

Paleodemographic analysis of a fossil porcupine (*Hystrix refossa* Gervais, 1852) population from the Upper Pleistocene site of Geula Cave (Mount Carmel, Israel)

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ABSTRACT

For decades zooarchaeological studies mainly focused on teeth age profiles to derive central hypotheses concerning human subsistence during the Pleistocene. Behavior was often related to hunting and/or scavenging strategies according to two models: attritional versus catastrophic. However, few studies have estimated basic demographic parameters using standard methods of population ecology, which are necessary for a more confident interpretation of animal paleopopulation structures. Thanks to a remarkably rich fossil bone assemblage from the Upper Pleistocene cave of Geula (Mount Carmel, Israel), in this paper we perform a paleodemographic analysis of *Hystrix refossa*, Gervais 1852 (Mammalia, Rodentia). We first consider phylogenetic and morphometric dental criteria for the comparison of Pleistocene porcupine species, followed by an examination of taphonomic conditions of the bone assemblage. We focus strongly on the age structure of the fossil population, presenting a new methodological approach that combines life tables and Leslie matrix models – one of the best-known methods in population ecology for assessing population growth and age distribution. We detail demographic parameters derived from cross-sectional life tables and past trends in the porcupine population at Geula Cave using simple matrix projection model. Finally, we were able to perform an elasticity analysis to identify which demographic component was potentially the most critical for influencing growth. We show that the population of *H. refossa* did not decline or shrink but was stable. Our results permit us to characterize Geula Cave as a natural shelter for porcupines, with limited evidence to scavenging and hunting by either hyenas or humans.

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1. Introduction

The fossil remains of porcupines are found at many archaeological sites in the Near East dating from the early Pleistocene onwards. However, where porcupines occur they are usually represented by only a few remains. They have been identified at such sites as Ksar 'Akil in Lebanon (Kersten, 1992), Douara Cave in the Syrian desert (Payne, 1983), Ubeidiya (Tchernov, 1986), Oumm Qatafa (Vaufrey, 1951), the Wadi Mughara Caves (Bate, 1937) and Kebara Cave in Israel (Wreschner et al., 1960), as well as from several more recent Israeli sites (Rabinovich and Horwitz, 1994; Tchernov, 1988). Unfortunately, none of these sites have provided

sufficient data for the analysis of paleodemography of porcupine populations. An exception is the Upper Pleistocene deposits of Geula Cave (Mount Carmel, Israel). With 837 remains including 112 fetal/newborn elements, the porcupine (*Hystrix refossa*) is more abundant at Geula than at any other site in the Near East.

Geula Cave provides a unique opportunity to study the paleodemography of *H. refossa* since the taphonomic processes are well documented and the sample is large enough to apply time-specific models or cross-sectional life tables, as developed by Deevey (1947), and to use a Leslie matrix model (Leslie, 1945). We detail step-by-step the application of the method which has the potential to advance our understanding of paleodemography in paleobiological contexts, but which has rarely been applied to paleobiological data. Starting from the premise that the mortality profiles of predator-free populations differ from those of populations subject to predation, the primary goal of this article is to present an analysis of the population dynamics of porcupines at Geula. This study should provide insight into whether the Geula porcupines are

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a non-predated population which regularly lived in the cave, or if the age structure reflects predation or scavenging by humans and/or the spotted hyena.

2. The site: Geula Cave

Geula Cave is situated along the northern slopes of Mount Carmel, at an altitude of 200 m above sea level and 15 m above Wadi A-Tin, which flows into the Giborim River, in the suburbs of the city of Haifa, Israel (Fig. 1). This cave was originally very large but was damaged by quarrying activities during the 19th century. Two of the chambers of the original cave remain intact and were excavated by Wreschner during the years 1958–1964. Based on geological observations, Wreschner et al. (1960) concluded that the two chambers, named Geula A and B, represent the rear part of the cave. Geula A was devoid of any archaeological sediment. Three sedimentary layers were identified in chamber B: A, B1 and B2, all of which contained Middle Paleolithic (Upper Mousterian) material, while the fourth and lowest layer (named C) was sterile. Radiocarbon dates derived from charred bones provided an age of $42,000 \pm 1,700$ years B.C. (Gr. N° 4221) for stratum B1 (Wreschner, 1967). However, this early date might be altered if re-dated using contemporary radiocarbon methods.

