



Improving mortality profile analysis in zooarchaeology: a revised zoning for ternary diagrams



Emmanuel Discamps^{a, b, *}, Sandrine Costamagno^c

^a University of Bergen, AHKR Institute, N-5020 Bergen, Norway

^b Université de Bordeaux – CNRS, UMR 5199 PACEA, F-33405 Talence, France

^c Université Toulouse Jean Jaurès – CNRS, UMR 5608 TRACES, F-33405 Toulouse, France

ARTICLE INFO

Article history:

Received 13 October 2014

Received in revised form

18 March 2015

Accepted 19 March 2015

Available online 28 March 2015

Keywords:

Zooarchaeology

Mortality profile

Hunting tactics

Subsistence strategies

Palaeolithic

Stone Age

Age structure

ABSTRACT

Mortality profiles have figured prominently among tools used by zooarchaeologists to investigate relationships between hominids and prey species. Their analysis and interpretation have been considerably influenced by M.C. Stiner's approach based on ternary diagrams. Part of this method included the demarcation of "zones" in ternary diagrams identifying specific mortality patterns (e.g. attritional, catastrophic, prime-dominated, etc.). Since its introduction some twenty-five years ago, this zoning has, however, received little critical attention. Mathematical modelling as well as a reassessment of the ecological data used to define these zones reveal several problems that may bias interpretations of mortality profiles on ternary diagrams.

Here we propose new, mathematically supported definitions for the zoning of ternary diagrams combined with species-specific age class boundaries based on ethological and ontological data for seven of the most common hominid prey (bison, red deer, reindeer, horse, zebras, African buffalo and common eland). We advocate for the use of new areas (JPO, JOP, O and P zones) that produce more valid interpretations of the relative abundance of juveniles, prime and old adults in an assemblage. These results contribute to the improvement of the commonly used method of mortality profile analysis first advanced by M.C. Stiner.

© 2015 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

1.1. Mortality profiles in zooarchaeology

Mortality profiles are widely used in zooarchaeology, serving as a key line of evidence for exploring relationships between past societies and the animal species they exploited (e.g. Frison, 1978; Stiner, 1991b; Brugal and David, 1993; Stiner, 1994; Morel and Müller, 1997; Turner et al., 2002; Steele, 2004; Fernandez et al., 2006; Bignon, 2008; Hill et al., 2008; Bunn and Pickering, 2010b; Street and Turner, 2013). Age-frequency distributions are commonly used to document choices made by human populations in terms of prey acquisition strategies (e.g. Reher, 1973; Klein, 1982; Stiner, 1990; Brugal and David, 1993; Fernandez et al., 2006; Driver and Maxwell, 2013) or herd management (e.g. Payne, 1973;

Halstead, 1998; Greenfield, 2005; Vigne and Helmer, 2007; Marom and Bar-Oz, 2009).

Based on data from contemporary wild populations, two theoretical models have been proposed to describe the demography of stable large mammal cohorts (Deevey, 1947; Caughley, 1966, 1977). The first corresponds to the age profile of a typical stable living population, often referred to as a "catastrophic" or "living structure" pattern. The second basic mortality type is characterized by an under-representation of prime adults alongside larger numbers of young and old individuals, which corresponds to "attritional" mortality factors implicating elevated mortality rates for juvenile and old individuals. In the fossil record, these basic mortality types were first used by palaeontologists to shed light on the mortality factors underlying the formation of faunal assemblages (e.g. Kurtén, 1953; Voorhies, 1969), and later by zooarchaeologists in order to considerably enrich discussions concerning past hunting strategies (e.g. Reher, 1970, 1973; Klein, 1982; Stiner, 1990):

– "Catastrophic" profiles are generally considered illustrative of mortality events related to natural disasters (Voorhies, 1969;

* Corresponding author. University of Bergen, AHKR Institute, Postboks 7805, N-5020 Bergen, Norway

E-mail address: ediscamps@gmail.com (E. Discamps).

Lyman, 1987), mass kills (e.g. Reher, 1970; Levine, 1983; Costamagno et al., 2006; Hill et al., 2008; Kuntz and Costamagno, 2011; Rendu et al., 2012) or non-selective hunting episodes (e.g. Klein, 1978, 1981; Stiner, 1990; Costamagno, 2003). Solitary ambush predators do not track their prey but generally capture them during chance encounters, meaning that these predators are more likely to generate mortality profiles resembling the expected age structure of a living population, i.e. catastrophic profiles (Stiner, 1990).

- “Attritional” mortality profiles can have several causes, including disease, malnutrition, accidents and predation (Clutton-Brock et al., 1982; White et al., 1987; Stiner, 1991b; Delgiudice et al., 2006). Social cursorial carnivores (e.g. wolves, wild dogs and spotted hyenas), which engage in long chases of their quarry, are also more prone to produce attritional mortality profiles (Stiner, 1990). While Klein (1978) interpreted attritional profiles in Palaeolithic sites as reflecting the inability of hominids to hunt prime-age adults, Stiner (1991a) interpreted them as the product of scavenging.

Additional mortality types have also been recognized in archaeological assemblages. For instance, old-dominated mortality profiles have been considered typical signatures of scavenging (Klein, 1982; Klein and Cruz-Urbe, 1991; Stiner, 1991a, 1994), as primary predators often leave behind very little of the fragile skeletons of young individuals. Stiner (1990, 1991a) also showed that several archaeological sites exhibit a strong bias towards prime adults, with the selection of the most profitable prey considered evidence for the emergence of specific hunting strategies (selective ambush techniques) during the Late Mousterian. Prime-mortality profiles have since been recognized in older archaeological assemblages (e.g. Wallertheim cf. Gaudzinski, 1995; Le Lazaret cf. Valensi and Psathi, 2004; Bocksteinschmiede cf. Krönneck et al., 2004; see also Steele, 2004) as well as in natural accumulations (e.g. Wolverton, 2001, 2006; Kahlke and Gaudzinski, 2005).

1.2. Methods used to identify mortality patterns

While the analysis of mortality profiles is not limited to the identification of a specific mortality pattern (e.g. catastrophic or attritional mortality), these broad categories often guide behavioural interpretation. Because of their significant interpretative power, it has long been considered important to both elaborate and improve the tools available to zooarchaeologists for identifying different theoretical mortality patterns (e.g. Klein, 1982; Lyman, 1987; Stiner, 1990; Steele and Weaver, 2002). Zooarchaeologists working with Palaeolithic assemblages have favoured two types of graphical representations to identify these patterns, histograms and ternary plots. Although other graphical solutions can be used to represent age distributions (e.g. survivorship curves cf. Deevey, 1947; Caughley, 1966; Spinage, 1972; Millard and Zammuto, 1983), they have rarely been applied to mortality analyses in zooarchaeology (although see Lyman, 1987; Fernandez and Legendre, 2003; Fernandez et al., 2006). For instance, survivorship curves, commonly used in Neolithic contexts (e.g. Payne, 1973; Vigne and Helmer, 2007; Marom and Bar-Oz, 2009), feature far less often in Palaeolithic studies (e.g. Klein, 1978). Similarly, the alternative advanced by Klein et al. (1981), which relies on boxplots of crown heights representing age distribution of adults, is still rarely employed (Klein and Cruz-Urbe, 1996; Steele, 2005; Klein et al., 2007).

Histograms are commonly used to represent the relative or absolute frequency of individuals in a series of age classes. Generally, age classes are defined either as a given duration in years or months (e.g. Voorhies, 1969; Lyman, 1987; Turner, 2002) or as a

proportion of total life expectancy (Klein, 1982). In a histogram where age classes are of similar duration, the shape of the age profile provides an initial assessment of the corresponding mortality pattern. The curve of a catastrophic profile is typically “L-shaped” (i.e. half-pyramidal), characterized by a progressive decrease in the number of individuals in each subsequent age class (Fig. 1a). Conversely, the curve of attritional profiles is most often “U-shaped” (Fig. 1b), with juvenile and old individuals being best represented and prime adults rare. It is important to note that the “L” or “U” shape of an age profile can only be recognized on histograms where age classes are of similar duration. However, depending on the ageing method used, the precision in age estimates is not always sufficient for individuals to be ascribed to classes of equal duration. In such cases, “corrected” age profiles are sometimes produced by dividing raw class frequencies by the percentage of lifespan represented by a given class in order to render them comparable with theoretical profiles (Bignon, 2006a; Vigne and Helmer, 2007, Fig. 5).

While H.C. Greenfield (1988), in his study of Neolithic domestic animal production strategies, was the first to rely on a three-age system where assemblages are plotted on ternary diagrams, it was M.C. Stiner (1990, 1991a, 1994) who popularized the method. In promoting its clear advantages for the comparison of mortality profiles from small samples, she proposed three age groups (juveniles, prime adults and old adults), which “correspond to major life history phases in artiodactyls and equids” (Stiner, 1990: 311). Individuals with deciduous teeth were considered as juveniles, those with the full complement of permanent teeth as prime adults and individuals with more than half of their crown worn away as old adults. These broad age classes are interesting as they correspond to nutritional trade-offs faced by hunters as well as non-human predators. Juveniles and old adults have lower fat levels than prime adults, and juveniles have a lower body weight, while prime adults provide the most calories, yet are less vulnerable to predation. By comparing a large number of age profiles from both archaeological sites and modern wildlife datasets on ternary diagrams, Stiner (1990) was able to discuss niche separation in prey age selection between different predators. While this was not the main objective of her analyses, Stiner (1990) also identified various zones on ternary diagrams that were correlated with basic mortality patterns (Fig. 1c). In addition to areas delimiting profiles reflecting a bias towards one of the three main age groups (juvenile, prime and old dominated), she demarcated the expected range of variation for both U- and L-shaped profiles: “The U-shaped mortality model and the natural cases of mortality [...] occur in the lower left-central region of the graph [...] The living-structure model, live census data, and cases of mass (catastrophic) death are distributed in the lower right-central region of the graph” (Stiner, 1990: 319). Since 1990, Stiner’s zoned ternary diagrams have been widely used in zooarchaeological studies, especially in Palaeolithic research (e.g. Lyman, 1994; Marean, 1997; Speth and Tchernov, 1998; Díez et al., 1999; Lubinski, 2000; Munro, 2001; Steele and Weaver, 2002; Kahlke and Gaudzinski, 2005; Adler et al., 2006; Wolverton, 2006; Hill et al., 2008; Byers and Hill, 2009; Steele and Klein, 2009; Rendu, 2010; Driver and Maxwell, 2013). When used in mortality profile analyses, ternary diagrams almost systematically employ Stiner’s zonation. While the position of an age profile according to Stiner’s zones is seldom the only line of evidence mobilised for interpreting mortality profiles, it has been used to identify an age profile as L-shaped, U-shaped, prime dominated, old dominated or juvenile dominated. This age profile can then subsequently be evoked as further evidence of a particular prey acquisition strategy. For example, when profiles from archaeological sites fall in the “L-shaped zone” on ternary plots, they could be interpreted as evidence for non-selective hunting episodes,

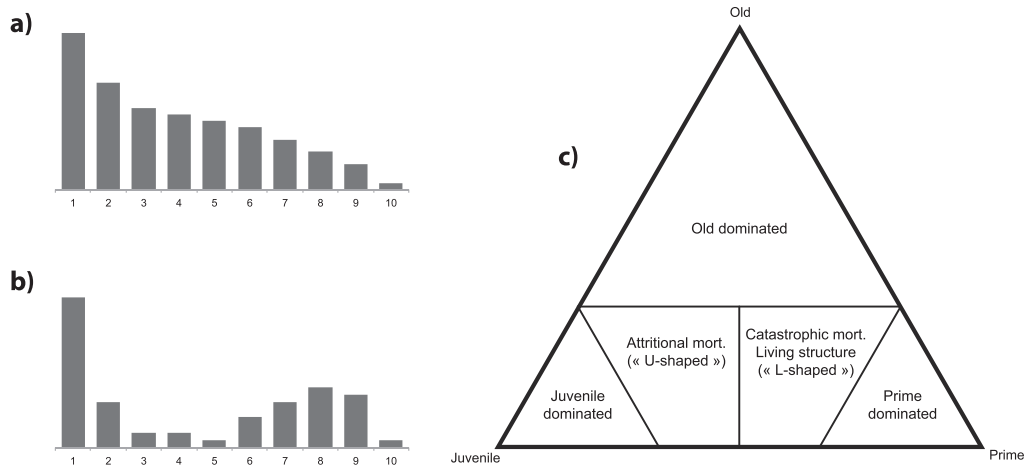


Fig. 1. Commonly used theoretical mortality patterns. L-shaped (a), U-shaped (b) and Stiner's (1990) zoning of ternary diagrams (c).

including mass kill events. Yet Stiner's method was originally not specifically intended as a tool to attribute a single age profile to a given theoretical mortality pattern (e.g. catastrophic or attritional profiles).

The purpose of the present paper is to (a) examine whether Stiner's zones can be used for the identification of mortality patterns (such as L-shaped or U-shaped profiles) on ternary diagrams and (b) define new zones on ternary diagrams that can help zooarchaeologists interpret the relative proportions of 3 age cohorts.

