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Back-casting sociality in extinct species: new perspectives using mass death assemblages and sex ratios

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Despite 150 years of interest in the ecology of dinosaurs, mammoths, proto-hominids and other extinct vertebrates, a general framework to recreate patterns of sociality has been elusive. Based on our recent discovery of a contemporary heterospecific mass death assemblage in the Gobi Desert (Mongolia), we fit predictions about gender-specific associations and group living in extant ungulates to extinct ones. We relied on comparative data on sex-ratio variation and body-size dimorphism, basing analyses on 38 additional mass mortality sites from Asia, Africa, Europe and North America that span 50 million years. Both extant and extinct species died in aggregations with biased adult sex ratios, but the skew (from 1:1) was greater for extinct dimorphic taxa, suggesting that sociality in these extinct species can be predicted from spatial and demographic traits of extant ones. However, extinct rhinos, horses and zebras were inconsistent with predictions about adult sex ratios, which underscores the inherent difficulty in back-casting historic patterns to some monomorphic taxa. These findings shed light not only on the sociality of extinct species but provide a sound, although limited, footing for interpretation of modern death assemblages within the context of the emerging science of taphonomy and palaeobehaviour.

Keywords: taphonomy; palaeoecology; behaviour; death assemblages; ungulates, sex ratios

1. INTRODUCTION

Attempts to reconstruct the behaviour of extinct mammals, birds and large reptiles have been especially challenging in the absence of living relatives (Coombs 1990; Van Valkenburgh & Hertzel 1993). Nevertheless, traits such as body-size and sexual dimorphism, and demographic variables including adult sex ratios (ASRs) in living species may enable some level of behavioural reconstruction (Hopson 1975; Dodson 1996). A previously under-used but recognized resource that may permit an improved level of interpretation is modern death assemblages (Behrensmeyer *et al.* 1979; Haynes 1991; Fox *et al.* 1992). Even Charles Darwin commented on mass mortality sites, having reported a South American site involving equids and camelids and being perplexed about why individuals might perish in groups (Darwin 1845). Such death events, however, not only enable comparisons across multiple sites but have the advantage, when treated collectively, of boosting sample sizes to facilitate more rigorous statistical approaches. Equally as critical, death assemblages are also represented in both contemporary and past faunas, thus offering an important temporal dimension, and they include species diverse in life histories, across geological periods, and spatially across multiple continents.

To back-cast patterns of sociality in long-extinct species first requires that relationships be interpreted for extant ones, information that already exists due to a plethora of study on ASRs and spatial structure of modern equids, cervids, bovids and other ungulates (Eisenberg 1981; Berger 1986; Clutton-Brock 1989; Martin 2000). If life-history traits are associated with ASR at catastrophic death sites and correlated with social groupings away from such sites, the development of more complex models of sociality may be applicable to extinct taxa. Our goal is modest—to initiate a more unified approach to gauge simple levels of sociality in extinct vertebrates.

We attempt this by developing an empirical framework through reliance on modern species and then exploring how well it may be back-cast to extinct ones. The focus is on ungulates because they are comparatively abundant in the fossil record, much is known about extant species, and sufficient information is available about spatial relationships in relation to sex ratios and life-history traits. Specifically we apply predictions about the relationship between sexual body-size dimorphism and social groupings in extant ungulates to extinct ones. In doing so, we generate expectations about the extent to which ASRs should deviate from unity based on current models, and then examine how well these expectations are matched by contrasting empirically derived sex-ratio data from mass death assemblages between modern and extinct species.

2. METHODS, RATIONALE AND ASSUMPTIONS

To generate sufficient samples for comparative analyses, we relied on the published literature and our own observations from