All lithics ($n = 171$) recovered from Geula Cave are associated to what was once termed the “Levallois–Mousterian”, but today it is being referred to as Levantine Mousterian. Three fragmented human bones identified as archaic *Homo sapiens* were found in layer B2 and have been described by Arensburg (2002). Paleontological studies were carried out by Wreschner et al. (1960), as well as Petter and Heintz (1969) on the large mammal remains, which includes those of carnivores. Heller (1970) and Frenkel (1970) conducted the analysis of the small vertebrates remains. Recently, a re-analysis of the large mammal remains was conducted by Monchot (2005). This assemblage was composed of 12,505 remains, most of which was unidentifiable bone fragments and only 2186 (17.5%) of which could be identified and analyzed (Table 1). The most interesting find is the remarkable faunal list comprising numerous species of carnivores, dominated by the spotted hyena and a classic spectrum of southern Levantine herbivores, with gazelle and Mesopotamian fallow deer being the most numerous. However, the porcupine, whose remains were found in exceptional abundance, is clearly the most common taxon. A preliminary zooarchaeological and taphonomic study clearly shows that Geula Cave served as both a hyena den and a porcupine lair, a unique phenomenon in Mount Carmel and in the Middle and Near East. The low density of lithic remains confirms the short occupation by hominins at a time when the cave was abandoned by carnivores (Monchot, 2005).

3. Material: the porcupine population

3.1. Taxonomy

The taxonomy of the fossil *Hystricidae* is debated since most specimens of *Hystrix* are represented by small collections of teeth exclusively. Intra-specific variability in shape, size, and enamel patterns of the occlusal surfaces makes biometric and morphological comparisons problematic, especially in instances where stages of attrition are not indicated. The genus *Hystrix* is represented in Europe by four fossil species (*Hystrix parvae*, *Hystrix primigenia*, *H. refoffa* and *Hystrix vinogradovi*) and one extant species, *Hystrix cristata* (Van Weers, 1994). In the Southern Levant, however *Hystrix indica* is the only porcupine that exists today (Mendelsohn and Yom-Tov, 1999). The porcupine remains from the Geula Cave were initially ascribed to a new species, *Hystrix angressi*, established