2. The demarcation of mortality patterns on ternary diagrams

2.1. Mathematical modelling of theoretical mortality patterns

Since its original proposition by Stiner (1990), the demarcation of specific areas pertaining to different mortality types on ternary plots has received little critical attention. Although Stiner (1990) used examples of profiles from wildlife studies to demarcate the different zones of the ternary diagram, it is equally possible to assess the distribution of mortality patterns on ternary diagrams using mathematical models.

The relationships between the proportions of the 3 age cohorts on a ternary diagram are shown in Fig. 2a (P_j , P_p , P_o : proportions of

juveniles, prime adults and old adults, respectively). If we consider the definitions of L-shaped and U-shaped profiles, the first should correspond to the " $P_j > P_p > P_o$ " zone (juveniles > prime adults > old in proportion), the second to the " $P_j > P_o > P_p$ " zone (juveniles > old > prime adults), with prime-dominated assemblages corresponding to the " $P_p > P_o > P_j$ " and " $P_p > P_j > P_o$ " zones. However, the 3 age cohorts used in ternary diagrams seldom correspond to the same fraction of the potential ecological longevity or PEL (Stiner, 1990; Costamagno, 1999, Table 1). For instance, if juveniles are defined as individuals between 0 and 2 years of age and prime adults as between 2 and 6 years, differences in age class duration (2 and 4 years, respectively) might in itself explain an under-representation of juveniles. In such a case, the mortality profile should not be considered evidence for the preferential selection of adults (i.e. a prime-dominated profile). Using age classes of unequal duration leads to profiles that are less straightforward to interpret (Fig. 2b). This does not mean that zooarchaeologists must use age classes of equal duration, which would in any case be difficult considering the precision of ageing methods, but rather that defining zones corresponding to certain mortality types on ternary diagrams should take into account the duration of each age cohort relative to PEL.

In order to test Stiner's zones, we used randomization techniques to produce a large number of mortality profiles that fall within the 'basic' mortality types commonly used in

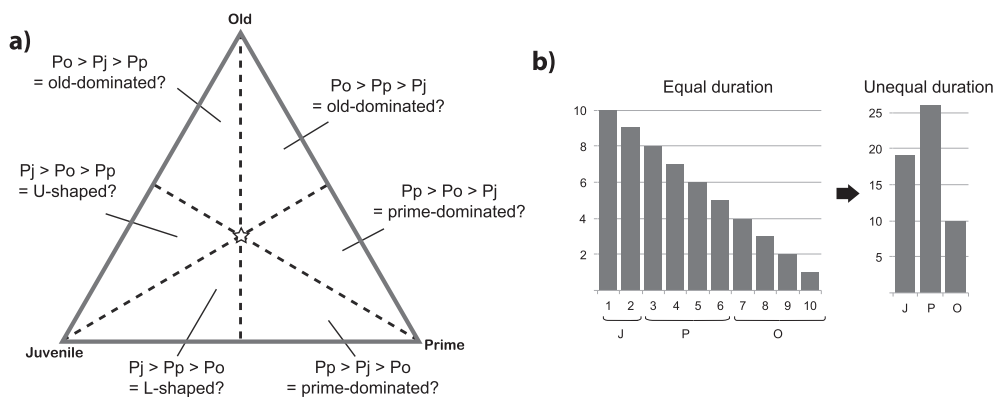


Fig. 2. a) Mathematical relationships between the proportions of the 3 age cohorts on a ternary diagram (P_j : juveniles; P_p : prime adults; P_o : old adults). The star indicates the point where the 3 classes are proportionally equal. b) Example of a typical L-shaped age profile as seen on histograms with 10 classes of equal duration or 3 of unequal duration. Using age classes of unequal duration leads to uncharacteristic profiles that are less straightforward to interpret (in this example $P_p > P_j > P_o$).

Table 1

Proportional lifespan of each age cohort for the different species considered (bold numbers with, in parentheses, class limit in years, with the upper limit of the old class representing the mean longevity). Estimated proportions of individuals within each age class of several natural modern populations are also included (with corresponding numbers from Fig. 8).

		Juvenile	Prime	Old
Bison and African Buffalo	Proportion of each class (with limits in years)	15% (0–3)	45% (3–12)	40% (12–20)
	1 Białowieża, bison (Kraśiński, 1978)	26.3%	59.1%	14.6%
	2 Akagera, buffalo (Spinage, 1972)	37.2%	54.4%	8.4%
Horse, Mountain and Plains zebras	Proportion of each class (with limits in years)	8% (0–2)	52% (2–15)	40% (15–25)
	1 Montana, horse (Garrott and Taylor, 1990)	32.8%	57.3%	9.9%
	2 Nevada, horse (Garrott, 1991)	33.1%	62.1%	4.8%
	3 Oregon, horse (Garrott, 1991)	30.6%	66.5%	2.9%
	4 Wyoming, horse (Garrott, 1991)	36.1%	63.9%	0%
	5 Akagera, zebra (Spinage, 1972)	20.4%	73.9%	5.7%
Red deer	Proportion of each class (with limits in years)	12.5% (0–2)	62.5% (2–12)	25% (12–16)
	1 Rhum 1957 (Lowe, 1969)	30%	68.3%	1.7%
	2 Mount St Helen (Lyman, 1987)	27.4%	71.2%	1.4%
Reindeer	Proportion of each class (with limits in years)	18.8% (0–3)	50% (3–11)	31.2% (11–16)
	1 Barff (Leader-Williams, 1980)	66.6%	33.2%	2.5%
	2 Busen (Leader-Williams, 1980)	61.6%	37.5%	8.9%
	3 Svalbard (Reimers, 1983)	42.1%	55.8%	2.1%
Eland	Proportion of each class (with limits in years)	13.9% (0–2.5)	58.3% (2.5–13)	27.8% (13–18)
	1 Loskop Dam (approximation, Underwood, 1975)	41.9%	57%	1.1%

zoarchaeology. Our mathematical modelling considered mortality profiles with relatively common characteristics: 10 age classes; the first two correspond to juveniles, classes 3 to 6 to prime adults and classes 7 to 10 to old adults. The number of individuals for the 10 age classes in each random age profile was computed using a random number generator (any number between 1 and 1000). Age profiles that follow a specific mathematical law were then selected in order to assess the distribution of L- and U-shaped profiles (see below). The resulting profiles were then plotted on a ternary diagram.

The mathematical definition of L-shaped mortality profiles is fairly straightforward. For L-shaped profiles, we selected 10,000 random profiles with decreasing numbers of individuals in each subsequent class from classes 1 to 10. Once plotted, these profiles (Fig. 3a) reveal a clear problem with the current definition of the “L-shaped zone” in that a majority of the random profiles fall within the ‘classic’ “U-shaped zone”.

Mathematically defining U-shaped profiles proved slightly more complicated. We selected 10,000 random U-shaped profiles for which: 1) the number of individuals decreases from class 1 to 6, 2) the number of individuals increases from class 6 to 10 and 3) the number of individuals in class 10 is inferior to the number of individuals in class 2. While this simulation does not necessarily integrate all theoretically possible U-shaped profiles, Fig. 3b does show that a large proportion of them are found outside the ‘classic’ U-shaped zone, with several profiles even falling within the ‘classic’ L-shaped area.

2.2. Problems with the zoning of ternary diagrams?

Simulations pinpointed potential problems in the current zoning of ternary diagrams. Issues with the ‘classic’ zoning commonly used by zooarchaeologists were first recognised by Costamagno (1999) and then Discamps (2011). Fig. 4 shows an example of an age profile that would typically be identified as L-shaped on a histogram, but which, when plotted on a ternary diagram, falls within the “U-shaped” zone defined by Stiner (1990). This type of problem can have important repercussions for the interpretation of mortality profiles in terms of hunting techniques. In this particular case, a catastrophic profile would be categorized as attritional. Additionally, very distinct mortality profiles are found at the exact same spot on a ternary diagram. Fig. 4 shows such a

case, where U- and L-shaped profiles are located at the same spot on the diagram. This is to be expected if we bear in mind that the use of ternary diagrams induces a substantial loss of resolution in the analysis of mortality profiles (Klein, 1995). In the following, we investigate why such discrepancies are apparent between the zones defined by Stiner (1990) and the simulated age profiles presented above.

Stiner's method was not originally developed as a tool to demarcate zones pertaining to specific mortality patterns. While the original zones (Stiner, 1990) were devised with reference to two theoretical profiles, the majority of the profiles come from wildlife studies in which the mortality factors identified should theoretically have produced L-shaped (catastrophic mortality and ambush predators) or U-shaped (attritional mortality and cursorial predators) profiles. These wildlife profiles were then used to demarcate the expected range of L-shaped and U-shaped profiles. Stiner's approach is in itself sound, although the specific examples of age profiles she selected in wildlife studies do not meet the theoretical expectations. Fig. 5 represents 12 of the 13 mortality profiles used to define the “U-shaped zone”. A re-assessment of the original data from living populations shows the selected profiles only to be clearly categorized on histograms as U-shaped in 3 out of 12 cases (NF, WM1 and HWS). Profiles NW and HWN are actually more similar to L-shaped profiles. Despite the U-shaped appearance of WM2, it is much closer to an L-shaped profile when differences in the duration of age classes are taken into account. HZS, composed of only 12% of old individuals and 41% of prime adults, is hardly classifiable as a U-shaped profile. The remaining profiles are more difficult to classify but are nevertheless not clearly U-shaped. Moreover, interpreting histograms of this type is often problematic as the relative duration of each age class is not always known (profiles marked with a * in Fig. 5). Actual U-shaped profiles are concentrated in the upper-left part of the area defined by Stiner as the “U-shaped zone” (Fig. 5).

In fact, in some of the wildlife studies, the identified mortality factors did not produce the type of profile theoretically expected. The NW profile, assumed to be tied to attritional mortality factors (wolf skulls found in Israel), is closer to an L-shaped profile. Mortality profiles of hyena prey, considered representative of attritional mortality, are highly variable (e.g. U-shaped, L-shaped) and depend largely on the demographic characteristics of the prey populations, a phenomenon previously recognized by Kruuk (1972). The same

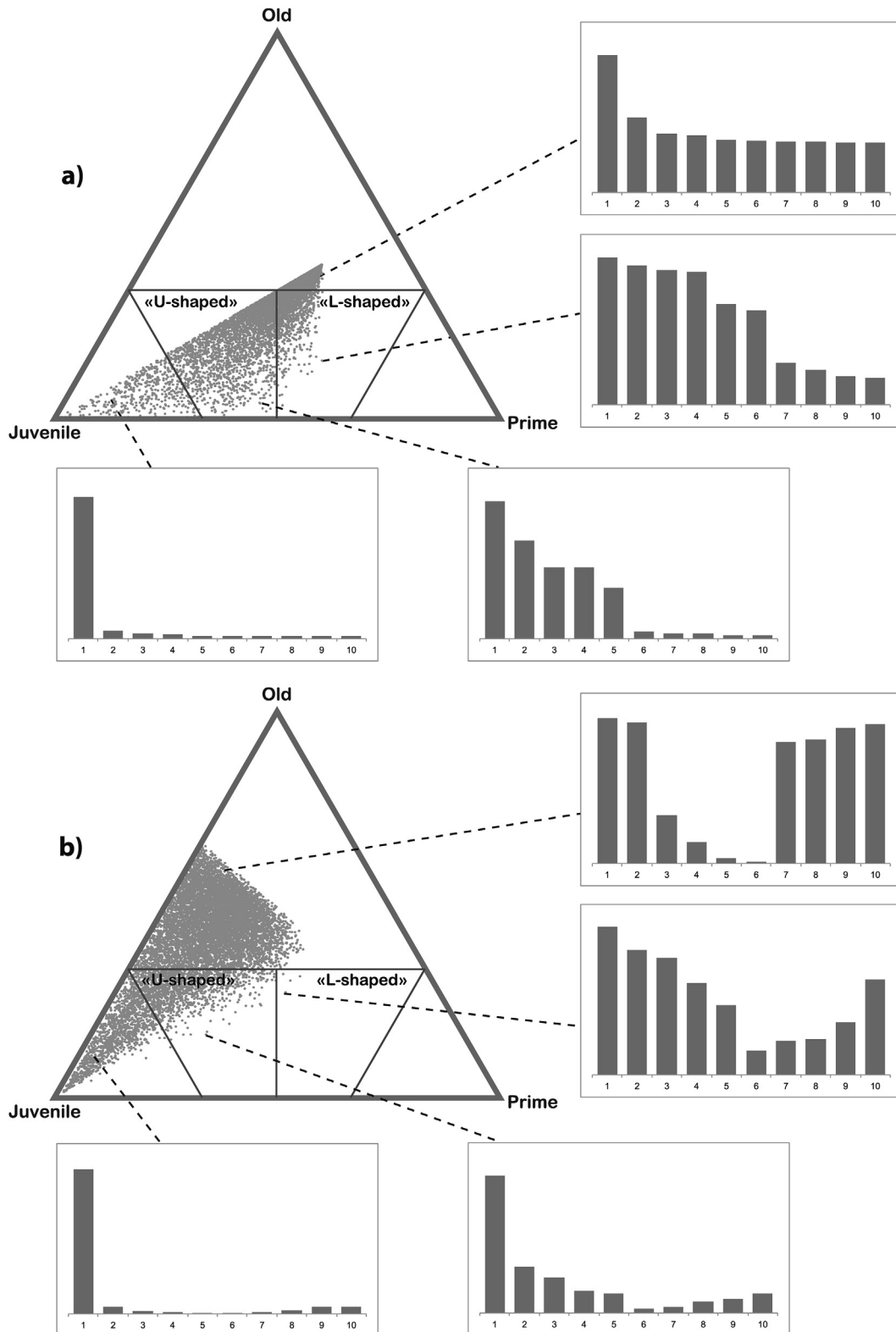


Fig. 3. Mathematical simulations for a) L-shaped and b) U-shaped profiles (cf. text for details). In both cases, 10,000 random profiles are represented on a ternary diagram with Stiner's zoning (1990), as well as 4 profiles representing the extreme limits of the scatter plot (histograms).