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Figure 1. Overview of Valley of Shavart site, discovered in October 1999, of death assemblage involving 38 goittered gazelles, khulons and domestic free-roaming Bactrian camels in the Gobi Desert of Mongolia (Dornogob Aimag, about 80 km south-east of Mandakh, 43, 45, 10.6 N latitude; 108, 37, 10.3 W longitude). The assemblage is at an artesian site with small, ephemeral pools and intermittent water flow through partially vegetated sand dunes. Bones were concentrated over about 0.06 km^2, where 63% of sites with standing water ($n = 16$) had skeletal material, 25% of the seeps ($n = 12$) had surface bones, and none of the sites with flowing water ($n = 4$) or dug by khulans ($n = 8$) had surface bones; foxes (red and Corsac), wolves and vultures had scavenged much of the material. The number of individuals (including unsexed juveniles) and the adult sex ratio (ASR; males:females) was as follows: khulans 19, five juveniles (ASR = 6:5, three unsexed); camels 11, five juveniles (2:3, one unsexed); gazelles eight, three juveniles (2:2, one unsexed). All carcasses or bones had been at the site for at least several weeks; partially mummified carcasses are khulans. Death was due to entrapment in mud, and followed by starvation or perhaps predation. In the foreground is a partially mummified khulan in mud, and rows of skulls of camels and gazelles.

a catastrophic mortality site in Mongolia's Gobi Desert, which, not unlike Darwin's (1845) find from South America, also included equids and a camel (figure 1). The database was enhanced in several instances with information from unpublished observations of wildlife biologists who had also discovered mass deaths (see table 2). Specifically, we used data on ASRs and life-history traits identifiable from the fossil record—body-size and sexual dimorphism. Excluded were cases where ASR was unknown, such as in several Miocene and Pliocene sites (Voorhies 1969; Pratt & Hulbert 1995), could not be inferred (Klein & Cruz-Uribe 1996), or group size was too small for statistical testing (Haynes 1991). Also omitted were population-level mortalities because they failed to reflect social structure at any type of perceptible spatial level. For example, more than 6000 elephants and 500 pronghorns died at Kenyan and Montanan sites at densities of about 11 and 40 km^{-2}, respectively, but carcasses were neither clumped nor in groups (Corfield 1973; Martinka 1967).

With respect to the number of individuals identified by gender at any single death site, samples were small (less than 35 individuals at *ca.* 80% of the sites; see table 2), which rendered the possibility of a type II error (e.g. failing to reject the null hypothesis) concerning an assumed parity in ASR as high. That is, it might have been tempting to conclude variance in ASR was lacking when, given a larger sample, the variation from parity would have been detectable. Thus, we checked the extent to which ASR deviated from a 1:1 expectation using standard binomial tests; but when the probability of a type II error appeared high ($p < 0.10$) we calculated the minimum sample size to achieve significance at that level. The requisite samples were then contrasted between groups that differed in physical traits to evaluate whether ASR varied consistently between organisms with different life histories. Additionally, to be conservative and thereby minimize potential phylogenetic effects, we restricted all contrasts involving different species to the generic level. For example, sheep (bighorn, Dall, argali) of the genus *Ovis*, deer (*Odocoileus*), and mountain zebras and khulons (*Equus*) were each counted as only single data entries.

The extent to which patterns of sexual segregation and social aggregations were associated with ASR at sites of catastrophic mortality was explored through the development of a simple model (outlined in § 3(a)). Predictions were tested empirically using information on extant species. The primary assumptions, explored more fully in § 3, are (i) body size and dimorphism are associated; (ii) sexual dimorphism is linked with gender-specific spatial segregation; and (iii) social aggregations are reflected first by sexual segregation and, subsequently, by ASR at mass death sites.

Table 1. *Relationships between sexual dimorphism and segregation (in time or space) in extant ungulates*

(G-test: $G_{\text{adj}} = 23.59$; $p < 0.001$.)

		sexual dimorphism	
		yes	no
sexual	yes	21[a]	0
segregation	no	1[b]	7[c]

[a] Bighorn, bison, buffalo, caribou, chamois, chiru, elk/red deer, goittered gazelle, giraffe, huemal, ibex, kudu, moose, mountain goats, musk ox, mule deer, pronghorn, Sika deer, Tibetan gazelle, waterbuck, yak.

[b] Reeve's muntjac.

[c] Black rhinos, blue duiker, all equids (*Equus*), collared peccary, dik dik, guanaco, klipspringer.

Sources in Appendix 1 as Berger 1986; Berger & Cunningham 1994; Bowyer *et al.* 1996; Komers & Brotherton 1997; McCullough *et al.* 2000; Schaller 1998; and J. Berger, unpublished data.