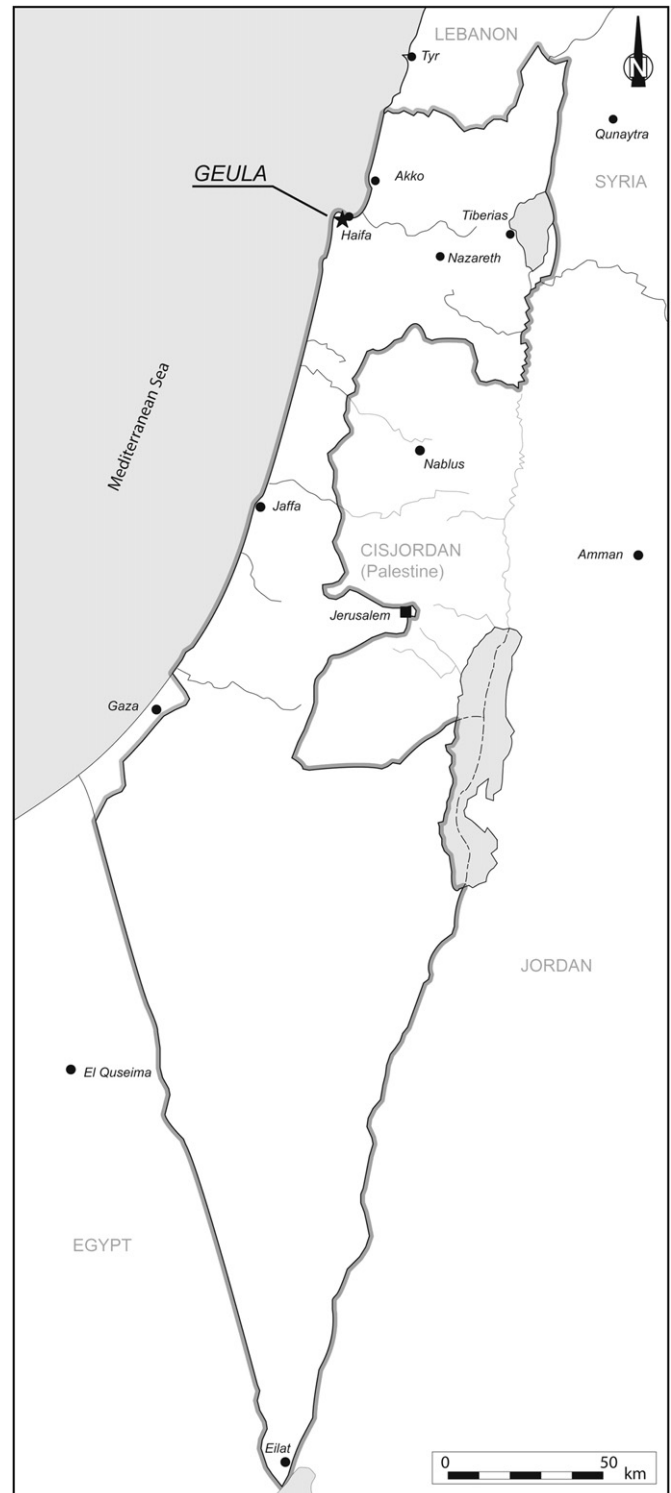


Fig. 1. Location of Geula Cave.

by Frenkel (1970) and based on a pair of maxillaries (the holotype), as well as hundreds of cranial and post-cranial parts. *H. angressi* was found to be considerably larger than most known species of porcupine, including *Hystrix vinogradovi* from the last interglacial of central Europe, yet smaller than the African early Pleistocene species *Hystrix major*. Frenkel found a close similarity between *H. angressi* and *H. cristata* with regard to the nasal bones, the high and narrow occiput and the similar position in the root of the

Table 1

List of the main species from Geula Cave (Mount Carmel, Israel). NISP = Number of Identified Specimen; MNIC = Minimum Numbers of Individuals combining stratigraphic information and the tooth wear stages.

Species		NISP	% NISP	MNIC	% MNIC
Ungulates					
<i>Dama mesopotamica</i>	Fallow deer	309	14.13	15	8.82
<i>Gazella gazella</i>	Gazelle	221	10.11	13	7.65
<i>Bos primigenius</i>	Aurochs	209	9.56	9	5.29
<i>Sus scrofa</i>	Wild boar	118	5.4	9	5.29
<i>Cervus elaphus</i>	Red deer	44	2.01	6	3.53
<i>Capreolus capreolus</i>	Roe deer	38	1.74	4	2.35
<i>Capra aegagrus</i>	Wild goat	13	0.59	3	1.76
<i>Alcelaphus buselaphus</i>	Hartebeest	5	0.23	2	1.18
<i>Dicerhorinus</i> sp.	Rhinoceros	22	1.01	3	1.76
Equids	Horse/Donkey	21	0.96	4	2.35
<i>Hippopotamus amphibius</i>	Hippopotamus	1	0.05	1	0.59
Carnivores					
<i>Crocota crocuta</i>	Spotted hyena	107	4.89	9	5.29
<i>Panthera pardus</i>	Leopard	7	0.32	3	1.76
<i>Canis aureus</i>	Golden jackal	4	0.18	3	1.76
<i>Vulpes vulpes</i>	Common fox	33	1.51	4	2.35
cf. <i>Caracal caracal</i>	Caracal	1	0.05	1	0.59
<i>Martes foina</i>	Beech marten	12	0.55	4	2.35
<i>Vormela peregusna</i>	Marbled polecat	2	0.09	2	1.18
<i>Genetta genetta</i>	Common genet	2	0.09	1	0.59
cf. <i>Mellivora capensis</i>	Honey badger	2	0.09	1	0.59
<i>Herpestes ichneumon</i>	Egyptian mongoose	1	0.05	1	0.59
Primates					
<i>Homo sapiens</i>	Modern human	3	0.14	1	0.59
Hyracoids					
<i>Procavia capensis</i>	Rock hyrax	12	0.55	3	1.76
Rodents					
<i>Hystrix refoffa</i>	Porcupine	837	38.29	58	34.12
Lagomorphs					
<i>Lepus capensis</i>	Brown hare	2	0.09	1	0.59
Reptilia					
<i>Testudo graeca</i>	Greek tortoise	160	7.32	9	5.29
Total		2186	100	170	100

mandibular incisor. However, Tchernov (1986) suggested that *H. angrissi* was a size variant of *H. indica* and that no species other than *H. indica* occupied the eastern Mediterranean region during the Pleistocene. Like the other aforementioned species, the dimensions and morphology of the Geula remains concur with *H. refoffa*, and consequently this species is now listed as a synonym of *H. refoffa* (Van Weers, 1994, 2005).