can be said for mortality profiles produced by wolves, which may be U- or L-shaped or even old-dominated in some cases (in Pimlott et al., 1969 study, old adults represent 46% of wolf-killed white tail deer). Additionally, some differences highlighted by Stiner (1990)

between cursorial and ambush predators reflect analytical choices. For instance, Bunn and Pickering (2010a, their figure 4) show that differences observed by Stiner between lion- and hyena-hunted wildebeest is a consequence of the boundaries used for the

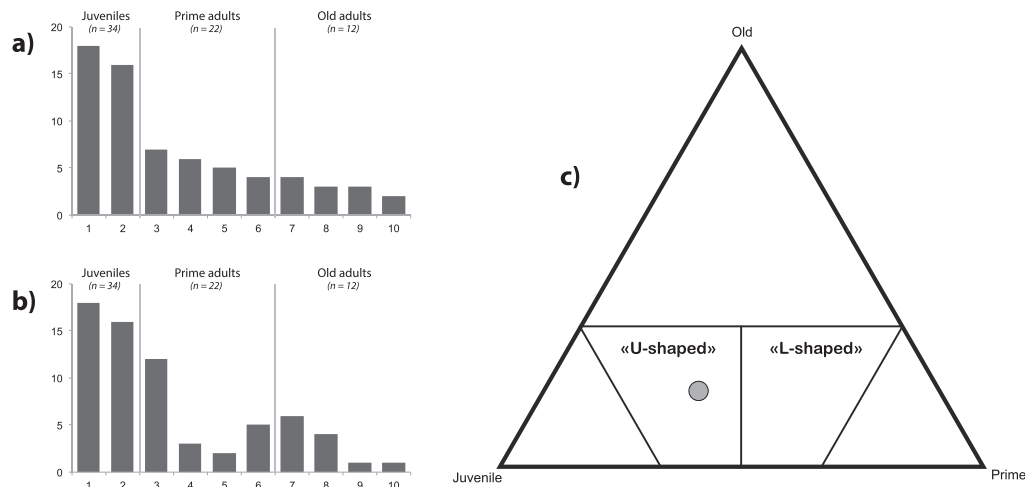


Fig. 4. Examples of problems with the commonly used zoning. The L-shaped profile (a) is placed on a ternary diagram in the U-shaped area defined by Stiner (1990). Profiles (a) and (b) illustrate problems due to the limited resolution of ternary diagrams sharing the same number of juveniles, prime and old adults, such that both profiles fall in exactly the same spot on the ternary diagram, despite one being more L-shaped (a) and the other U-shaped (b).

age classes in one of the studies (data from Schaller, 1972), and that there is in fact no statistically significant difference between mortality profiles created by these two predators.

The above highlights that the current zoning of ternary plots inaccurately distinguishes the different theoretical mortality patterns such as catastrophic and attritional mortality profiles.

2.3. Towards new definitions for ternary diagram zones

Despite these problems, it is possible to demarcate zones on ternary diagrams that are useful for zooarchaeologists to identify mortality patterns. As shown by Stiner (1990), ternary diagrams provide a powerful means for comparing the relative abundance of 3 different age classes of a large number of age profiles. Here we propose a new zoning of ternary plots aimed at improving Stiner's method. Instead of identifying 'classic' theoretical mortality patterns, such as catastrophic or attritional profiles, our zonation provides a means for distinguishing particular profile types defined by the relative proportions of juvenile, prime and old individuals.

This new zoning is devised on the basis of mathematical relationships in order to overcome difficulties in interpreting ternary diagrams with age cohorts of unequal duration. Fig. 6 describes the manner in which the new zones are demarcated for a typical unglut population where juveniles represent 20% of the PEL, prime adults 40% and old adults 40%:

- First, the mathematical relationships between the observed proportions of each class (P_j , P_p , P_o ; proportions of juveniles, prime adults and old adults, without taking into account biases produced by unequal class duration) were determined such that the corrected proportions (P_{jc} , P_{pc} , P_{oc} ; proportions corrected for age class duration, defined as corrected proportion = observed proportion of the class/fraction of the PEL represented by the given class) are equal (i.e. $P_{jc} = P_{pc} = P_{oc}$). This holds true at a single point on the diagram that is defined by the PEL fractions of the different classes. In this specific case, the point is located at 20% juveniles, 40% prime adults, 40% old adults: if $P_j = 20\%$, $P_p = 40\%$ and $P_o = 40\%$, then $P_{jc} = P_j/\text{fraction of PEL} = 20\%/20\% = P_{pc} = 40\%/40\% = P_{oc}$.
- Secondly, the 3 lines running through this point and the corners of the triangle are then drawn. The line passing through the old adult corner of the triangular diagram includes cases where the

corrected proportion of juveniles and prime adults are equal ($P_{jc} = P_{pc}$; Fig. 6a) and delimits zones where $P_{pc} > P_{jc}$ (right) and $P_{pc} < P_{jc}$ (left). The line going through the juvenile corner includes points where $P_{pc} = P_{oc}$ and delimits zones where $P_{oc} > P_{pc}$ and $P_{oc} < P_{pc}$ (Fig. 6b). Finally, the line going through the prime adult corner contains points where $P_{jc} = P_{oc}$ and delimits zones where $P_{oc} > P_{jc}$ and $P_{oc} < P_{jc}$ (Fig. 6c).

- The combination of these areas results in zones with particular mathematical relationships between P_{jc} , P_{pc} and P_{oc} (Fig. 6d). Differences between Figs. 2a and 6d demonstrate how zones 'shift' when biases produced by age classes of unequal duration are taken into account.

This mathematically-based zoning for ternary diagrams demarcates:

- the JPO – “Juveniles-Prime-Old” – zone ($P_{jc} > P_{pc} > P_{oc}$), which primarily includes L-Shaped profiles but also a few U-shaped ones;
- the JOP – “Juveniles-Old-Prime” - zone ($P_{jc} > P_{oc} > P_{pc}$) that includes U-shaped profiles;
- the P – “Prime” – zone ($P_{pc} > P_{oc} > P_{jc}$ or $P_{pc} > P_{jc} > P_{oc}$) with profiles that are dominated by prime adults (age class duration bias taken into account);
- the O – “Old” – zone ($P_{oc} > P_{pc} > P_{jc}$ or $P_{oc} > P_{jc} > P_{pc}$) comprising profiles dominated by old adults (age class duration bias taken into account).

Plotting randomly generated L- and U-shaped profiles (see Section 2.1) on ternary diagrams allows us to empirically test their position according to these new zones. All the simulated L-shaped profiles fall within the JPO zone, a pattern that can in fact be demonstrated mathematically (see annex 1). While the majority of simulated U-shaped profiles fall within the JOP zone, some lie in the JPO zone (Fig. 7). Interestingly, it is possible to visualize the approximate delimitation of zones JOP and JPO on the basis of Stiner's examples from wildlife studies (diagonal dotted line on Fig. 5a). Additionally, in Section 3 below, we review age profiles of living populations for different species (Table 1): they all fall in the JPO zone (Fig. 8).

Stiner (1990) defined juvenile-, prime- and old-dominated zones where individuals of the “dominant” class represent more

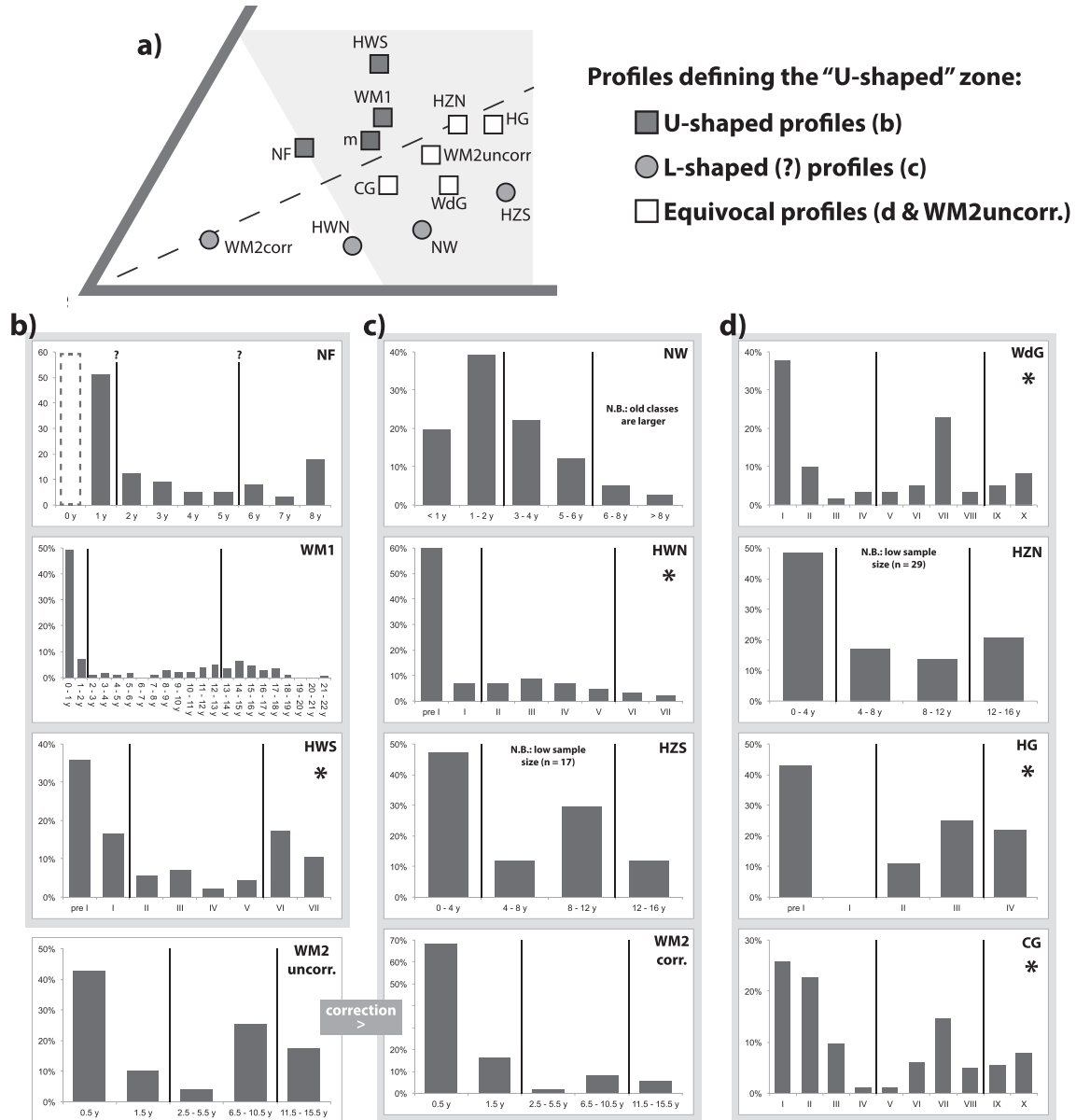


Fig. 5. a) Mortality profiles used by *Stiner (1990)* to define the U-shaped zone (light grey area) on a ternary diagram (m: U-shaped model from *Stiner, 1990*). b) Histograms of the 3 mortality profiles that can be considered as U-shaped (NF: fallow deer in the absence of predators, cf. *Chapman and Chapman, 1975*; WM1: wolf-killed moose, cf. *Peterson et al., 1984*; HWS: hyena-killed wildebeest, Serengeti, cf. *Kruuk, 1972*). c) Histograms of the 4 mortality profiles that actually appear more L-shaped (NW: wolf in the absence of predators, cf. *Mendelssohn, 1982*; HWN: hyena-killed wildebeest, Ngorongoro, cf. *Kruuk, 1972*; HZS: hyena-killed zebra, Serengeti, cf. *Kruuk, 1972*; WM2: wolf-killed moose, cf. *Fuller and Keith, 1980*). d) Histograms of the 4 mortality profiles that are rather equivocal (WdG: wild dog-killed Thompson's gazelle, cf. *Kruuk, 1972*; HZN: hyena-killed zebra, Ngorongoro, cf. *Kruuk, 1972*; HG: hyena-killed Thompson's gazelle, cf. *Kruuk, 1972*; CG: cheetah-killed Thompson's gazelle, cf. *Schaller, 1972*). The WM2 profile is presented uncorrected (WM2 uncorr., with age classes of unequal duration) and corrected (WM2 corr., corrected for age class duration). Mortality profiles marked by an * are those for which interpretation is hampered by the uncertain time span of each age class. We have excluded one of the profiles considered as U-shaped by *Stiner (1990)* due to small sample size (n = 14) and uncertain mortality factors (tiger kills plus some scavenging). Vertical bars in the histograms represent age class boundaries used by *Stiner (1990)* for each profile. We were unable to define them with any certainty for the NF profile.

