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Quaternary International

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## A parametrical model to describe a stable and stationary age structure for fossil populations

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### ARTICLE INFO

#### Article history:

Available online xxx

#### Keywords:

Mathematical models  
Age structure population  
Leslie matrix  
Fossil sample

### ABSTRACT

A parametric family of models based on the Weibull model was proposed to describe the age structure of a fossil population. This descriptive approach was combined with a population dynamics model based on the Leslie matrix. The stability and sustainability conditions were algebraically stated to provide an equilibrium equation for any species. The model parameters for a sustainable population were determined via numerical methods. These values represent the survival and mortality profiles for a sustainable population and are comparable between different populations. This approach tests whether an observed mortality profile might correspond to the natural mortality pattern of a stable population. Finally, the model performance was tested for three fossil *Bison priscus* populations (Il'Skaya, Mauran and Coudoulous) using literature data.

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### 1. Introduction

Building mortality profiles to study age at death patterns is a typical component for most faunal analyses. The age distribution of a species in an assemblage provides information on the pre- and post-depositional history of the fossil specimens, including prey selection, accumulation mode, and prey herd behaviour. Assessing the mortality profiles and sex ratios in zooarchaeological populations is often difficult, but several methods, such as histograms, boxplots and triangular graphs are currently used to describe and compare mortality and living population profiles (Lyman, 1987, 1994; Pike-Tay, 2000; Steele, 2003; Discamps and Costamagno, 2015). The way in which palaeontologists and zooarchaeologists analyse the mortality profiles has been influenced by the identification of age structure of the past populations. Age structures are often compared to two theoretical models based on observations of stable wild large mammal populations (Kurtén, 1953). For the first model, often called a “catastrophic” profile, the number of dead individuals per age class is proportional to their

abundance in the population; therefore, the age structure for the living population is preserved in the fossil assemblage. The second model (often called an “attritional” profile) corresponds to deaths via natural attrition of the herd that mainly affect the youngest and oldest members of the population (Klein, 1982a,b; Stiner, 1990). However, mortality profiles in fossil records are affected by a number of uncertainties (Klein and Cruz-Urbe, 1983; Levine, 1983; Hamlin et al., 2000; Lubinski, 2000; Steele and Weaver, 2002), and inaccuracies in the age at death estimates for individuals and both pre- and post-depositional biases affect fossil assemblages. Dental eruption, dental attrition, epiphyseal fusion and skeletochronology usually provide reliable and adequately accurate estimates for the age at death of individuals in fossil assemblages. However, while some of these techniques are thought to provide punctual age estimates, most provide interval age estimates and cannot be used for statistical inferences. A refinement of traditional methods with new tools is required to mitigate mortality profile interpretation problems. To date, different analytical methods have been employed to discuss the mortality profiles. Mathematical approaches with life tables and the Leslie matrix were used to model fossil populations in classical studies (Kurtén, 1953, 1954, 1983; Van Valen, 1963, 1964, 1965; Voorhies, 1969; Koike and Ohtaishi, 1987). The graphical solutions called “survivorship curves” extracted from the life tables (Deevey, 1947; Caughley, 1966), have been rarely applied to mortality analysis by

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zooarchaeologists and palaeontologists. More recent studies addressing more specific questions such as the growth, stability and elasticity of sample populations employ new refinements of these techniques (Monchot and L  chelle, 2002; Fernandez and Legendre, 2003; Fernandez et al., 2006; Monchot et al., 2012; Rodr  guez-G  mez et al., 2013, 2014a, 2014b).

Here, we present a new method that proposes mathematically supported refinements to analyse the fossil assemblage age structure from another viewpoint. We test whether an observed mortality pattern might correspond to the natural attrition mortality for a population stable over the long term. The mortality profiles are usually employed by palaeontologists to identify the factors affecting the faunal assemblages and their formation and by zooarchaeologists to open discussions concerning the prey selection strategies and the predator's behaviour. Our method can help zooarchaeologists to interpret the hunting and/or scavenging strategies, the prey preference and the predation pressure of humans and others predators (solitary ambush predators, social cursorial carnivores, scavengers, etc.). Moreover, using the approach presented here researchers could evaluate the viability of a specific hunting strategy for a herd population in the wild or the

et al. (2013). The values for these variables may be obtained for a fossil species from allometric relationships or comparing to a closely related living species, as detailed in Rodr  guez-G  mez et al. (2013). For example, Table 1 estimates these variables for three large mammal species. The fecundity and maximum lifespan for *Bison priscus* were assumed to be similar to those estimated by Rodr  guez-Gomez et al. (2013) for *Bison voigteditensis*.