3.2. Skeletal representation

Several complete mandibles, palatal parts, many isolated teeth, and a considerable number of limb bones were identified (Table 2). As observed in some Pleistocene prehistoric sites (e.g., Zourah Cave, Aouraghe, 2001) or in natural contexts (e.g., Saint-Vallier, Huguency, 2004; Pirro Nord, Rook and Sardella, 2005; Fish Hoek lair, Kerbis Peterhans and Singer, 2006), the mandibles and the isolated teeth (in particular the lower molars) are over-represented when compared with the long bones. No differences were observed in the distribution between the right and left sides in the NISP (Kolmogorov–Smirnov = 0.457, $p > 0.10$). These arguments suggest that the animals died *in situ* with few post-depositional disturbances rather than a transport of carcasses to the site by predators.

3.3. Taphonomy

A common surface modification observed on 145 mammalian specimens (Monchot, 2005: Table 3) from Geula Cave is gnawing by

Table 2

H. refoffa skeletal element frequencies in number of identified specimens (NISP) and Minimum Number of Individuals of frequency (MNIF). In bracket, elements belong to juveniles (Deciduous teeth, unfused bones or foetal/newborn bones). % Surv. = % survival calculated as = $MNI \times 100/36$ (maximum MNI estimated by the right upper incisor).

Skeletal elements	Left	Right	Ind/un.	Total	MNIF	% Surv.
Skull fragment	7	4	28	39	—	—
Maxillary with teeth	5	2	3 (R + L)	10	8	22.2
<i>Isolated upper teeth</i>						
Incisor	26	36	—	62	36	100
P4	—	—	11	11	6	16.7
M2	5	4	7	16	9	25
M3	—	—	15	15	8	22.2
Mandibles without teeth	6	5	7	18	6	16.7
Mandibles with teeth	15	17	—	32	17	47.2
<i>Isolated lower teeth</i>						
Incisor	32	26	—	58	32	88.9
dP4	—	—	9	9	5	13.9
P4	5	8	6	19	11	30.6
M1	17	11	2	30	18	50
M2	6	7	—	13	7	19.4
M3	10	10	—	20	10	27.8
Lower/upper molar (M1)	—	—	32	32	—	—
Enamel fragment of molar	—	—	4	4	—	—
Enamel fragment of incisor	—	—	54	54	—	—
Ribs	—	—	1	1	—	—
Vertebra	—	—	27	27	—	—
Scapula	2	—	(4)	6	2 + (2)	11.1
Humerus	12 + (12)	7 + (7)	1 + (5)	44	12 + (15)	75
Radius	9	6	(16)	31	9 + (8)	47.2
Ulna	11 + (5)	7 + (5)	(4)	32	11 + (7)	50
Carpal	—	—	19	19	—	—
Metacarpal 2	—	—	8	8	4	11.1
Metacarpal 3	—	—	15	15	8	22.2
Metacarpal 4	—	—	15	15	8	22.2
Metacarpal 5	—	—	9	9	5	13.9
Coxal	2	—	—	2	2	5.6
Femur	7 + (9)	13 + (7)	3 + (7)	46	15 + (13)	77.8
Patella	1	1	—	2	1	2.8
Tibia	5	7	(3)	15	7 + (2)	25
Fibula	4	4	3	11	6	16.7
Talus	4	5	—	9	5	13.9
Calcaneus	5	2	—	7	5	13.9
Metatarsal 2	—	—	10	10	5	13.9
Metatarsal 3	—	—	18	18	9	25
Metatarsal 4	—	—	16	16	8	22.2
Metatarsal 5	—	—	4	4	2	5.6
Phalanx	—	—	19	19	—	—
Metapodial	—	—	1	1	—	—
Fetal long bone indet.	—	—	28	28	—	—
Total	222	201	414	837	36/58^a	100

^a 58 correspond to the maximum of MNI after dental recombination (see Table 4 for more details).