3. RESULTS AND DISCUSSION

(a) *Morphological features and sociality in extant species*

A relationship between body size and dimorphism has been repeatedly demonstrated among diverse ungulates (Eisenberg 1981; Clutton-Brock 1989), although artiodactyls reflect greater diversity in sexual dimorphism than perissodactyls (Jarman 1983; Berger 1986; MacFadden 1992). Nevertheless, for 28 genera where patterns of male and female spatial or feeding segregation were known, differences in sexual segregation are strongly associated with body-size dimorphism (table 1), results that affirm the relationship between body-size dimorphism and gender-specific spatial associations.

Although the potential for such a pattern has not been systematically explored for extinct species, extant monomorphic and dimorphic taxa also tend to differ in types of sociality (figure 2). Not only are species of dimorphic taxa polygynous, but they tend to occur in unisex groups (e.g. sex ratios deviate most from 1:1) comprised primarily of adult males, or adult females with young and/or subadults (Clutton-Brock 1989; McCullough 1999) that live separately except during the mating season (Berger & Cunningham 1994). Although juveniles may live with females, the most observable consequence is that adult females and males live separately (Bowyer *et al.* 1996). These patterns indicate that knowledge of body size and dimorphism permit prediction of social aggregations as illustrated in our simple model (figure 2).

(b) *Adult sex ratios at mass death sites reflect social aggregations*

Because data on ASRs including modern equids such as khulons, zebras and horses, as well as for other species, are available from catastrophic death sites and extant populations, and attendant patterns of sociality are known (table 2), possible associations between ASR and sociality can be derived. If ASR reflects patterns of sociality, then assemblages of dimorphic species should (i) be characterized by skewed sex ratios since groups are primarily unisexual, and (ii) differ from groupings of monomorphic species, the latter tending to reflect greater variability (figure 2).

We tested these predictions empirically using data from sites where mass deaths were a consequence of volcanic eruptions (Mt St Helens), landscape level fire (Yellowstone), drowning, snow storms, quagmires and human procurement (table 2). Except for the few instances involving several thousand bison, the maximum number of individuals with known ASR data was much less—the largest samples being 144 elk (fire), 42 bighorn sheep (disease) and 26 mule deer (snow chute), but sites of mortal assemblages generally contained far fewer individuals (table 2).

Analyses to examine the first prediction reveal that dimorphic species, whether extant or extinct, deviated from a 1:1 sex ratio at mortality sites (table 2). Out of 21 discrete events involving extant dimorphic species, skewed sex ratios occurred in 90% ($p < 0.001$), a finding consistent with the tenet that sexual segregation results in groups composed primarily of males or females.

A test of the second prediction involving sociality in monomorphic ungulates is more complex because these species occur in a greater variety of social aggregates (figure 2). For example, the modern camelids and equids (hemiones, zebras and horses) have social systems atypical of dimorphic species. Mountain and Plain's zebras, and horses (whether true or feral), guanacos and vicunas live in year-round bands where within-band sex ratios deviate from 1:1; in contrast, ephemeral mixed-sex groups devoid of permanent associations, which typify the more arid-adapted equids, have ASRs closer to parity (figure. 2). Among these are mixed-sex congregations of up to 1000 or more individuals, although smaller groups of fluid membership characterize Grevy's zebras, khulans and African asses (Andrews 1933; Berger 1986). These fundamental differences in group membership (bands consisting of a stallion and harem versus ephemeral groups) are not a consequence of population-level variation in ASR since the ASR among extant equids fails to differ between species living in year-round harems and those in ephemeral groups. (Out of 22 populations based on existing literature ($n = 7$ for kiangs, khulans and feral asses, and 15 for Mountain and Plain's zebras and feral horses), mean ASR is 0.82 ± 0.19 and 0.73 ± 0.5, respectively (t-test, $t = 0.63$, $p = 0.54$).) The critical point, however, is that for ASR to be diagnostically useful in assessing social groupings, differences in ASR must be reflected at mass death sites.