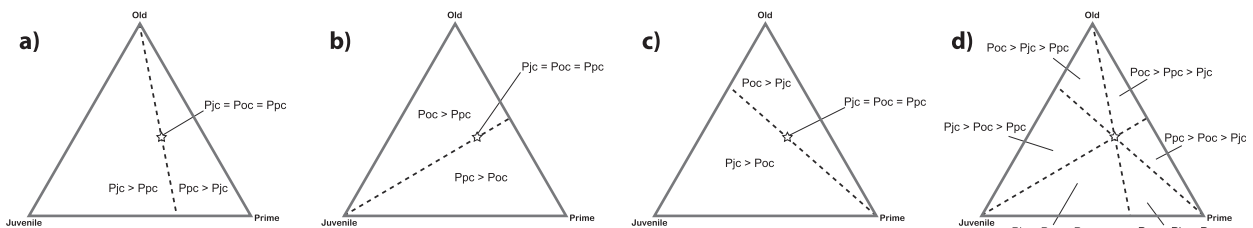


Fig. 6. Subsequent steps involved in establishing the new zones (cf. text for more details). Pjc: corrected proportion of juveniles, Ppc: corrected proportion of prime adults, Poc: corrected proportion of old adults.

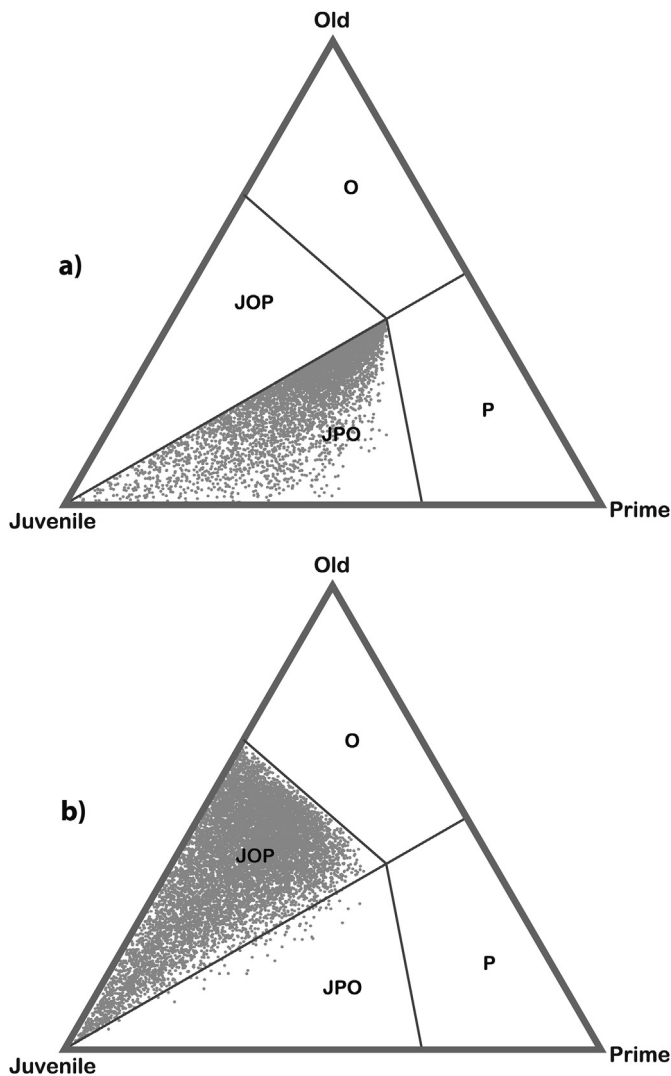


Fig. 7. L-shaped (a) and U-shaped (b) profiles from mathematical simulations plotted on a ternary diagram with the newly defined zones (JOP, JPO, P and O).

than 66% for the first two and more than 33% for the latter. The zones defined here are based on mathematical relationships as opposed to fixed arbitrary values. Prime and old adults are most frequent in zones P and O, respectively, once age class duration bias is taken into account. No “juvenile-dominated zone” is defined, as zones JPO and JOP are both dominated by juveniles (age class duration bias taken into consideration). Assemblages composed almost exclusively of juveniles would cluster at the bottom left-hand corner of the ternary diagram.

Despite not being able to systematically distinguish L-shaped from U-shaped profiles (as this is not possible on ternary diagrams, cf. above and Fig. 4), this revised zoning clearly distinguishes certain profile types:

- a profile within the JOP zone can be considered U-shaped;
- a profile within the JPO zone can either be U- or L-shaped, the latter being more likely;
- a profile outside of the JPO zone cannot strictly speaking be an L-shaped profile (cf. annex 1);
- profiles in the JOP or JPO zone are dominated by juveniles, those in the P zone by prime adults and in the O zone by old adults (age class duration bias taken into consideration).

It is important to note that, in order to use this new zoning, it is not necessary to compute corrected frequencies for age profiles. The uncorrected proportions are used to plot the age profile on the ternary diagram, and the demarcation of the zones allows for an interpretation of the “corrected” proportions of the 3 cohorts without any manipulation of the raw data. Ternary diagrams remain a powerful means for exploring ordinal-scale differences between age profiles (Lyman, 1987; Stiner, 1990). The new zoning proposed here aims to explore ordinal-scale relationships between “corrected” proportions of the 3 age cohorts (in other words, detecting for instance whether juveniles are more abundant than prime adults when the age class duration bias is taken into consideration).

3. Zoning adapted to each species

The definition of age class boundaries is critical in a 3-class system as even the slightest change in boundaries may impact interpretations. The necessity of defining species-specific age classes to properly take into account ontogeny and ethology has been mentioned on several occasions (Costamagno, 1999; Bunn and Pickering, 2010a; Driver and Maxwell, 2013). Driver and Maxwell’s (2013) review of bison kill sites perfectly illustrates this key point: mortality profiles appear primarily as either L-shaped or prime dominated depending on the boundary chosen between juveniles and prime adult classes (if fixed at 4 years in Stiner’s original definition or 2 years when bison biological traits are more fully considered, cf. Figs. 1 and 2 in Driver and Maxwell, 2013). Similarly, Bunn and Pickering (2010a) highlighted problems in the definition of the prime/old boundary, suggesting this limit should vary depending on the research question at hand. For example, when assessing hunting selectivity (i.e., the preferential selection of a given animal social group), the prime/old boundary ought to be defined as the moment when individuals modify their physical position in the herd (e.g. by isolating themselves), which is around 50–60 % of the PEL for buffalo. However, when evaluating the hunting capabilities of hominids (i.e. whether they were capable of hunting the most dangerous animals), this boundary should be adjusted to reflect the fact that buffalos remain physically viable up to 75% of their PEL, and may therefore be just as dangerous to hunt as a younger prime adult.

Several authors have recently proposed species-specific class boundaries based on ethological and biological data (Costamagno, 2001; Adler et al., 2006; Hill et al., 2008; Bunn and Pickering, 2010a; Discamps, 2011; Driver and Maxwell, 2013). While this is a significant step forwards, little consensus has been reached in terms of what criteria are most appropriate for fixing these boundaries. The zones proposed in Section 2.3 utilise the PEL fractions of each age cohort (see above) and thus have to be adapted to each species considered in mortality profiles. In the following, we propose new ternary diagram zones specifically adapted to 7 species frequently hunted by hominids during the Middle and Late Palaeolithic in Eurasia and North America and the Middle and Late Stone Age in Africa: bison (*Bison priscus/bonanus/bison*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), horse (*Equus caballus*), zebras (*Equus quagga/zebra/capensis*), African buffalo (*Synceus caffer*) and common eland (*Tragelaphus oryx*) (Fig. 8). The age group boundaries for each species were fixed with reference to biological and ethological traits from contemporary populations that seem the most important for hunters (e.g. when an individual forms part of an animal social group or remains solitary, or when it moves from one group to another) or scavengers (e.g. at which time(s) an individual is more likely to die of natural causes). As age is one of the criteria that shape the composition of animal social groups (e.g. matriarchal groups, bachelor groups, harems),

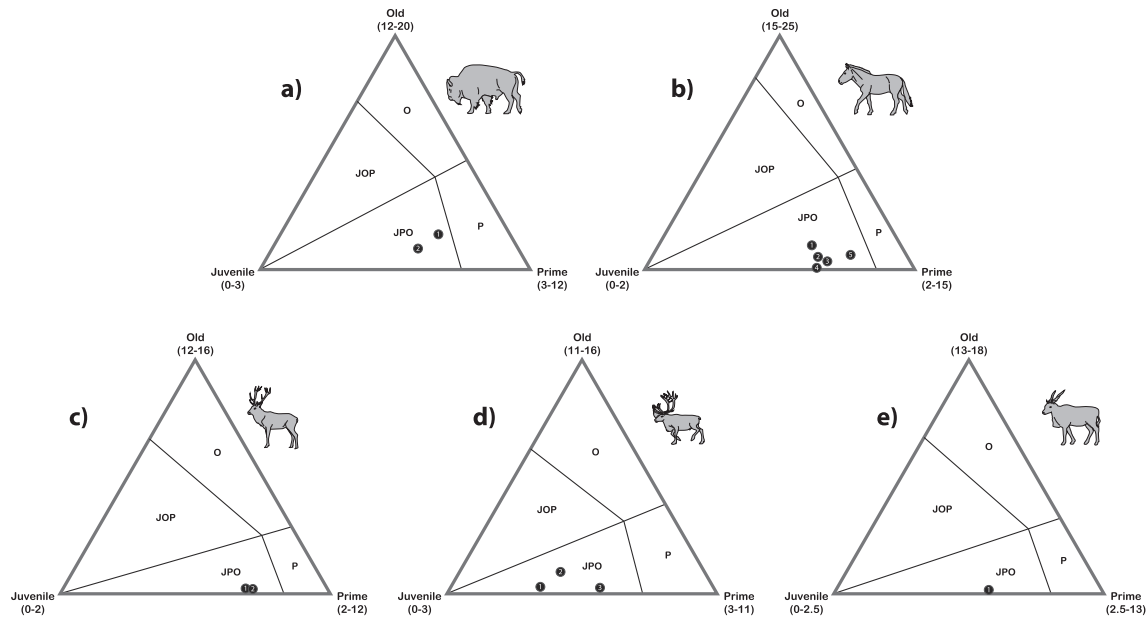


Fig. 8. Suggested species-adapted zoning of ternary diagrams for a) bison and African Buffalo, b) horse and mountain/plains zebras, c) red deer, d) reindeer and e) eland. Reference populations of each species are plotted on the corresponding ternary diagram (cf. Table 1).

mortality profiles can equally shed light on the type of social group targeted if age cohorts boundaries are set appropriately.

We used average PEL values as in most ungulate species males have a shorter life expectancy than females, and PEL estimates vary according to different wildlife studies. The juvenile/prime limit was set primarily by taking into consideration the age of sexual maturity, which correlates with important behavioural changes (e.g. solitary/grouped individuals). The age at which maximal body weight is reached was not factored into our model as several studies have shown it often occurs at a very advanced age (Dzieciolowski, 1970; Skogland, 1983; Bender et al., 2003; Fichant, 2003). The prime/old limit is often less straightforward to define. Contrary to many authors who use a set limit (often between 50 and 75 % of the PEL, e.g. Lyman, 1987; Stiner, 1990; Marean, 1997; Bunn and Pickering, 2010a), we determined a species-specific range based on (a) wildlife studies demonstrating populations that comprise a prime-age phase during which survival is relatively high and constant compared to other age classes and (b) senescence, which refers to the decline in age-specific survival and fecundity with age (Promislow, 1991; Loison et al., 1999). In this conception, old individuals are more likely to be isolated as a consequence of decreased fecundity, to die of natural causes due to a decrease in age-specific survival or to be generally weaker.

The PEL of European bison (*Bison bonasus*) varies in wild individuals, from around 14–16 years for males and up to 24 years for females (Kraśniński, 1978; Pucek et al., 2004). For the American bison (*Bison bison*), both sexes typically live up to 20 years (Mitchell and Gates, 2002), which is the mean value we retained for all bison species. In both European and American bison populations, females are sexually mature at around 2–3 years of age, but generally don't give birth to their first calf before 3–4 years (Kraśniński and Raczyński, 1967; Mitchell and Gates, 2002; COSEPAC, 2004). Bulls are sexually mature at 4–6 years of age and, while they do not take part in reproduction for behavioural reasons (Kraśniński and Raczyński, 1967), they nevertheless join bull groups as early as 3 years of age (Kraśniński and Kraśnińska, 1992). For both European and American bison populations, we considered individuals less than 3 years of age as juveniles and set the lower limit of the old adult

group at 12 years. Fecundity declines after this point, especially for males (Kraśniński and Raczyński, 1967; COSEPAC, 2004), who tend to be less aggressive and submit to younger bulls (Maher and Byers, 1987).