porcupine in a similar fashion to that described in the literature (Diedrich, 2009; Maguire et al., 1980; Brain, 1981; Rabinovich and Horwitz, 1994). They include different types of gnawing damage, such as using the broad, chisel-shaped upper and lower incisors, and scooping or hollowing out of cancellous bone, usually accompanied by damage around the bone shaft margins. *H. cristata* commonly chews on bones for calcium and to sharpen its incisors (Nowak, 1999). In the Geula assemblage, all sizes of ungulate bone have been affected by porcupine damage, which is found on a wide range of skeletal parts. In particular, the porcupines preferentially

Table 3
Dimensions of *H. refossa* isolated teeth in mm with frequency (N), mean, standard deviation (SD), range (Minimum and Maximum), Skew. (Skewness), Kurt. (Kurtosis), coefficient of bimodality (B) and coefficient of variation (CV). The coefficient of bimodality is calculated as $B = (\text{Skewness}^2 + 1)/(\text{Kurtosis} + 3)$ (Bryant, 1991).

Isolated teeth	N	Mean	SD	Mini	Maxi	Skew.	Kurt.	B	CV
<i>Lower P4</i>									
Length	18	10.956	0.931	9.2	12.3	-0.252	-0.933	0.515	0.085
Breadth	18	8.144	0.551	7.0	9.2	0.094	-0.405	0.325	0.068
Height	17	16.029	3.336	7.0	19.0	-1.250	1.123	0.596	0.208
Ratio H/L	17	1.485	0.369	0.593	1.891	-0.927	0.024	0.512	0.248
<i>Lower M1</i>									
Length	13	9.162	1.036	7.1	10.7	-0.562	-0.507	0.528	0.113
Breadth	13	7.408	0.368	7.0	8.3	1.383	0.924	0.742	0.050
Height	12	12.392	1.065	6.5	17.5	-0.140	-1.220	0.573	0.298
Ratio H/L	12	1.349	0.342	0.607	1.786	-0.615	-0.147	0.483	0.254
<i>Lower M2</i>									
Length	13	9.854	0.685	8.7	11.0	-0.144	-0.987	0.507	0.070
Breadth	13	7.692	0.480	6.9	8.3	-0.326	-0.853	0.515	0.062
Height	13	17.138	3.095	13	23.1	0.209	-0.585	0.432	0.181
Ratio H/L	13	1.738	0.282	1.275	2.287	0.298	-0.470	0.430	0.162
<i>Lower M3</i>									
Length	19	9.695	0.774	8.3	11.0	-0.133	-0.623	0.428	0.080
Breadth	19	7.337	0.724	6.1	8.4	-0.351	-0.923	0.541	0.099
Height	17	13.882	2.504	9.7	18.1	0.240	-0.823	0.486	0.180
Ratio H/L	17	1.459	0.371	0.936	2.157	0.519	-0.845	0.589	0.255
<i>Upper P4</i>									
Length	10	10.140	0.664	9.2	11.0	-0.064	-1.542	0.689	0.065
Breadth	10	8.530	0.827	7.6	9.9	0.684	-1.001	0.734	0.097
Height	10	15.640	3.512	9.4	20.6	-0.090	-0.699	0.438	0.225
Ratio H/L	10	1.563	0.421	0.855	2.239	-0.016	-0.774	0.449	0.270
<i>Upper M1</i>									
Length	11	9.091	0.604	8.2	10.0	0.070	-1.133	0.538	0.066
Breadth	11	7.455	0.572	6.3	8.2	-0.308	-0.315	0.408	0.077
Height	10	11.850	2.210	9.1	15.0	0.113	-1.287	0.591	0.187
Ratio H/L	10	1.286	0.177	0.989	1.531	-0.295	-1.083	0.567	0.138
<i>Upper M2</i>									
Length	15	9.933	0.584	8.7	10.6	-0.503	-0.692	0.543	0.059
Breadth	15	8.233	0.739	7.0	9.2	-0.249	-1.238	0.603	0.090
Height	14	13.036	2.498	8.0	17.5	-0.354	-0.315	0.419	0.192
Ratio H/L	14	1.332	0.315	0.769	2.011	0.119	0.068	0.331	0.236
<i>Upper M3</i>									
Length	15	8.880	0.845	7.1	10.0	-0.702	-0.364	0.566	0.095
Breadth	15	7.260	0.533	6.4	8.1	-0.174	-0.759	0.460	0.073
Height	15	10.100	2.096	6.0	14.1	-0.139	-0.111	0.353	0.207
Ratio H/L	15	1.156	0.315	0.632	1.831	0.875	0.811	0.463	0.272