We examined this possibility for extant species, treating monomorphic and dimorphic species separately, expecting a skew in ASR for dimorphic but not monomorphic species. (The sole *a priori* expectation was for extant equids living in year-round harems since a single male is associated with multiple females; Berger 1986.) Despite the small sample sizes at individual die-off sites (table 2), a greater disparity in ASR was highly characteristic of dimorphic species. Effect sizes for species in which ASR parity in social aggregations was expected (median = 331, $\bar{x} = 539 \pm 195$ (s.e.m)) were much greater than for species expected to be in unisex groups (Mann–Whitney U-test, median = 6, $\bar{x} = 107 \pm 99$, $p < 0.013$). This difference suggests that species predicted to have biased

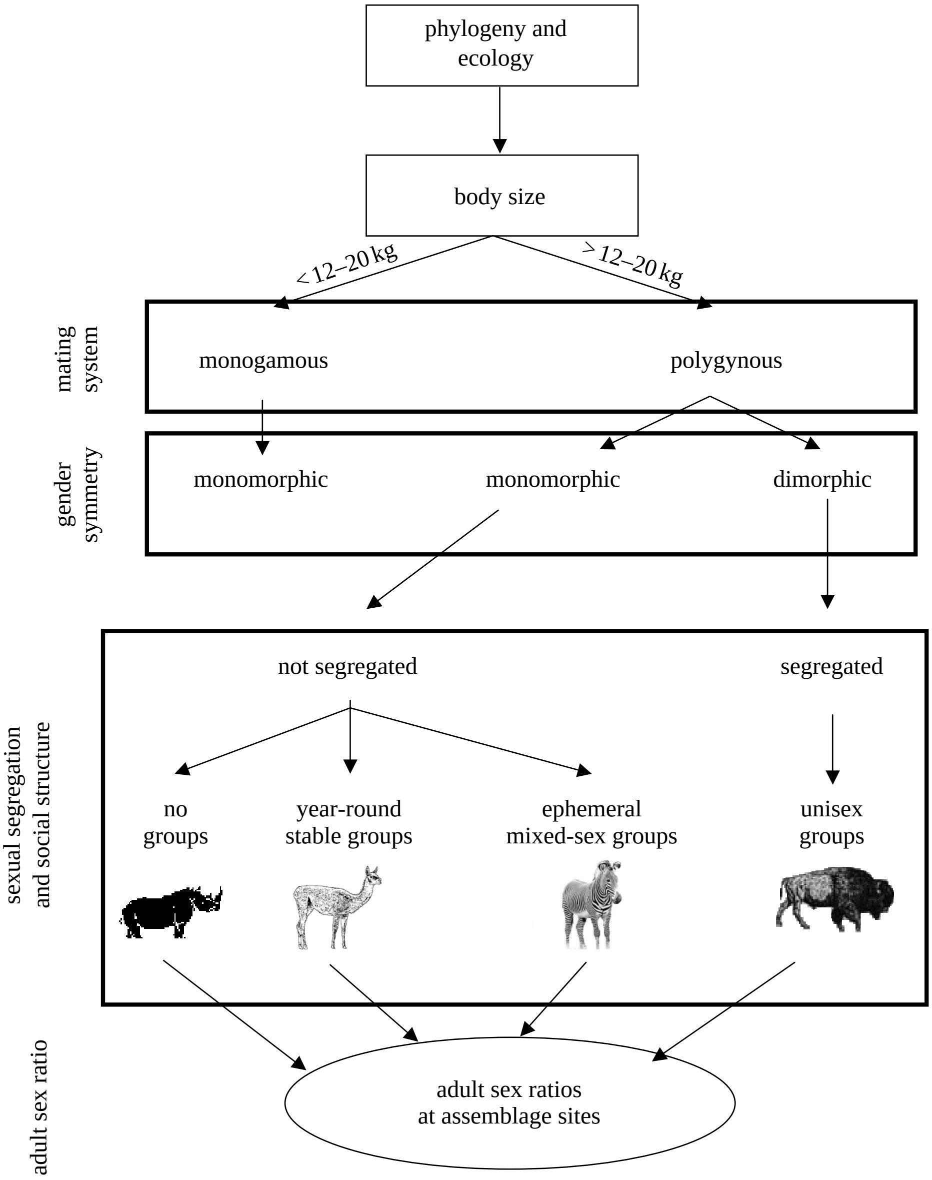

Figure 2. Synopsis of relationships involving body size, mating systems and sexual dimorphism that result in different types of social groupings and adult sex ratios in ungulates. Group types are (i) none; (ii) year-round bands in which membership is stable and one or more adult males thwart associations between females and rival males; (iii) ephemeral mixed-sex groups, but with only short-term or no permanent associations among or between members of either sex; and (iv) unisex groups that are segregated throughout most of the year and with membership being either primarily adult females and associated young and subadults, or adult males only. Grouping classifications and critical body mass for dimorphism from literature (Janis 1982, 1989; Berger 1986; Eisenberg 1981; Clutton-Brock 1989; MacFadden 1992; Komers & Brotherton 1997).

within-group ASR deviated more from unity than those in which parity was expected. Hence, despite about half the die-off sites consisting of fewer than 15 individuals, the expected variation in ASR by body size morphs held, indicating not only that the variation in ASR in extant species was robust but that a basis exists to apply our model (figure 2) to extinct species.

To check for congruence in expected social aggregations between extant and extinct species, we used data from contemporary death sites and two types of historic assemblages representing events from the Holocene to the Eocene: (i) procurement sites, in which early humans were responsible for one-time kill episodes, and (ii) natural traps or catastrophic assemblages that represented similar episodes but in the absence of humans. Although the human kill sites may have been based on optimal prey choices (Speth 1983), there is little reason to suspect within-group sex ratios (of prey) to be heavily altered if the species was dimorphic. The data from natural traps or catastrophic assemblages represented one-time events. To derive expectations of sociality from extinct species (table 2), we used as an analogue the most closely related modern species (e.g. extant monomorphic rhinos for extinct monomorphic rhinoceratids). *A priori* predictions were not derived for extinct monomorphic equids because male and female crania of extant equids are not distinct (Eisenmann & Turlot 1978; Klein & Cruz-Uribe 1996). Hence, to simply suggest a pattern of sociality based on ASR in the absence of inductive criteria is tautological. Nevertheless, to evaluate how well

Table 2. *Relationships between expected and observed patterns of groupings (from figure 2) using adult sex ratios (ASRs) from single catastrophic mortality events in extant and extinct ungulates*

(Sexual dimorphism is present (+) or absent (–), and expected patterns derived from models of extant species or nearest related taxa for extinct ones. 'Observed' reflects the direction of sex-ratio bias and proportion of adult males:females; ?, the appropriate model is uncertain; na, not applicable; n, minimum group size (includes juveniles and subadults), and n^* is the additional sample required for effect size to be significant at $^{*}p < 0.10$, $^{**}p < 0.05$, $^{***}p < 0.001$ (binomial test). Where ASR was equal, a sample of 1 was added to cause a skew. Note the congruence between expected and observed in mule deer and ibex would have been diminished if the timing of deaths had not occurred during the putative rut, which, by definition, is when males and females are together. References: 1, Lee, R. (Arizona Department Fish Game, in litt.); 2, Mensch 1969; 3, Swift *et al.* 2000; 4, Allen 1875; 5, Haynes 1988; 6, Van Vuren & Bray 1985; 7, Berger & Cunningham 1994; 8, Haynes 1988; 9, Cole & Houston 1969; 10, Taber *et al.* 1982; 11, Smith, B. (US Fish Wildlife Service, in litt.); 12, French & French 1996; 13, Berger 1986, unpublished; 14, Chamberlain 1971; 15, Jones 1954; 16, Bleich & Pierce 2001; 17, Penzhorn 1979; 18, Reher 1971; 19, Reher 1974; 20, Nimmo 1971; 21, Saunders 1992; 22, Mihlbachler 1999; 23, MacFadden 1992, 1996; 24, McDonald 1996; 25, Gingerich 1981; 26, Straus 1987; 27, Barnosky 1985; 28, Agenbroad 1990, personal communication; 29, Fox *et al.* 1992; 30, Voorhies 1969; 31, Hulbert 1982; 32, Hulbert 1984; 33, Mead 2001. yr BP, years before present.)

