diceros*, although only males above 9 years (24% PL) mate (Hitchins and Anderson 1983). In *Rhinoceros* and *Ceratotherium*, females first give birth between 6 and 8 years, but males do not typically mate until after 11–15 years (Owen-Smith 1975; Laurie et al. 1983; Dinerstein and Price 1991). The
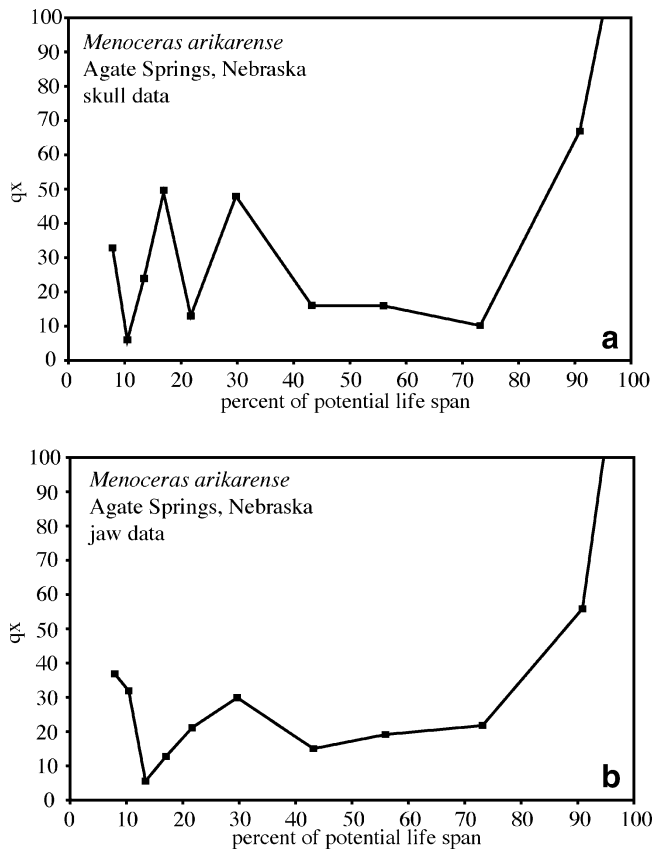
Fig. 7 Sex-combined age specific mortality rate curves (qx) for *Menoceras arikarense* based on age estimates of skulls (**a**) and jaws (**b**).

timing of maturity with respect to relative potential lifespan of fossil rhinos is likely to have been at least roughly similar to other rhinos (approximately between 15 and 35% PL). Therefore, increased mortality rates within this age range encompass the earliest reproductive years of females and the life-history transition from adolescence to adulthood in males.

It is interesting to note that in *Diceros*, a monomorphic species, horn wounds appear to be a significant cause of death in both sexes. Data on adult *Diceros* mortality suggest that 50% of male and 30% of female deaths are a result of horn wounds (Hitchins and Anderson 1983; Berger 1994; Berger and Cunningham 1994b). Socially mediated mortality in sexually dimorphic rhinos, such as *Rhinoceros* and *Ceratotherium*, is more sex-specific. Combat mortality is reported to represent between 31 and 50% of deaths among males in *Ceratotherium* and *Rhinoceros* (Owen-Smith 1988; Dinerstein 1991, 2003; Dinerstein and Price 1991). Intragender aggression is less frequent among females than it is among males of these species (Dinerstein and Price 1991; Owen-Smith 1975).

The elevated mortality rate among young adults that is apparent in the life table and Fig. 7 is largely attributable to the abundance of young males in this collection. Although direct fighting cannot be confirmed as the specific cause of elevated localized young adult mortality in the fossil *Menoceras* assemblage, the pattern of mortality reflected by the assemblage is consistent

with modern rhinos and strongly suggest that intraspecific competition was a more significant cause of male mortality than female mortality.

Conclusions

The abundant fossil rhino record allows one to indirectly relate sexual dimorphism to aspects of sociality via mortality patterns of large fossil assemblages. Horn and/or incisor inflicted wounds are a significant cause of socially mediated mortality among modern rhinos; however, there is no apparent relationship between the frequency of socially mediated mortality and the degree of sexual dimorphism. Among modern rhinos, a high frequency of socially mediated deaths (due to horn and/or incisor wounds) is seen among relatively monomorphic (*Diceros*) and sexually dimorphic (*Ceratotherium* and *Rhinoceros*) rhinos. In the fossil record, some sexually dimorphic rhinos (*Teleoceras*, *Menoceras*) show elevated rates of young male mortality, likewise suggesting a high frequency of socially mediated deaths (this paper and Mihlbachler 2003). However, another sexually dimorphic rhino (*Aphelops*) lacks evidence for elevated young male mortality (Mihlbachler 2003). There remains no clear relationship between sexual dimorphism and sociality (to the extent that they are reflected by mortality patterns) among living or extinct species of rhinos. This suggests that the absence of a strong relationship between dimorphism and sociality among rhinos, and possibly all modern perissodactyls, is a general characteristic of the group, and it has less to do with recent anthropogenic disturbances or extinction bias, perhaps with the exception of the extinction of all small rhinos given that body size may be a confounding factor.

Unlike ruminant artiodactyls, where sexual dimorphism and sociality are correlated, both sexes of rhinos may benefit selectively from horns, particularly females in the defense of calves from modern predators or in conficts with other rhinos. Selective benefits from horns for females, in addition to male benefits in establishing dominance hierarchies, would explain the rather low levels of sexual dimorphism seem in living rhinos. Significantly, *Menoceras* is much smaller than any living rhino and clearly shows a higher degree of sexual dimorphism in its nasal bone (and presumably its horns) than in any other rhino, living or extinct, for which sexual dimorphism has been documented. This suggests that horn function was more sex-specific in *Menoceras*. *Menoceras* females may have simply been too small to effectively fend off the large predators of its time regardless of the presence of horns, thus robbing females of the selective advantages of horns, but still allowing males to utilize horns effectively in establishing dominance hierarchies within the species. This suggests that body size may be a confounding factor in relating sexual dimorphism with sociality in rhinos. At any rate, analysis of sexual dimorphism in other small species of extinct rhinos is needed to confirm this. The smaller size and increased sexual dimorphism in *Menoceras* does suggest, however, that it may have evolved a more gregarious type of sociality than modern rhinos, perhaps similar to herding artiodactyls. However, the mortality patterns of *Menoceras* resemble those of other rhinos, with elevated rates of young male mortality. The effect that a more gregarious form of sociality in *Menoceras* would have had on mortality is unclear. While *Menoceras* mortality patterns clearly suggest a high rate of male competition, and consequently polygyny, concluding that *Menoceras* formed artiodactyl-like social groups, such as herds, remains a matter of speculation.

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