gnawed the astragalus, calcaneus and phalanges, which appear to be sculpted as a result. Gnawing damage also appears on deer antlers, gazelle horn cores and even fragments of wild boar canines (Monchot, 2005; Monchot and Aouraghe, 2009). It is difficult to know whether porcupine activity in the cave was preceded by that of hyenas or humans since, to some degree, porcupines collect food remains left by sympatric carnivores (Diedrich, 2009; Kerbis Peterhans and Singer, 2006). Conversely, as described by Brain (1981) for South African cave sites, the porcupines at Geula Cave may have been the primary agents responsible for introducing and gnawing the bones in the cave leaving only fragments behind.

4. Methodology: ageing a porcupine population

4.1. Sequence of tooth eruption and degree of attrition

Both fossil and living porcupines have semi-hypsodontal cheek teeth and a dental formula of 1.0.1.3./1.0.1.3. Among porcupines, as with all mammals, the order of eruption of the teeth, in both the lower and the upper jaws start from front to back. Incisors appear first, followed by pd4, and ending with the third molar (M3). By one and a half years, the pd4 is replaced by the permanent P4. All the cheek teeth exhibit a similar pattern of four to five enamel cusps. Following tooth wear, enamel folds appear. These are initially contiguous, but individualized. With continued wear, each fold

becomes isolated from the external enamel and forms an isolated island. Evidently, the first tooth to appear is always the most worn. The overall trend is such that the number of folds decreases as the tooth wears down, until all folds have disappeared, and in certain stages of wear the first 'islands' appear, which eventually reach a maximum. In older specimens, the number of 'islands' is diminished until the last one has disappeared in a totally worn tooth.

Frenkel (1970) proposed a system of ageing porcupines by separating the teeth into five distinct groups based on degrees of attrition (Fig. 2). However, Frenkel's system does not provide enough information for the identification of actual age categories in months. We have added a sixth category for fetal remains since none were identified in the original study. Another ageing system, proposed by Van Weers (1990), recognizes 39 wear patterns, divided into 8 classes for the upper molars, and 6 classes with many subdivisions for the lower molars of *Hystrix brachyura*. This extremely large number of patterns is not applicable to the remains from Geula because the attrition stages in *H. brachyura* differ from those observed in *H. refossa*. Moreover, in many classes it is difficult to make a correlation between the two species since we do not have an understanding of the duration of each wear group.

The aforementioned semi-hypsodonty varies between teeth. The lingual portion of the upper cheek teeth is higher-crowned than the labial portion, the opposite of that is observed for the lower cheek teeth. Furthermore, the enamel height differs