species	reference	location	size	expected	observed	n	n^*	period	cause/comment	fit
extant										
bighorn (*Ovis canadensis*)	1	Sonoran Desert, USA	+	unisex	m < f (0.12)	9	*	1990s	drowning (tinaja)	+
bighorn sheep	1	Sonoran Desert, USA	+	unisex	m < f (0.16)	6	8	1990s	drowning (tinaja)	+
bighorn sheep	1	Sonoran Desert, USA	+	unisex	m < f (0)	5	1	1990s	drowning (tinaja)	+
bighorn	2	Mohave Desert, USA	+	unisex	m < f (0.10)	34	***	1960s	drowning (tinaja)	+
bighorn	3	Mohave Desert, USA	+	unisex	m < f (0.13)	42	***	1990s	most from disease	+
bighorn	3	Mohave Desert, USA	+	unisex	young	13	na	1990s	lambs only (drowned)	
bison (*Bison bison*)	4	Great Plains, USA	+	unisex	m < f (–)	*ca.* 2000	na	1870s	mass drowning (river flood)	+
bison	5	Wood Buffalo, Canada	+	unisex	m < f (0.17)	*ca.* 3000	***	1970s	mass drowning (flood)	+
bison	6	Great Basin, USA	+	unisex	m = f (1.07)	34	1000 +	1930s	in lake bottom	–
bison	7	Badlands, USA	+	unisex	m < f (0)	6	2	1980s	drowning (frozen pond)	+
elephant (*Loxodonta africanus*)	8	Hwange, Zimbabwe	+	unisex	m < f (0)	215	***	1980s	drought, starvation	+
elephant	8	Hwange, Zimbabwe	+	unisex	m < f (0)	21	na	1980s	drought, starvation	+
elephant	8	Hwange, Zimbabwe	+	unisex	m < f (0)	12	na	1980s	drought, starvation	+
elephant	8	Hwange, Zimbabwe	+	unisex	m < f (0)	51	***	1980s	drought, starvation	+
elk (*Cervus elaphus*)	9	Glacier, USA	+	unisex	m < f (0)	40	***	1960s	drowning (frozen lake)	+
elk	10	Mt St Helens A, USA	+	unisex	m < f (0.10)	26	***	1980s	volcanic eruption	+
elk	10	Mt St Helens B, USA	+	unisex	m < f (0)	8	2	1980s	volcanic eruption	+
elk	10	Mt St Helens C, USA	+	unisex	m < f (0)	6	4	1980s	volcanic eruption	+
elk	10	Mt St Helens D, USA	+	unisex	m < f (0)	13	*	1980s	volcanic eruption	+
elk	11	Yellowstone area, USA	+	unisex	young	8	na	1990s	calves only in quagmire	
elk	12	Yellowstone Park, USA	+	unisex	m < f (0.12)	144	***	1988	fire	+
goittered gazelle (*Gazella subguttorosa*)		Gobi Desert, Mongolia	+	unisex	m = f (1.0)	8	na	1990s	quagmire, starvation	
horses (feral) (*Equus caballus*)	13	Great Basin, USA	–	year round	m < f (0.25)	6	9	1980s	snowstorm	+
horses (feral)	13	Great Basin, USA	–	year- round	m < f (0.29)	21	9	1970s	snow, starvation	+
horses (feral)	13	Great Basin, USA	–	year- round	young	8	na	1980s	foals only in quagmire	

(*Cont.*)

Table 2 (*Cont.*)