Wild red deer can live up to 20 years (Fichant, 2003), however individuals over the age of 16 are extremely rare (Clutton-Brock et al., 1982). Accordingly, 16 was retained as the average PEL value for this species. Although females reach sexual maturity at 2 years of age, fecundity is low among 3- and 4-year-old hinds (Clutton-Brock et al., 1982: 83). Stags are sexually mature at around 3 years old but only begin to hold harems after the 5-year mark (Gibson and Guinness, 1980). Full sexual maturity also corresponds to stags reaching their full body weight (Dzieciolowski, 1970). Young males leave the familial herd during their second year (Fichant, 2003). Individuals younger than 2 years old were thus considered as juveniles. The prime/old boundary is harder to fix; body size decreases after 8 and 9 years for females and males, respectively (Dzieciolowski, 1970), fecundity and body fat severely decline in females older than 12 years (Dzieciolowski, 1970) and males experience a decrease in physical strength (Fichant, 2003). Consequently, males older than 11 years are no longer able to hold harems (Clutton-Brock et al., 1982: 117). Unlike Clutton-Brock et al. (2002), who considered >10-year-old individuals as old adults, we fixed this limit at 12 years old. Our limits are comparable to those recommended by Steele (2002).

Reindeer PEL is highly variable, ranging from around 12 to 20 years depending on the population (Miller, 1974). PEL also varies according to sex. For instance, in Kaminuriak populations, males rarely survive beyond 12 years of age while females may live up to 16 years (Miller, 1974), and, in the Norwegian Svalbard, PEL ranges between 12 and 17 years depending on the sex (Reimers, 1983). We set the average PEL for reindeer at 16 in order to account for this variability. Sexual maturity is reached at 3 and 2.5 years of age for males and females, respectively, with female fecundity increasing up until 7 years of age (Bergerud, 2000 in Thomas and Gray, 2002). Although reindeer groups are more or less gregarious and the composition of social groups varies according to ecotype, the basic social unit is always composed of females accompanied by their <1-

year-old calves. Yearlings are generally excluded from matriarchal groups and form bands of juveniles that remain at the periphery (Miller, 1974). However, in forest ecosystems, calves can remain with their mother during their first two years (Shoesmith and Storey, 1977 in Murray, 1993). We defined the juvenile/prime limit at 3 years of age based on sexual maturity rather than behaviour, as the latter varies depending on the ecotype. In both barren-ground and woodland caribou, only 2–3 % of females and males survive beyond 12 and 10 years of age, respectively (Messier et al., 1988; Thomas and Barry, 1990). Mortality rates in barren-ground caribou increase considerably after 10–11 years, and females cease reproduction (Reimers, 1983). We set the boundary between prime and old adults at 11 years of age.

Horse class limits were defined on the basis of several ethological studies (Amann et al., 1979; Berger, 1986; Duncan, 1992; Bennett and Hoffman, 1999). The lifespan of wild horses rarely exceeds 25 years, which is the mean PEL value we retained. Mares are fertile at 3–4 years of age, although, up until 5 years, few pregnancies are ever carried to full term (Klingel, 1975). Sexual maturity is attained in the fifth year for males, which is also when individuals reach their adult weight. Horse social organization is highly structured. Harems are composed of females with calves and one stallion. At about 2 years old, young males leave to join male bachelor groups. Unlike males, subadult females are not forced to leave their maternal herd but often join other harems after 2 years of age (Goodloe et al., 2000). As these behaviours heavily influence the composition of social groups, individuals over 2 years old were considered as adults in our model. While horses are fertile throughout their lives, lower fertility rates are observed in females from 18 years on (Berger, 1986). Beyond 10–12 years of age, the stallion is generally dethroned by a younger male. Fernandez (2001) classified individuals >12 years old as old adults. However, as the stallion's change in status has little effect on the demographic composition of social groups, we, like Bignon (2006a), defined old adults as individuals over 15 years of age, which corresponds to an increased mortality rate (Garrott and Taylor, 1990).

The strong behavioural similarities between mountain zebras (*Equus zebra*), plains zebras (different subspecies of *E. quagga*, cf. Groves and Bell, 2004) and horses (Groves, 1974; Klingel, 1975) support the use of the same class limits for these species. The horse behavioural patterns outlined above are generally true for zebra populations (cf. Grubb, 1981; Penzhorn, 1988; Estes, 1991; Skinner and Chimimba, 2005). Moreover, zebra ethology further reinforces our class boundaries for equids (i.e. 0–2, 2–15, 15–25 years). Zebras may live up to at least 21 years in the wild, often reaching 26–29 (Grubb, 1981; Jones, 1993). Juvenile mountain zebras leave their maternal herd around 22 months (Penzhorn, 1988; Lloyd and Rasa, 1989), and plains zebras around 1–3 years (Grubb, 1981). Stallions maintain their dominant status in the herd for up to 15 years.

The African buffalo PEL, which is sex-dependent, has been estimated to be around 15–26 years for wild populations (Mentis, 1972; Spinage, 1973; Grubb, 1981; Jones, 1993; Prins, 1996; Apps, 2000). We adopted an average value of 20 years, which best fits with most wildlife studies. Females are fertile at around 4–5 years, and while bulls are sexually mature as early as 3.5–5.5 years, they do not breed before 7–8 years of age (Taylor, 1985; Estes, 1991; Apps, 2000; Skinner and Chimimba, 2005). Adult body weight is only reached at around 5 years of age for females, while males increase in body size throughout their life (Sinclair, 1977). Buffaloes congregate in large mixed herds or in bachelor bands of adult bulls (Sinclair, 1977; Estes, 1991; Skinner and Chimimba, 2005). Large herds may split into smaller groups, and the physical position of individuals in the herd depends largely on age and sex. Calves, whether male or female, stay close to their mother until they are at least 2 years old. Female adults often stay in the larger herds, while

young bulls reaching puberty (around 3 years old) tend to form small independent bachelor groups, eventually rejoining the herd for mating. Bulls older than 10–12 years of age often leave the herd to form small sedentary groups or adopt a solitary life style, at which time they cease to procreate and are put at a greater risk of predation (Sinclair, 1977). We therefore considered individuals younger than 3 years of age as juveniles, and more than 12 years old as old adults. These class boundaries are identical to those adopted for bison given the strong ethological similarities between these two Bovinae species.

For the common eland, PEL estimates range from 12 to 25 years, but most often fall between 15 and 20 years (Mentis, 1972; Underwood, 1975; Attwell and Jeffery, 1981; Estes, 1991; Jones, 1993; Apps, 2000; Pappas, 2002). We opted for an average value of 18 years. Females first breed at around 2.5 years (Underwood, 1975; Estes, 1991; Pappas, 2002). Males are sexually mature at around 18 months, however, restrained by older dominant males, they rarely breed before 4 years of age (Pappas, 2002; Skinner and Chimimba, 2005). Adult body weight is reached at around 3.5 years, although males grow throughout their life (Underwood, 1975). Elands are found in large mixed herds (nursery/breeding herds), notably in the summer, but these bands may split into smaller groups the rest of the year (Underwood, 1975; Hillman, 1987; Estes, 1991; Skinner and Chimimba, 2005). The composition of social groups is highly variable as inter-group movements are frequent. Juveniles stay together at least for their first 2 years, forming clusters within the large herds. At around 2–3 years old, elands tend to leave the large nursery herds to join smaller groups of adults, a pattern which is particularly true for males (Hillman, 1987). We thus considered individuals younger than 2.5 years of age as juveniles, which corresponds to the juvenile/"subadult" limit of Underwood (1975). The boundary between prime and old adults is extremely difficult to fix. Unlike buffaloes (cf. supra), old bulls may mate throughout their life and do not necessarily isolate themselves from large herds (Hillman, 1987). Females are no longer fertile after 15 years (Scotcher, 1982). Attwell and Jeffery (1981) considered individuals as "senescent" from about 13 years old, when feeding efficiency is impaired by worn teeth. We have adopted this value for our prime/old limit, as it correlates with an increase in the likelihood of death by natural causes.

This ethological data highlights the fundamental importance of sex and seasonality in the composition of animal social groups, and hence related difficulties in defining age groups that allow direct interpretations in terms of animal social bands targeted by hunters. We do not claim the age class limits suggested here to be universally applicable and every analyst should adapt age classes depending on the behavioural factors they wish to investigate. Three parameters should however be made available in order to facilitate inter-study comparisons: the PEL considered, as well as the juvenile/prime and prime/old boundaries, information that can easily be included in the ternary diagrams themselves (see Figs. 8 and 9).

In practice, matching age class boundaries with patterns of dental attrition can be problematic. However, it is important to note that the resolution of ageing methods is often sufficient to distinguish the age classes proposed above. This holds true for dental ageing methods commonly used for bison (e.g. Frison and Reher, 1970; Frison et al., 1976; Gifford-Gonzalez, 1991; Todd et al., 1996), buffalo (e.g. Grimsdell, 1973; Taylor, 1988), equids (Levine, 1982; Guadelli, 1998; Fernandez and Legendre, 2003; Bignon, 2006b), red deer (e.g. Quimby and Gaab, 1957; Lowe, 1967; Klein et al., 1981; Brown and Chapman, 1991; Steele and Weaver, 2012), reindeer (e.g. Miller, 1974; Pike-Tay et al., 2000) and eland (e.g. Kerr and Roth, 1970; Attwell and Jeffery, 1981; Jeffery and Hanks, 1981). When data from tooth eruption and wear is combined, young individuals are easily

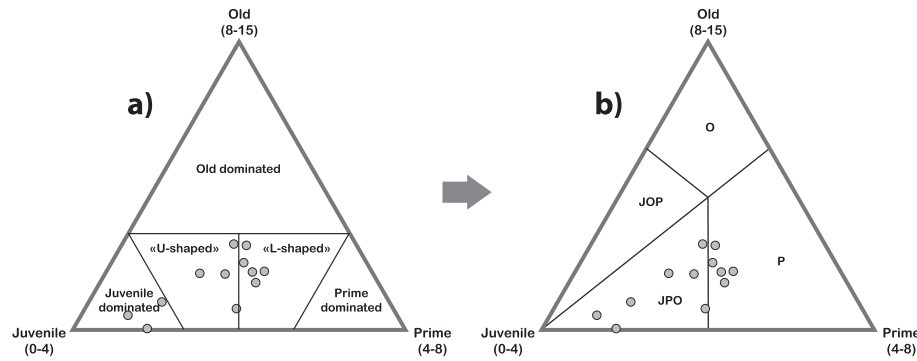


Fig. 9. Bison kill sites dataset from Driver and Maxwell (2013, Tables 2 and 3) with Stiner's zoning (a) and the new zoning of ternary diagrams (b). Confidence intervals have been omitted for clarity.

discerned from adults. Additionally, while distinguishing prime from old adults is often more complicated and somewhat prone to error, wear patterns (notably the loss of molar infundibula) and crown height measurements provide means for separating the two.

4. Discussion

4.1. Example of the effect of the new zoning on interpretations

The revised zoning presented above may considerably alter previous interpretations of mortality profiles. For example, when Driver and Maxwell (2013:105, their figure 1) compiled mortality data from bison kill sites, they highlighted the fact that “assemblages [fall] within a range of zones, including “living structure”, “U-shaped” and, in rare cases, “juvenile-dominated”. [...] Most bison kill sites [...] do not conform to the classic catastrophic mortality profile” (Fig. 9). In fact, when the same zoning described in Section 2.3 is applied, 7 profiles fall within the JPO zone, which includes the L-shaped profiles, and 5 in the P zone, all in close proximity to the JPO zone (Fig. 9). Not a single profile is found in the JOP zone that includes most of the U-shaped profiles, revealing that the mortality profiles of bison kill sites considered are not so unusual, as they apparently mostly conform to catastrophic mortality profiles.

4.2. Limitations of zoned ternary diagrams

Despite the fact that the new zones advocated here improve the validity of interpretations drawn from ternary diagrams, several important limitations remain. Certain theoretical mortality patterns are commonly assumed to correspond to hunting episodes “without selection” (e.g. L-shaped) and others to episodes “with selection” (e.g. U-shaped, prime-dominated). However, the analysis of mortality profiles using zones on ternary diagrams is not sufficient to securely determine if a given age class was preferentially selected or not. Valid conclusions can only be drawn when mortality profiles are compared with demographic data from modern reference populations corresponding to different animal social groups. Even though all the living populations from Fig. 8 fall within the JPO zone, this zone should not be systematically linked to unselective hunting. For instance, several “sub-groups” of the prime-adult class may be preferentially targeted (e.g. youngest prime adults).

Several other limitations pertain to long-recognized biases in mortality profiles that can severely hamper interpretation of mortality profiles.

4.2.1. Demographic variability of the prey population

The “slope” and “shape” of a living-structure mortality profile may vary if the animal population is stable, decreasing or growing

following seasonal or long-term environmental changes or as a response to human or non-human predation pressure (Peterson et al., 1984; Lyman, 1987; Stiner, 1990; Blumenschine, 1991; Lyman, 1994; Lubinski, 2000; Hill et al., 2008; Wolverton, 2008; Driver and Maxwell, 2013). For example, significant predation pressure can induce an under-representation of young and/or old adults in the prey population (Driver and Maxwell, 2013). In such cases, the selective hunting of the most vulnerable individuals (i.e. juveniles and old adults) might remain undetected as the resulting age profile, likely L-shaped, will fall within the JPO zone instead of the JOP one. Moreover, herd demography largely depends on the season and animal social group. Mass hunting of different sub-populations without selection will produce dissimilar “catastrophic” profiles depending on the targeted animal social group (Levine, 1983). For example, mass kills of a bachelor group of male horses would produce profiles situated towards the lower right-hand corner of the graph (i.e. prime-dominated) instead of inside the JPO zone, where profiles traditionally considered as the signature of unselective hunting (L-shaped) would be expected. The demography of the hunted population thus has to be taken into consideration before any preferential selection of a particular age group can be demonstrated. This is made possible partly by identifying the hunting season and the animal social group targeted.