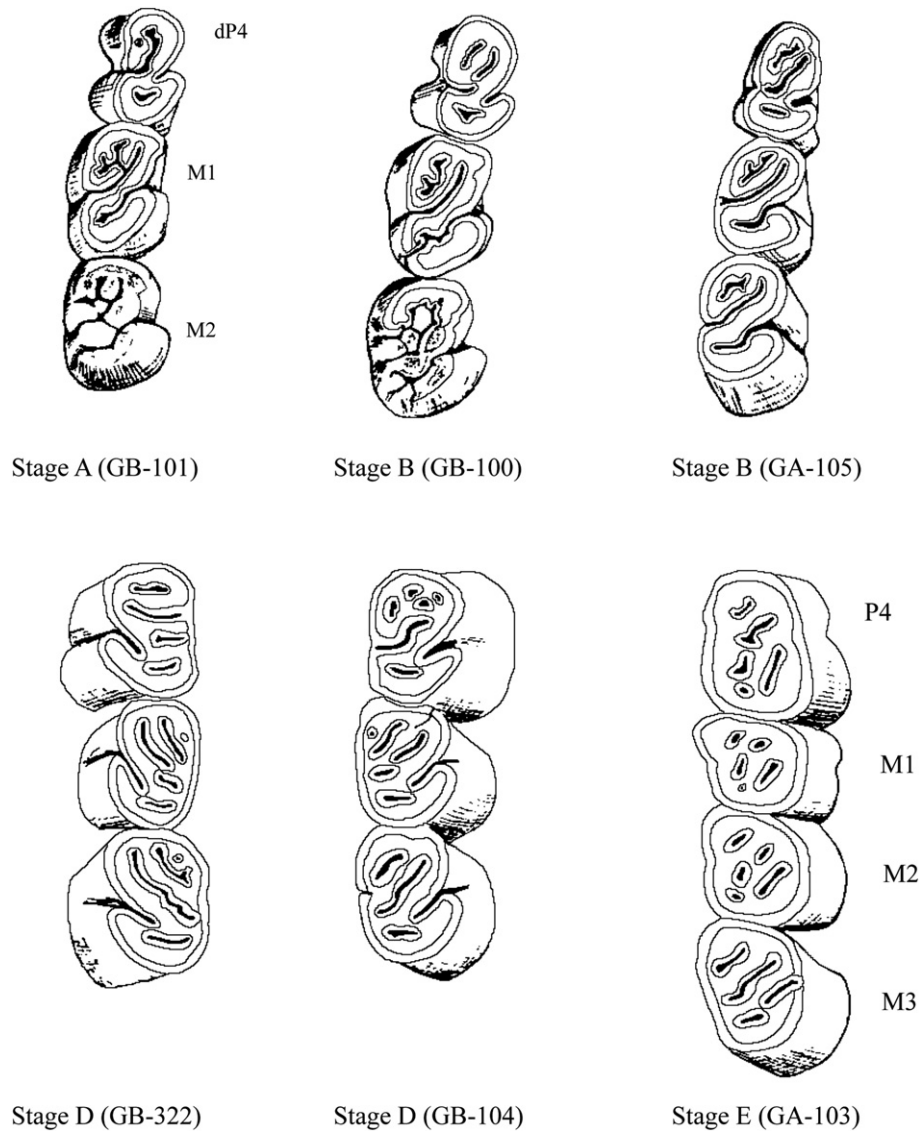


Fig. 2. Attritional wear stages observed on select porcupine mandibles from Geula Cave (after Frenkel, 1970: Plate III). Stage A = one or more enamel islands become isolated on dP4. Stage B = one or two enamel islands become isolated only on dP4 and on M1. Stage C = at least on island becomes isolated on M1 and M2 with P4 generally in the process of eruption. Stage D = only one loop on M1 and M2 is in the contact with the external enamel surrounding the tooth. Stage E = all the loops on all teeth are transformed into islands (one loop on M3 may not yet be isolated).

between the labial and lingual faces of the lower cheek teeth (Sen, 2001). Hypsodonty is usually estimated on mammalian cheek teeth by means of the ratio of maximum enamel height versus the maximum occlusal length on the most intact and unaltered teeth possible. However, Van Weers (1990, 1993) proposed to use crown height, which is the height of the tooth body without the roots (anteriorly, from the inter-root area to the occlusal surface), instead of enamel height. According to Van Weers' (1990) procedure, the occlusal breadth, length and height were measured with calipers to the closest millimeter. No occlusal measurement could be taken on very young molars, or on teeth with damaged occlusal surfaces.

The standard univariate statistics for each measured cheek tooth are presented in Table 3 and constitute an original reference sample for *H. refoffa*. The lower/upper M3 appears to be slightly smaller than the remaining teeth, contrary to the lower/upper P4, which appears to be the longest and broadest tooth. With respect to morphology, the dimensions do not show significant

differences between the lower and upper M1 and M2 (Student's *t* test, length $M_1/M_2 = 2.00$, $p > 0.05$; length $M^1/M^2 = 3.58$, $p > 0.05$), we felt confident to treat the teeth as one whole sample, as suggested by Van Weers (1990) for the Malayan porcupine. Values of *B*, the coefficient of bimodality, greater than 0.555 may indicate a bimodal or polynomial distribution (Bryant, 1991). Some values of *B* clearly show a non-normal distribution, confirming the relationship between age, tooth wear and crown height. However the small size of the sample in each tooth age interval does not allow us to present statistical results by age group (i.e., non-significant).

We assigned individuals to an age interval using teeth in mandibles as well as isolated teeth, on the basis of Frenkel's wear stages and age-specific sequences of tooth replacement by analogy with Cape porcupines of known-age (*Hystrix africaeustralis*) born in captivity at the Experimental Farm of the University of Pretoria. Age of the latter group of animals was determined during bi-weekly examinations conducted by Van Aarde (1985). We also

took fetal bones into account in the first age interval. By applying knowledge of the biology of *H. cristata* (Nowak, 1999) and *H. africae australis* (Van Aarde, 1987), we established the first age interval at 0–5 months, to represent newborn animals; individuals from 5 to 8 months were considered as juveniles; animals between 8 and 18 months, when sexual maturity is attained, were classified as immature animals; and the next age groups, respectively from 18 to 30 and from 30 to 48 months, were grouped as adults. In the wild, the lifespan of the Cape porcupine is less than 10 years (Van Aarde, 1987) but considering that there have been cases of individuals reaching ages up to 15 years (Nowak, 1999) we have chosen to regroup the oldest adults from 48 to 144 months (i.e., a maximum longevity of 12 years).