species	reference	location	size	expected	observed	*n*	n^*	period	cause/comment	fit
khulon (*E. heminous*)		Gobi Desert, Mongolia	–	ephemeral	m = f (1.20)	19	331	1990s	quagmire, starvation	+
moose (*Alces alces*)	14	Ontario, Canada	+	no group	m < f (0.30)	15	*	1970s	quagmire; higher frequency of females	–
mule deer (*Odocoileus hemionus*)	15	Sierra Nevada, USA	+	unisex	m < f (0.35)	26	**	1950s	icefield deaths during migration and rut	+
mule deer	16	Sierra Nevada, USA	+	unisex	m < f (3.0)	17	*	1990s	icefield deaths during migration and rut	+
zebra (mountain) (*E. zebra*)	17	Craddock, South Africa	–	year round	m < f (0)	10	2	1970s	snow storm; lack of males could mean unisex	–
Holocene										
bison (*Bison bison* ?)	18	Glenrock, USA	+	unisex	m < f (0.14)	113	***	Holocene	human procurement site	+
bison	19	Casper, USA	+	unisex	m < f (0.06)	74	***	Holocene	human procurement site	+
pronghorn (*Antilopcapra americana*)	20	Green River, USA	+	unisex	not unisex	79	na	300 yr BP	late season kill site; males likely present	
mammoth (*Mammoth columbi*)	21	Dent, USA	+	unisex	juveniles	13	na	Holocene	eight juveniles and three adults; males unlikely	
mammoth	21	Colby, USA	+	unisex	juveniles	6	na	Holocene	three juveniles and three adults; males unlikely	+
Eocene to Pleistocene										
rhino (*Aphelops*)	22	Mixon Bone Bed, USA	–	no group	m = f (1.0)	?	na	Late Miocene	shallow water	+
horse or zebra (*Cormohipparion occidentale*)	23	Johnson Quarry, USA	–	?	m = f (1.0)	10	331	Mid-Miocene	ASR suggests ephemeral	?
horse or zebra (*Equus simplicidens*)	24	Hagerman Fossils, USA	–	?	m < f (0.61)	54	**	Late Pliocene	possible water; ASR suggests year-round	?
horse or zebra (*Hipparion tehonense*)	23	McAdams Quarry, USA	–	?	m = f (1.0)	40	1000 +	Late Miocene	even ASR suggests ephemeral	?
horse or zebra (*Hyracotherium tapirnum*)	25	Huerfano Basin, USA	+	unisex	m < f (0.57)	24	40	Early Eocene	body-size dimorphism unusual[a]	?
ibex (*Capra pyrenaica*)	26	Pyrenees site A, France	+	unsiex	m < f (0)	28	na	21 000 yr BP	kill site; 33% juveniles; hence nannies and young	+
ibex	26	Pyrenees site B, France	+	unisex	m < f (0)	14	***	21 000 yr BP	kill site	+
ibex	26	Pyrenees site C, France	+	unisex	m = f (1.0)	37	1000 +	12 500 yr BP	kill site during late fall/winter, possible rut	+
Irish elk (*Megaloceros giganteus*)	27	Ballybetagh Bog, Ireland	+	unisex	m < f (1.0)	100	***	Late Pleistocene	winterkill at marsh site	+
mammoth	28	Hot Springs, USA	+	unisex	m < f (52)	0.52	***	26 000 yr BP	males only at trap site	+
mammoth	29	Waco, USA	+	unisex	m < f (0)	15	*	Late Pleistocene	mostly females and young along shoreline	+
antelope (*Merycodus furcatus*)	30	Verdigre, USA	+	unisex	m = f (0.83)	273	36	Early Pliocene	winter deaths due to possible flood[b]	+
horse or zebra (*Neohipparion*)	31	Love Bone Beds, USA	–	?	m = f (1.0)	229	*	Late Miocene	ASR assumed; all ages present	
horse or zebra (*Parahippus leonensis*)	32	Thomas Farm Beds, USA	–	?	m = f (1.16)	89	na	Mid-Miocene	sinkhole; may be attritional	
rhino (*Teleoceras major*)	33	Ashfall Fossil Beds, USA	–	no group	m < f (0.46)	35	*	Miocene	volcanic; possible hippo-like herds	–
rhino (*Teleoceras* spp.)	33	Love Bone Beds, USA	–	no group	m < f (3.0)	50	na	Late Miocene	shallow water; possible male groups	–

[a] Given the unexpected dimorphism (15%) for a small-bodied equid (< 15 kg; MacFadden 1996), neither Artiodactyl nor Perissodactyl models appear appropriate.

[b] Using modern pronghorn as an analogue (Byers 1997) for the extinct merycodonts, winter congregations would include both sexes.