#### b. Mortality profiles.

Three fossil populations of steppe bison (*Bison priscus*) were selected from three different sites to illustrate the use and performance of the presented method: Il'Skaya (Hoffecker et al., 1991), Mauran and Coudoulous (Brugal and David, 1992). The mortality profiles for these populations are described in Munson and Marean (2003) as histogram summaries of the data which they extracted from Hoffecker et al. (1991) and Brugal and David (1992). They provide percentage frequencies per age cohort. However, the percentage frequencies have been transformed into proportions in order to make a probabilistic interpretation. All of these data are shown in Table 2.

**Table 1**  
Physiological variables for *Mammuthus* sp., *Sus scrofa* and *Bison priscus*. The values inside the cells represent the fecundity defined as the number of female offspring per female. The first row represents the age in years and the maximum lifespan for each species corresponds to the older age for which a fecundity value is written. Lifespan is defined as the age at which a non-representative proportion of the population remains alive (5%). The justification for these values is the same as in (Rodr  guez-G  mez et al., 2013).

Age	1	2	3	...	11	...	16	17	...	26	...	60
<i>Mammuthus</i> sp.	0	0	0	0	0	0	0.5	0.10	0.10	0.10	0.10	0.10
<i>S. scrofa</i>	0.175	1.75	1.75	1.75	1.75	1.75						
<i>Bison priscus</i>	0	0	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26		

sustainability of a management strategy for a domestic population. Furthermore, the refinement proposed in this work could help to differentiate among the theoretical mortality profiles widely used in the literature.

We use a Leslie Matrix to model the population dynamics because of its widely recognized suitability for describing population dynamics (Caswell, 2000; Keyfitz and Caswell, 2005). The introduction of this matrix projection model was developed by Bernardelli (1941), Lewis (1942) and Leslie (1945, 1966, 1948) [bib\\_Leslie\\_1966](#). In this sense, the main goal of this study was to show how the living age structure of a fossil population may be reconstructed from an attritional mortality profile assuming this age structure can be mathematically modelled using a survival model. This modelling approach also addresses other relevant questions. For example, the demographic parameters such as life expectancy at birth, birth rate or mortality rate can be determined based on the survival model instead of the original data.

## 2. Materials

The data used can be classified into two different structures:

#### a. Physiological variables.

Any species can be characterized by two variables, lifespan ( $n$ ) and fecundity at age  $i$  ( $a_i$ ). The lifespan is the age when a non-representative proportion of the population remains alive (5%). We arbitrarily set the value to 5% because this value is commonly used as the border for improvable situations. The fecundity ( $a = [a_1, \dots, a_n]$ ) is the number of female offspring per female. Both variables are defined similarly in Rodr  guez-G  mez

**Table 2**  
Mortality profiles for the *Bison priscus* populations from the Il'Skaya, Mauran and Coudoulous sites (the proportion of individuals observed in each age interval). The expected mortality profiles have been found based on the survival profile of a stable population following a Weibull model. This survival profile has and associated (CDF) cumulative density function (they are complementary). The mortality for each interval may be computed as the difference between the proportion of individuals in the interval and the proportion of individuals in the next interval of the CDF. See also Fig. 1.

Age	Observed mortality profiles			Expected mortality profiles		
	Il'Skaya	Mauran	Coudoulous	Il'Skaya	Mauran	Coudoulous
[0,1.6]	0.28	0.35	0.54	0.34	0.31	0.60
(1.6, 3.2]	0.33	0.17	0.24	0.18	0.19	0.10
(3.2, 4.8]	0.15	0.16	0.06	0.12	0.13	0.05
(4.8, 6.4]	0.09	0.08	0.09	0.09	0.10	0.04
(6.4, 8]	0.11	0.09	0.03	0.06	0.07	0.03
(8,9.6]	0.02	0.09	0.03	0.05	0.05	0.02
(9.6,11.2]	0	0.05	0.01	0.03	0.04	0.02
(11.2,12.8]	0	0.01	0	0.03	0.03	0.01
(12.8,14.4]	0	0	0	0.02	0.02	0.01
(14.4,16]	0.02	0	0	0.02	0.02	0.01
>16				0.06	0.04	0.11

## 3. Methods

### 3.1. Population age structure, the survival models

A robust description of the age structure for a fossil population is required as a first step. The next consideration is how the data were obtained. As stated above, the methods used to estimate the age of individual fossils (dental eruption, dental attrition, epiphyseal fusion and skeletochronology) produce interval age estimates.

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