4.2.2. Effects of taphonomic processes, site function and transport decisions

The preferential destruction of deciduous teeth by gelifraction (Guadelli and Ozouf, 1994; Guadelli, 2008; Mallye et al., 2009) or carnivore consumption (Blumenschine, 1991; Munson, 2000; Munson and Garniewicz, 2003) is often evoked to explain the under-representation of juveniles (Munson and Marean, 2003; Kahlke and Gaudzinski, 2005). While it is simple enough to omit younger individuals from mortality profiles on a histogram, it is much more difficult on a ternary diagram (Steele and Weaver, 2002). Site function can also play a role in the representativeness of mortality profiles. Contrary to most kill sites, residential camps are often associated with faunal assemblages that represent several hunting episodes. Apart from cases where the same age class was consistently targeted, mortality profiles from palimpsests present a greater likelihood of representing the general living population (L-shaped), and can thus be wrongly interpreted as indicating unselective hunting (Costamagno, 1999). The repeated use of kill sites can also produce non-catastrophic profiles when different herds are targeted (Wilson, 1980). Additionally, the somewhat connected effect of transport decisions can also impact mortality profiles (Reher and Frison, 1980; Marean, 1997): the transported profile (i.e. heads transported from kill sites to residential sites) does not always correspond to the death profile, as several factors influence

transport decisions (Binford, 1978; Speth, 1983; Bunn et al., 1988; O'Connell et al., 1990; Bartram, 1993; Monahan, 1998).

The key issues raised above highlight the importance of equifinality in the analysis of mortality profiles and the shortcomings of relying solely on this type of evidence for interpreting specific hunting strategies. In fact there is no clear link between the different theoretical 'classic' mortality patterns (L-shaped, U-shaped, etc.) and potential interpretations concerning acquisition strategies (selective or unselective kills, hunting tactics, etc.). As such, the commonly assumed links "L shaped = catastrophic mortality" and "U-shaped = attritional mortality" cannot be taken as a given. Likewise, a prime- or old-dominated profile is not necessarily connected to a preferential selection of prime or old individuals, as identical patterns can result from taphonomic biases (e.g. Bunn and Pickering, 2010a) or the specificity of the prey population, including differences in the targeted animal social group (cf. Levine, 1983) or in the demography of the natural population following significant non-human predation pressure (cf. Hill et al., 2008). As noted by several scholars (e.g. Blumenschine, 1991; Lyman, 1994; Marean, 1997; Steele, 2004; Hill et al., 2008; Wolverson, 2008), additional data on site formation processes, faunal taphonomy, sex ratio, skeletal profiles, body size or hunting season should be integrated if mortality patterns are to be properly interpreted.

4.3. Advantages of ternary plots

While the interpretation of mortality patterns using ternary diagrams can be problematic compared to other graphical representations, they do offer several valuable advantages:

- Sample sizes are often too small in Palaeolithic contexts for mortality patterns based on ten age classes to be reliably explored (Klein and Cruz-Urbe, 1984; Lyman, 1987). The use of three age classes, despite the resulting loss of resolution, allows for data from small faunal assemblages to be integrated more easily, as the minimum sample size is lower (Stiner, 1998).
- The use of three age classes limits the impact of problems linked to ethological variability (cf. Section 3) and ageing methods, such as the use of overly precise age classes or difficulties associated with isolated teeth, which are often the most abundant dental remains recovered from archaeological sites.
- Ternary diagrams constitute a powerful and efficient way of comparing dozens of mortality profiles in a single illustration. Furthermore, it is possible to statistically test the relevance of mortality profiles on a ternary diagram (Steele and Weaver, 2002; Weaver et al., 2011) in a much more direct and convenient way than other methods (Klein, 1978; Marom and Bar-Oz, 2009).
- Relying on the relative proportions of juveniles, prime and old adults for discussing age-driven prey selection can be complicated by the fact that these age cohorts are generally of unequal duration. The zoning proposed here allows the relative importance of each age group to be quickly and easily determined from ternary diagrams while taking into account this age class duration bias.
- Finally, ternary diagrams can be adapted to address different research questions using the same dataset, adjust to different hunted populations or overcome taphonomic biases.

5. Conclusion

The way in which zooarchaeologists analyse and interpret mortality profiles has been considerably impacted by the development of analytical methods based on ternary diagrams by Stiner (1990). Part of this method involved the use of interpretative

"zones", which delimited specific mortality patterns (attritional, catastrophic, etc.). Our revision of these commonly used zones reveals some significant problems that can bias interpretations. For example, the 'classic' U-shaped zone actually comprises numerous L-shaped profiles. Additionally, it is not always possible to securely distinguish L- and U-shaped mortality profiles on a ternary diagram. Furthermore, differences between the respective duration of each age cohort (i.e. age class duration bias) impede the consistent interpretation of ternary plots. We advocate for the use of new areas (JPO, JOP, O and P zones) that overcome this age class duration bias, resulting in more robust interpretations of the relative abundance of juveniles, prime and old adults in an assemblage. Even if 'traditional' concepts (e.g. U-shaped/attritional and L-shaped/catastrophic profiles) are somewhat abandoned in our revised zoning, ternary diagrams are still useful for reconstructing subsistence strategies as they are based on three age cohorts that present distinct advantages and drawbacks for hunters (cf. 1.2). With that said, the importance of biases and uncertainties affecting mortality profiles and ageing methods, as well as the undoubtedly variable character of past animal communities, must be built into analyses. Zones on ternary diagrams are only heuristic devices, useful but imperfect. In the end, discerning and interpreting relative differences between faunal assemblages remains the overall goal of the analysis.

Building upon Stiner's theoretical and methodological contribution, our study proposes new, mathematically supported definitions for the zoning of ternary diagrams combined with species-specific age class boundaries based on ethological and ontological data. This new zoning permits mortality profiles from a large number of assemblages to be more reliably compared. The position of a profile on a ternary diagram in this revised zoning allows the relationships between relative proportions of juveniles, prime and old adults to be identified while taking into account age class duration bias. It is however only through the combination of several zooarchaeological datasets (e.g. mortality profiles, site function, seasonality, skeletal-part profiles, taphonomy, sex-ratio) and comparisons with modern data from reference populations corresponding to various animal social groups that the preferential selection of a given age class or a specific hunting tactic can be demonstrated with any certainty.

Acknowledgements

Financial support was provided to ED by the AHKR department at the University of Bergen, Norway. This research is part of the European Research Council Advanced Grant TRACSYMBOLS, no. 249587, awarded under the FP7 programme at the University of Bergen, Norway. We thank Marie-Claire Dawson and Brad Gravina for English language editing and useful comments. We are also grateful to Steve Wolverson and two anonymous reviewers for constructive comments.

Annex 1. Mathematical verification of L-shaped profiles

In this demonstration, mortality profiles were considered using a 10-class system, where juveniles are defined as classes 1 and 2, prime adults 3 to 6 and old adults 7 to 10.

A theoretically perfect L-shaped mortality profile should have decreasing numbers of individuals from class 1 to 10.

If the number of individuals (n) in class 3 (youngest prime individuals) is "x", and the number of individuals (n) in class 7 (youngest old individuals) is "y", then these 3 equations are satisfied for a perfect L-shaped profile:

$$N(\text{juveniles}) \geq (x + 2) + (x + 1), \tag{1}$$

therefore $N(\text{juveniles}) \geq 2x + 3$

$$N(\text{prime}) \leq x + (x - 1) + (x - 2) + (x - 3), \tag{2}$$

therefore $N(\text{prime}) \leq 4x - 6$

$$N(\text{prime}) \geq (y + 4) + (y + 3) + (y + 2) + (y + 1), \tag{3}$$

therefore $N(\text{prime}) \geq 4y + 10$

$$N(\text{old}) \leq y + (y - 1) + (y - 2) + (y - 3), \tag{4}$$

therefore $N(\text{old}) \leq 4y - 6$

If we consider corrected numbers for differences in the duration of the 3 main cohorts:

$$N_{\text{corr}}(\text{juveniles}) = N(\text{juveniles})/0.2, \text{ therefore (eq (1))}$$

equals $N_{\text{corr}}(\text{juveniles}) \geq (2x + 3)/0.2,$
 therefore $N_{\text{corr}}(\text{juveniles}) \geq 10x + 15$ (5)

$$N_{\text{corr}}(\text{prime}) = N(\text{prime})/0.4, \text{ therefore (eq (2)) equals}$$

$N_{\text{corr}}(\text{prime}) \leq (4x - 6)/0.4, \text{ therefore}$
 $N_{\text{corr}}(\text{prime}) \leq 10x - 15$ (6)

$$N_{\text{corr}}(\text{prime}) = N(\text{prime})/0.4, \text{ therefore (eq (3)) equals}$$

$N_{\text{corr}}(\text{prime}) \geq (4y + 10)/0.4, \text{ therefore}$
 $N_{\text{corr}}(\text{prime}) \geq 10y + 25$ (7)

$$N_{\text{corr}}(\text{old}) = N(\text{old})/0.4, \text{ therefore (eq (4)) equals}$$

$N_{\text{corr}}(\text{old}) \leq (4y - 6)/0.4, \text{ therefore}$ (8)
 $N_{\text{corr}}(\text{old}) \leq 10y - 15$

The combination of eq (5) and eq (6) demonstrates that a theoretical L-shaped profile always satisfies the equation $N_{\text{corr}}(\text{juveniles}) > N_{\text{corr}}(\text{prime})$ because $10x + 15 > 10x - 15$.

The combination of eq (7) and eq (8) demonstrates that a theoretical L-shaped profile always satisfies the equation $N_{\text{corr}}(\text{prime}) > N_{\text{corr}}(\text{old})$ because $10y + 25 > 10y - 15$.

These observations show that a theoretical L-shaped profile, when plotted on a ternary diagram, will necessarily fall within the JPO zone defined in Section 3 by $N_{\text{corr}}(\text{juveniles}) > N_{\text{corr}}(\text{prime}) > N_{\text{corr}}(\text{old})$.

References

Adler, D.S., Bar-Oz, G., Belfer-Cohen, A., Bar-Yosef, O., 2006. Ahead of the game. *Curr. Anthropol.* 47, 89–118.

Amann, R.P., Thompson, D.L., Squires, E.L., Pickett, B.W., 1979. Effects of age and frequency of ejaculation on sperm production and extragonadal sperm reserves in stallions. *J. Reprod. Fertil.* 27, 1–6.

Apps, P., 2000. *Smither's Mammals of Southern Africa: a Field Guide*. Struik Publishers, Cape Town.

Attwell, C.A.M., Jeffery, R.C.V., 1981. Aspects of molariform tooth attrition in eland and wildebeest. *S. Afr. J. Wildl. Res.* 11, 31–34.

Bartram, L.E., 1993. Perspectives on skeletal part profiles and utility curves from eastern Kalahari ethnoarchaeology. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, Southern Illinois University at Carbondale, Carbondale, pp. 115–137.

Bender, L.C., Carlson, E., Schmitt, S.M., Haufler, J.B., 2003. Body mass and antler development patterns of rocky mountain Elk (*Cervus elaphus nelsoni*) in Michigan. *Am. Midl. Nat.* 150, 169–180.

Bennett, D., Hoffmann, R.S., 1999. *Equus caballus*. *Mamm. Species* 628, 1–14.

Berger, J., 1986. *Wild Horse of the Great Basin*. University of Chicago Press, Chicago.

Bergerud, A.T., 2000. Caribou. In: Demarais, S., Krausman, P.R. (Eds.), *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, pp. 658–693.

Bignon, O., 2006a. De l'exploitation des chevaux aux stratégies de subsistance des Magdaléniens dans le Bassin parisien. *Gall. Préhist.* 48, 181–206.

Bignon, O., 2006b. Approche morphométrique des dents jugales déciduales d'*Equus caballus arcelini* (sensu lato, Guadelli 1991): critères de détermination et estimation de l'âge d'abattage. *Comptes Rendus Palevol* 5, 1005–1020.

Bignon, O., 2008. Chasser les chevaux à la fin du Paléolithique dans le Bassin parisien. In: *Stratégie cynégétique et mode de vie au Magdalénien et à l'Azilien ancien*. BAR International Series, vol. 1747 (Oxford).

Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York.

Blumenschine, R.J., 1991. Prey size and age models of prehistoric hominid scavenging: test cases from the Serengeti. In: Stiner, M.C. (Ed.), *Human Predators and Prey Mortality*. Westview Press, Boulder, pp. 122–147.

Brown, W.A.B., Chapman, N.G., 1991. The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. *J. Zool.* 224, 519–536.

Brugal, J.-P., David, F., 1993. Usure dentaire, courbe de mortalité et saisonnalité: les gisements du Paléolithique moyen à grands bovidés. In: Desse, J., Audouin-Rouzeau, F. (Eds.), *Exploitation des animaux sauvages à travers le temps. XIII^e rencontre internationale d'Archéologie et d'Histoire d'Antibes. IV^e Colloque international de l'Homme et de l'Animal*. APDCA, Juan-les-Pins, pp. 62–77.