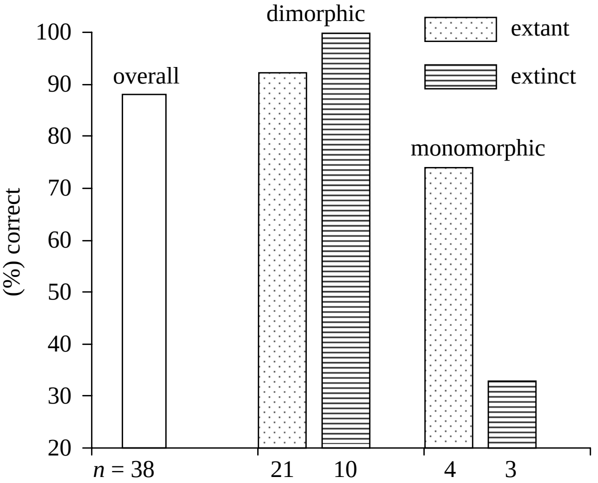

Figure 3. Comparison of the proportion of observed and expected adult sex ratios in ungulates from catastrophic mortality sites (data from table 2).

the model enables back-casting of sociality, extinct and extant species were considered collectively.

The overall match between expected patterns of grouping and observed ASR (figure 3) shows a high concordance (88%; binomial test, $p < 0.001$). Although the fit was better for dimorphic than monomorphic taxa ($G = 5.203$, $p < 0.025$), differences failed to exist between extant and extinct dimorphic species ($p < 0.50$) or between extinct and extant monomorphic ones ($p < 0.50$). The predicted patterns of ASR fit were only slightly improved for extant dimorphic species relative to extinct ones (figure 3), but this contrast was not statistically different ($G = 0.638$, $p < 0.25$); more than 90% of predictions in either category were correct (figure 3). Striking, however, was the discordance in ability to predict types of aggregations between extinct monomorphic and dimorphic species ($G = 3.04$, $p < 0.10$). Hence, while we may have been reasonably good at back-casting patterns of sociality in extinct species that were dimorphic in body size (by analogy with ASR at mass assemblages), our abilities to do so for monomorphic species were impaired.

(c) *Implications for the reconstruction of sociality in extinct species*

Extant monomorphic ungulates are less likely than dimorphic ones to be good models for back-casting sociality, a tenet best illustrated by the underlying confusion associated with two monomorphic perissodactyls. First, although black rhinos are solitary and typically die individually, mortalities may occasionally be concentrated near water, an observation noted as early as the 1830s, and well before and independent of recent poaching epidemics (Alexander 1838; Andersson 1856; Cunningham & Berger 1997). As a consequence, observations of aggregated mortalities may lead to the erroneous conclusion that modern black rhinos are group living. Nevertheless, the fact that Miocene rhinos died in 'herds' with varied ASR (table 2) suggests that modern monomorphic rhinos may be poor models for extinct ones. Second, additional uncertainty is associated with extinct monomorphic equids. Appropriate *a priori* models of social aggregations for these equids are more difficult to construct than models for sexually dimorphic artiodactyls because equids occur in more types of complex groupings and because the distinction between year-round bands and unisex groups is highly dependent on whether a single adult male may be represented in a group death. An additional dilemma for depicting past behaviour is our lack of understanding of factors and their potential interaction that predilect species or taxa towards dimorphism or monomorphism (Janis 1982, 1989). Concomitantly, a practical challenge will continue to be gender identification in extinct species that lack modern counterparts, especially when a bimodal distribution of morphological traits is absent, such as expected for monomorphic species.

Our results offer empirical support for the idea that components of a species' social organization can be inferred from life-history theory in combination with ASR from sites of catastrophic mortalities. That the degree of congruence between extant and extinct species in ASR from catastrophic death sites was greater in dimorphic, than in monomorphic, taxa suggests that (i) types of social groups among extant dimorphic species are reflective of similar patterns in the distant past, and (ii) among monomorphic perissodactyls, especially extinct equids and rhinoceratids, uncertainty about different selective and/or ecological forces confound interpretation of social groupings. Reconstruction of past social patterns will become increasingly challenging when extinct forms such as dinosaurs lack modern analogues. Nevertheless, these findings shed light not only on the presumed sociality of some extinct species but provide a scientific footing for the use of modern life histories in the emerging science of taphonomy and palaeobehaviour.

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