Bunn, H.T., Pickering, T.R., 2010a. Methodological recommendations for ungulate mortality analyses in paleoanthropology. *Quat. Res.* 74, 388–394.

Bunn, H.T., Pickering, T.R., 2010b. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. *Quat. Res.* 74, 395–404.

Bunn, H.T., Bartram, L.E., Kroll, E.M., 1988. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. *J. Anthropol. Archaeol.* 7, 412–457.

Byers, D.A., Hill, B.L., 2009. Pronghorn dental age profiles and Holocene hunting strategies at Hogup Cave. *Utah. Am. Antiq.* 74, 299–321.

Caughley, G., 1966. *Mortality patterns in mammals*. Ecology 47, 906–917.

Caughley, G., 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, London.

Chapman, D., Chapman, N., 1975. *Fallow Deer: Their History, Distribution and Biology*. Terence Dalton Limited, Lavenham.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982. *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.

Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415, 633–637.

COSEPAC, 2004. *Évaluation et rapport de situation du COSEPAC sur le Bison des prairies (Bison bison bison) au Canada*. Comité sur la situation des espèces en péril au Canada, Ottawa.

Costamagno, S., 1999. *Stratégies de chasse et fonction des sites au Magdalénien dans le sud de la France* (PhD dissertation). Université Bordeaux I.

Costamagno, S., 2001. *Exploitation de l'Antilope saïga au Magdalénien en Aquitaine: méthodes d'étude et applications archéologiques*. *Paleo* 13, 111–127.

Costamagno, S., 2003. *Exploitation de la grande faune au Magdalénien dans le sud de la France*. In: Costamagno, S., Laroulandie, V. (Eds.), *Mode de vie au Magdalénien : les apports de l'archéozoologie*, BAR International Series, vol. S1144, pp. 73–88. Oxford.

Costamagno, S., Meignen, L., Beauval, C., Vandermeersch, B., Maureille, B., 2006. Les Pradelles (Marillac-le-Franc, France): a Mousterian reindeer hunting camp? *J. Anthropol. Archaeol.* 25, 466–484.

Deevey, E.S.J., 1947. Life tables for natural populations of animals. *Q. Rev. Biol.* 22, 283–314.

Delgiudice, G.D., Fieberg, J., Riggs, M.R., Carstensen Powell, M., Pan, W., 2006. A long-term age-specific survival analysis of female white-tailed deer. *J. Wildl. Manag.* 70, 1556–1568.

Díez, J.C., Fernández-Jalvo, Y., Rosell, J., Cáceres, I., 1999. Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). *J. Hum. Evol.* 37, 623–652.

Discamps, E., 2011. *Hommes et hyènes face aux recompositions des communautés d'Ongulés (MIS 5-3): Éléments pour un cadre paléocologique des sociétés du Paléolithique moyen et supérieur ancien d'Europe de l'Ouest* (PhD dissertation). Université Bordeaux I.

Driver, J.C., Maxwell, D., 2013. Bison death assemblages and the interpretation of human hunting behavior. *Quat. Int.* 297, 100–109.

Duncan, P., 1992. *Horses and Grasses: the Nutritional Ecology of Equids and Their Impact on the Camargue*. Springer Verlag, New-York.

Dziedziolowski, R., 1970. Relations between the age and size of red deer in Poland. *Acta Theriol.* XV, 253–268.

Estes, R.D., 1991. *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates*. University of California Press, London.

Fernandez, P., 2001. *Étude paléontologique et archéozoologique des niveaux d'occupations moustériens au Bau de l'Aubesier (Monieux, Vaucluse) : implications biochronologiques et paléthnologiques* (PhD dissertation). Université Claude Bernard Lyon 1.

- Fernandez, P., Legendre, S., 2003. Mortality curves for horses from the Middle Palaeolithic site of Bau de l'Aubesier (Vaucluse, France): methodological, palaeo-ethnological approaches. *J. Archaeol. Sci.* 30, 1577–1598.
- Fernandez, P., Guadelli, J.-L., Fosse, P., 2006. Applying dynamics and comparing life tables for Pleistocene Equidae in anthropic (Bau de l'Aubesier, Combe-Grenal) and carnivore (Fouvent) contexts with modern feral horse populations (Aka-gera, Pryor Mountain). *J. Archaeol. Sci.* 33, 176–184.
- Fichant, R., 2003. *Le cerf. Biologie, comportement, gestion*. Editions du Gerfaut, Paris.
- Frison, G.C., 1978. *Prehistoric Hunters of the High Plains*. Academic Press, New York.
- Frison, G.C., Reher, C.A., 1970. Age determination of buffalo by teeth eruption and wear. In: Frison, G.C. (Ed.), *The Glenrock Buffalo Jump, 48C0304: Late Prehistoric Period Buffalo Procurement and Butchering on the Northwest Plains*, Plains Anthropol. Mem. vol. 7, pp. 46–50.
- Frison, G.C., Wilson, M., Wilson, D.J., 1976. Fossil bison and artifacts from an Early Altitheimal period arroyo trap in Wyoming. *Am. Antiq.* 41, 28–57.
- Fuller, T.K., Keith, L.B., 1980. Wolf predation dynamics and prey relationships in northeastern Alaska. *J. Wildl. Manag.* 44, 583–602.
- Garrott, R.A., 1991. Bias in aging feral horses. *J. Range Manag.* 44, 611–613.
- Garrott, R.A., Taylor, L., 1990. Dynamics of a feral horse population in Montana. *J. Wildl. Manag.* 54, 603–612.
- Gaudzinski, S., 1995. Wallertheim revisited: a re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhessen/Germany). *J. Archaeol. Sci.* 22, 51–66.
- Gibson, R.M., Guinness, F.E., 1980. Differential reproduction among red deer (*Cervus elaphus*) stags on Rhum. *Br. Ecol. Soc.* 49, 199–208.
- Gifford-Gonzalez, D., 1991. Examining and refining the Quadratic Crown height Method of age estimation. In: Stiner, M.C. (Ed.), *Human Predators and Prey Mortality*, Westview Press, Boulder, pp. 41–78.
- Goodloe, R.B., Warren, R.J., Osborn, D.A., Hall, C., 2000. Population characteristics of feral horses on Cumberland Island, Georgia and their management implications. *J. Wildl. Manag.* 64, 114–121.
- Greenfield, H.J., 1988. The origins of milk and wool production in the Old World: a zooarchaeological perspective from the Central Balkans. *Curr. Anthropol.* 29, 573–593.
- Greenfield, H.J., 2005. A reconsideration of the secondary products revolution in southeastern Europe: on the origins and use of domestic animal milk, wool, and traction in the central Balkans. In: Mulville, J., Outram, A. (Eds.), *The Zooarchaeology of Fats, Oils, Milk and Dairying*. Oxbow Books, Oxford, pp. 14–31.
- Grimsdell, J.J.R., 1973. Age determination of the African buffalo, *Syncerus caffer* Sparrman. *Afr. J. Ecol.* 11, 31–53.
- Groves, C.P., 1974. *Horses, Asses and Zebras in the Wild*. David & Charles, Newton Abbot.
- Groves, C.P., Bell, C.H., 2004. New investigations on the taxonomy of the zebras genus *Equus*, subgenus *Hippotigris*. *Mamm. Biol. Z. fur Saugetierkd.* 69, 182–196.
- Grubb, P., 1981. *Equus burchelli*. *Mamm. Species* 157, 1–9.
- Guadelli, J.-L., 1998. Détermination de l'âge des chevaux fossiles et établissement des classes d'âge. *Paleo* 10, 87–93.
- Guadelli, J.-L., 2008. La gélification des restes fauniques. Expérimentation et transfert au fossile. *Ann. Paléontol.* 94, 121–165.
- Guadelli, J.-L., Ozouf, J.-C., 1994. Etudes expérimentales de l'action du gel sur les restes fauniques : Premiers résultats. In: Patou-Mathis, M. (Ed.), *Outils peu élaborés en os et bois de Cervidés*, 6 Table Ronde. CEDARC, Paris, pp. 47–56.
- Halstead, P., 1998. Mortality models and milking: problems of uniformitarianism, optimality and equifinality reconsidered. *Anthropozoologica* 27, 3–20.
- Hill, M.E., Hill, M.G., Widga, C.C., 2008. Late Quaternary bison diminution on the Great Plains of North America: evaluating the role of human hunting versus climate change. *Quat. Sci. Rev.* 27, 1752–1771.
- Hillman, J.C., 1987. Group size and association patterns of the common eland (*Tragelaphus oryx*). *J. Zool.* 213, 641–663.
- Jeffery, R.C.V., Hanks, J., 1981. Age determination of eland *Taurotragus oryx* (Pallas 1766) in the Natal highveld. *S. Afr. J. Zool.* 16, 113–122.
- Jones, M.L., 1993. Longevity of ungulates in captivity. *Int. Zoo. Yearb.* 32, 159–169.
- Kahlke, R.D., Gaudzinski, S., 2005. The blessing of a great flood: differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *J. Archaeol. Sci.* 32, 1202–1222.
- Kerr, M.A., Roth, H.H., 1970. Studies on the agricultural utilization of semi-domesticated eland (*Taurotragus oryx*) in Rhodesia. Horn development and tooth eruption as indicators of age. *Rhod. J. Agric. Res.* 8, 149–155.
- Klein, R.G., 1978. Stone Age predation on large African bovids. *J. Archaeol. Sci.* 5, 195–217.
- Klein, R.G., 1981. Stone Age predation on small African bovids. *S. Afr. Archaeol. Bull.* 36, 55–65.
- Klein, R.G., 1982. Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in Stone Age archaeological sites. *Paleobiology* 8, 151–158.
- Klein, R.G., 1995. Neanderthal carnivory. *Science* 267, 1843–1844.
- Klein, R.G., Cruz-Uribe, K., 1984. *The Analysis of Animal Bones from Archaeological Sites*. University of Chicago Press, Chicago.
- Klein, R.G., Cruz-Uribe, K., 1991. The bovids from Elandsfontein, South Africa, and their implications for the age, palaeoenvironment and origins of the site. *Afr. Archaeol. Rev.* 9, 21–79.
- Klein, R.G., Cruz-Uribe, K., 1996. Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. *J. Hum. Evol.* 31, 315–334.
- Klein, R.G., Wolf, C., Freeman, L.G., Allwarden, K., 1981. The use of dental crown heights for constructing age profiles of red deer and similar species in archaeological samples. *J. Archaeol. Sci.* 8, 1–31.
- Klein, R.G., Avery, G., Cruz-Uribe, K., Steele, T.E., 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. *J. Hum. Evol.* 52, 164–186.
- Klingel, H., 1975. Social organization and reproduction in equids. *J. Reprod. Fertil.* 23, 7–11.
- Krasiński, Z.A., 1978. Dynamics and structure of the European bison population in the Bialowieza primeval forest. *Acta Theriol.* 23, 3–48.
- Krasiński, Z.A., Krasińska, M., 1992. Free ranging European bison in Borecka forest. *Acta Theriol.* 37, 301–317.
- Krasiński, Z.A., Raczynski, J., 1967. The reproduction biology of European bison living in reserves and in freedom. *Acta Theriol.* 12, 407–444.
- Krönneck, P., Niven, L.B., Uerpman, H., 2004. Middle Palaeolithic subsistence in the Lone Valley (Swabian Alb, Southern Germany). *Int. J. Osteoarchaeol.* 14, 212–224.
- Kruuk, H., 1972. *The Spotted Hyena, a Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
- Kuntz, D., Costamagno, S., 2011. Relationships between reindeer and man in southwestern France during the Magdalenian. *Quat. Int.* 238, 12–24.
- Kurtén, B., 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zool. Fenn.* 76, 1–122.
- Leader-Williams, N., 1980. Population dynamics and mortality of reindeer introduced into South Georgia. *J. Wildl. Manag.* 44, 640–657.
- Levine, M., 1982. The use of crown height measurements and eruption-wear sequences to age horse teeth. In: Wilson, B., Grigson, H., Payne, S. (Eds.), *Ageing and Sexing Animal Bones from Archaeological Sites*, BAR International Series, vol. 109, pp. 223–250. Oxford.
- Levine, M., 1983. Mortality models and the interpretation of horse population structure. In: Bailey, G. (Ed.), *Hunter-gatherer Economy in Prehistory: a European Perspective*. Cambridge University Press, Cambridge, pp. 23–46.
- Lloyd, P.H., Rasa, O.A.E., 1989. Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav. Ecol. Sociobiol.* 25, 411–420.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., Jullien, J.-M., 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80, 2539–2554.
- Lowe, V.P.W., 1967. Teeth as indicators of age with special reference to red deer (*Cervus elaphus*). *J. Zool.* 152, 137–153.
- Lowe, V.P.W., 1969. Population dynamics of the red deer (*Cervus elaphus* L.) on Rhum. *J. Anim. Ecol.* 38, 425–457.
- Lubinski, P.M., 2000. A comparison of methods for evaluating ungulate mortality distributions. In: Pike-Tay, A. (Ed.), *Innovations in Assessing Season of Capture, Age and Sex of Archaeofaunas*, pp. 121–134. Archaeozoologia, Paris.
- Lyman, R.L., 1987. On the analysis of vertebrate mortality profiles: sample size, mortality profile, and hunting pressure. *Am. Antiq.* 52, 125–142.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.
- Maher, C.R., Byers, J.A., 1987. Age-related changes in reproductive effort of male bison. *Behav. Ecol. Sociobiol.* 21, 91–96.
- Mallye, J.-B., Costamagno, S., Laroulandie, V., Beauval, C., 2009. Impact des processus périglaciaires sur la préservation des ossements. *Les Nouv. l'Archéol.* 118, 26–31.
- Marean, C.W., 1997. Hunter/gatherer foraging strategies in tropical grasslands: model building and testing in the East African Middle and Late Stone Age. *J. Anthropol. Archaeol.* 16, 189–225.
- Marom, N., Bar-Oz, G., 2009. Culling profiles: the indeterminacy of archaeological data to survivorship curve modelling of sheep and goat herd maintenance strategies. *J. Archaeol. Sci.* 36, 1184–1187.
- Mendelssohn, H., 1982. Wolves in Israel. In: Harrington, F.H., Paquet, P.C. (Eds.), *Wolves of the World: Perspective of Behavior, Ecology and Conversation*. Noyes, Park Ridge, pp. 173–195.
- Mentis, M.T., 1972. A review of some life history features of the large herbivores of Africa. *Lammergeyer* 16, 1–89.
- Messier, F., Huot, J., Le Henaff, D., Luttich, S., 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41, 279–287.
- Millard, J.S., Zammuto, R.M., 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64, 631–635.
- Miller, F., 1974. Biology of the Kamuriak Population of Barren Ground Caribou. Part 2: Dentition as an Indicator of Age and Sex; Composition and Socialization of the Population. In: *Canadian Wildlife Service Reports*, vol. 31 (Ottawa).
- Mitchell, J.A., Gates, C.C., 2002. Status of the Wood bison (*Bison bison athabasca*) in Alberta. Alberta Conservation Association. Alberta Wildlife Status Report 38.
- Monahan, C.M., 1998. The Hadza carcass transport debate revisited and its archaeological implications. *J. Archaeol. Sci.* 25, 405–424.
- Morel, P., Müller, W., 1997. Hauterive-Champrevéyres - un campement magdalénien au bord du lac de Neuchâtel. Etude archéozoologique. Musée cantonal d'archéologie, Neuchâtel.
- Munro, N., 2001. *A Prelude to Agriculture: Game Use and Occupation Intensity during the Natufian Period in the Southern Levant* (PhD dissertation). University of Arizona.

- Munson, P.J., 2000. Age-correlated differential destruction of bones and its effect on archaeological mortality profiles of domestic sheep and goats. *J. Archaeol. Sci.* 27, 391–407.
- Munson, P.J., Garniewicz, R.C., 2003. Age-mediated survivorship of ungulate mandibles and teeth in canid-ravaged faunal assemblages. *J. Archaeol. Sci.* 30, 405–416.
- Munson, P.J., Marean, C.W., 2003. Adults only? A reconsideration of Middle Palaeolithic 'prime dominated' reindeer hunting at Salzgitter Lebenstedt. *J. Hum. Evol.* 44, 263–273.
- Murray, N.A., 1993. The Behavioural Ecology of Reindeer (*Rangifer tarandus*) during the Last Glaciation in Britain and its Implication for Human Settlement, Subsistence and Mobility (PhD dissertation). University of Edinburgh.
- O'Connell, J.F., Hawkes, K., Blurton-Jones, N., 1990. Reanalysis of large mammal body part transport among the Hadza. *J. Archaeol. Sci.* 17, 301–316.
- Pappas, L.A., 2002. *Taurotragus oryx*. *Mamm. Species* 689, 1–5.
- Payne, S., 1973. Kill-off patterns in sheep and goats: the mandibles from Asvan Kale. *Anatol. Stud.* 23, 282–303.
- Penzhorn, B.L., 1988. *Equus zebra*. *Mamm. Species* 314, 1–7.
- Peterson, R.O., Woolington, J.D., Theodore, N., 1984. Wolves of the Kenai Peninsula, Alaska. In: *Wildlife Monographs*, vol. 8. Wiley, New Jersey.
- Pike-Tay, A., Morcomb, C.A., O'Farrell, M., 2000. Reconsidering the quadratic crown height method of age estimation for Rangifer from archaeological sites. *Archaeozoologia* VI, 145–174.
- Pimlott, D.H., Shannon, J.A., Kolenosky, G.B., 1969. The Ecology of the Timber Wolf in Algonquin Park, Ontario. Research Report (Wildlife) no. 87. Department of Lands and Forests, Toronto.
- Prins, H.H.T., 1996. Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making. Chapman & Hall, London.
- Promislow, D.E.L., 1991. Senescence in natural populations of mammals: a comparative study. *S Evolution* 45, 1869–1887.
- Pucek, Z., Belousova, I.P., Krasnińska, M., Krasniński, Z.A., Olech, W., 2004. European bison. Status Survey and Conservation Action Plan. IUCN/SSC Bison Specialist Group, IUCN, Gland and Cambridge.
- Quimby, D.C., Gaab, J.E., 1957. Mandibular dentition as an age indicator in rocky mountain elk. *J. Wildl. Manag.* 21, 435–451.
- Reher, C.A., 1970. Population dynamics of the Glenrock *Bison bison* population. In: Frison, G.C. (Ed.), *The Glenrock Buffalo Jump 48CO384: Late Prehistoric Period Buffalo Procurement and Butchering on the Northwestern Plains*, Plains Anthropol. Mem., vol. 7, pp. 51–55.
- Reher, C.A., 1973. The Wardell *Bison bison* sample: population dynamics and archaeological interpretations. University of Michigan Anthropological Papers. In: Frison, G.C. (Ed.), *The Wardell Buffalo Trap 48SU301: Communal Procurement in the Upper Green River Basin, Wyoming*. University of Michigan, Ann Arbor, pp. 89–105.
- Reher, C.A., Frison, G.C., 1980. The Vore Site, 48CK302, a Stratified Buffalo Jump in the Wyoming Black Hills. *Plains Anthropol. Mem.* 16.
- Reimers, E., 1983. Mortality in Svalbard reindeer. *Holarct. Ecol.* 6, 141–149.
- Rendu, W., 2010. Hunting behavior and Neanderthal adaptability in the Late Pleistocene site of Pech-de-l'Azé I. *J. Archaeol. Sci.* 37, 1798–1810.
- Rendu, W., Costamagno, S., Meignen, L., Soulier, M.-C., 2012. Monospecific faunal spectra in Mousterian contexts: implications for social behavior. *Quat. Int.* 247, 50–58.
- Schaller, G.B., 1972. *The Serengeti Lion: a Study of Predator/prey Relations*. University of Chicago Press, Chicago.
- Scotcher, J.S.B., 1982. Interrelations of Vegetation and Eland (*Taurotragus oryx* Pallas) in Giant's Castle Game Reserve (PhD dissertation). University of the Witwatersrand, Natal.
- Shoesmith, M.W., Storey, D.R., 1977. Movements and associated behaviour of woodland caribou in central Manitoba. Manitoba Department of Renewable Resources and Transportation Services.
- Sinclair, A.R.E., 1977. *The African Buffalo: a Study of Resource Limitation of Populations*. University of Chicago Press, Chicago.
- Skinner, J.D., Chimimba, C.T., 2005. *The Mammals of the Southern African Sub-region*. Cambridge University Press, Cape Town.
- Skogland, T., 1983. The effects of density dependent resource limitation on size of wild reindeer. *Oecologia* 60, 156–168.
- Speth, J.D., 1983. *Bison kills and Bone Counts: Decision Making by Ancient Hunters*. University of Chicago Press, Chicago.
- Speth, J.D., Tchernov, E., 1998. The role of hunting and scavenging in Neanderthal procurement strategies: new evidence from Kebara Cave (Israel). In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neandertals and Modern Humans in Western Asia*. Plenum Press, New York, pp. 223–239.
- Spinage, C.A., 1972. African ungulate life tables. *Ecology* 53, 645–652.
- Spinage, C.A., 1973. A review of the age determination of mammals by means of teeth, with especial reference to Africa. *East Afr. Wildl. J.* 11, 165–187.
- Steele, T.E., 2002. *Red Deer: Their Ecology and How They Were Hunted by Late Pleistocene Hominids in Western Europe* (PhD dissertation). Stanford University.
- Steele, T.E., 2004. Variation in mortality profiles of red deer (*Cervus elaphus*) in Middle Palaeolithic assemblages from Western Europe. *Int. J. Osteoarchaeol.* 14, 307–320.
- Steele, T.E., 2005. Comparing methods for analysing mortality profiles in zooarchaeological and palaeontological samples. *Int. J. Osteoarchaeol.* 15, 404–420.
- Steele, T.E., Weaver, T.D., 2002. The modified triangular graph: a refined method for comparing mortality profiles in archaeological samples. *J. Archaeol. Sci.* 29, 317–322.
- Steele, T.E., Klein, R.G., 2009. Late Pleistocene subsistence strategies and resource intensification in Africa. In: Hublin, J.-J., Richards, M.P. (Eds.), *The Evolution of Hominid Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, pp. 111–124.
- Steele, T.E., Weaver, T.D., 2012. Refining the Quadratic Crown height Method of age estimation: do elk teeth wear quadratically with age? *J. Archaeol. Sci.* 39, 2329–2334.
- Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. *J. Anthropol. Archaeol.* 9, 305–351.
- Stiner, M.C., 1991a. An interspecific perspective on the emergence of the modern human predatory niche. In: Stiner, M.C. (Ed.), *Human Predators and Prey Mortality*. Westview Press, Boulder, pp. 149–185.
- Stiner, M.C., 1991b. *Human Predators and Prey Mortality*. Westview Press, Boulder.
- Stiner, M.C., 1994. *Honor Among Thieves: a Zooarchaeological Study of Neanderthal Ecology*. Princeton University Press, Princeton.
- Stiner, M.C., 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *J. Archaeol. Sci.* 34, 303–326.
- Street, M., Turner, E., 2013. *The Faunal Remains of Gönnesdorf*. Verlag des Römisch-Germanischen Zentralmuseums, Mainz.
- Taylor, R.D., 1985. The Response of Buffalo, *Syncerus caffer* (Sparrman), to the Kariba Lakeshore Grassland (*Panicum repens* L.) in Matusadona National Park (PhD dissertation). University of Zimbabwe.
- Taylor, R.D., 1988. Age determination of the African buffalo, *Syncerus caffer* (Sparrman) in Zimbabwe. *Afr. J. Ecol.* 26, 207–220.
- Thomas, D.C., Barry, S.J., 1990. A life table for female barren-ground caribou in north-central Canada. *Rangifer Spec. Issue* 3, 177–184.
- Thomas, D.C., Gray, D.R., 2002. Update COSEWIC Status Report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, pp. 1–98.
- Todd, L.C., Rapson, D.J., Hofman, J.L., 1996. Dentition studies of the Mill iron and other early Paleoindian bison bonebed sites. In: Frison, G.C. (Ed.), *The Mill Iron Site*. University of New Mexico Press, Albuquerque, pp. 145–175.
- Turner, A., Gonzalez, S., Ohman, J.C., 2002. Prehistoric human and ungulate remains from Preston Docks, Lancashire, UK: problems of river finds. *J. Archaeol. Sci.* 29, 423–433.
- Turner, E., 2002. *Solutrè - an Archaeozoological Analysis of the Magdalenian Horizon*. Verlag des Römisch-Germanischen Zentralmuseums, Mainz.
- Underwood, R., 1975. *Social Behaviour of the Eland (Taurotragus oryx) on Loskop Dam Nature Reserve* (MSc thesis). University of Pretoria.
- Valensi, P., Psathi, E., 2004. Faunal exploitation during the Middle Palaeolithic in south-eastern France and north-western Italy. *Int. J. Osteoarchaeol.* 14, 256–272.
- Vigne, J.D., Helmer, D., 2007. Was milk a "secondary product" in the Old World neolithisation process? its role in the domestication of cattle, sheep and goats. *Anthropozoologica* 47, 9–40.
- Voorhies, M.R., 1969. *Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska*, pp. 1–69. Wyoming University Contributions in Geology Special Paper 1.
- Weaver, T.D., Boyko, R.H., Steele, T.E., 2011. Cross-platform program for likelihood-based statistical comparisons of mortality profiles on a triangular graph. *J. Archaeol. Sci.* 38, 2420–2423.
- White, G.C., Garrott, R.A., Bartmann, R.M., Carpenter, L.H., Allredge, A.W., 1987. Survival of mule deer in northwest Colorado. *J. Wildl. Manag.* 51, 852–859.
- Wilson, M.C., 1980. Population dynamics of the Garnsey site bison. In: Speth, J.D., Parry, W.J. (Eds.), *Late Prehistoric Bison Procurement in Southeastern New Mexico: the 1978 Season at the Garnsey Site (LA-18399)*. Museum of Anthropology, University of Michigan, Ann Arbor, pp. 88–128.
- Wolverton, S., 2001. Caves, ursids, and artifacts: a natural-trap hypothesis. *J. Ethnobiol.* 21, 55–72.
- Wolverton, S., 2006. Natural-trap ursid mortality and the Kurtén response. *J. Hum. Evol.* 50, 540–551.
- Wolverton, S., 2008. Harvest pressure and environmental carrying capacity: an ordinal-scale model of effects on ungulate prey. *Am. Antiqu.* 73, 179–199.