4.2. Mortality profiles (attritional pattern versus catastrophic pattern)

Several methods exist for assigning a specimen to an age interval (Pike-Tay, 2001; Ruscillo, 2006; various papers in Wilson et al., 1982). Mortality curves are usually constructed from dental remains of large mammals (essentially ungulates: Grayson, 1978, 1984; Ringrose, 1993; Lyman, 1994; Steele, 2004, 2005) or small mammals (rabbit-sized or smaller: Korth and Evander, 1986; Bryant, 1991; Weissbrod et al., 2005) since teeth are generally the best-preserved elements. Age profiles are then usually related to attritional or catastrophic mortality patterns (Brugal and David, 1993; Klein, 1982; Klein and Cruz-Urbe, 1983; Klein et al., 1983; Levine, 1983; Lubinski, 2000; Lubinski and O'Brien, 2001; Lyman, 1994; Steele and Weaver, 2002; Stiner, 1990). Attritional mortality characterizes a “living population” and is affected by ecological parameters such as neo-natal mortality, disease, predation, and in some instances, hunting by humans, all of which preferentially affect the most vulnerable individuals; specifically, the very young and the very old. In other species, sexual dimorphism has been shown to produce different mortality patterns (Barnosky, 1985; Mihlbachler, 2007); this in relation with the Rensch rule which shows that larger mammals tend to exhibit greater sexual dimorphism (Rensch, 1950). A typical attritional age profile takes the form of a “U”-shaped curve because young and old animals die off more often than prime adults. Conversely, catastrophic mortality is generated by natural events including bush fires (Spinage, 1972), floods (Haynes, 1985, 1987), volcanic eruptions (Lyman, 1987), or mass hunting strategies when game was hunted by chasing herds over a cliff (Olsen, 1989). This differs from the attritional mortality profile by exhibiting an “L”-shaped curve, reflecting the age distribution of the living “population” in which the number of individuals in each age group decreases regularly with age.

However, fossil age structures often result in different patterns than these two ideal U-shaped and L-shaped curves, with assemblage biases stemming from a multitude of possible causes (Fernandez, 2009; Monchot and L  chelle, 2002). Considering the potential weakness of such theoretical profiles, and the fact that they are not used in dynamic to evaluate impacted or stable populations, we advocate a new methodological approach using life tables and Leslie matrices.

4.3. Life tables and Leslie matrix

Application of life tables in an archaeological context is possible when the sample is large enough and the mode of accumulation is well documented (Fernandez and Legendre, 2003; Fernandez et al., 2006; Fernandez and Boulbes, 2010; Koike and Ohtaishi, 1987; Kurt  n, 1953, 1954, 1983; Van Valen, 1963, 1964, 1965; Voorhies, 1969). In this study, we used both cross-sectional life

tables (time-specific model) and the “Leslie” matrix models. Life tables were primarily introduced by biologists in order to determine the lifespan of insects (Pearl and Miner, 1935). They are constructed from direct observations of the age structure of dead (d_x) or living (l_x) animals. This approach was popularized by Deevey (1947) to estimate survival rates of mammal and bird populations. Three main models are employed according to the sampling and the nature of the population: *Age-specific*; *Composite*; *Static* or *Time-specific*. A stationary age structure through time is required excepted for the latter model, with constant survival and fecundity parameters (Caughley, 1966; Krebs, 2001; Ricklefs, 1997; Ricklefs and Miller, 1999; Sinclair, 1974). It is also assumed that the age structure of the sample corresponds to a local population in the absence of immigration and emigration (Caughley, 1977; Caughley and Sinclair, 1994). Opportunities to follow cohorts for long periods of time are rare and these strict assumptions are unlikely to be met in any population of wild mammals (Gaillard et al., 1998; McCullough et al., 1994; Menkens and Boyce, 1993). At Geula, the sample from three archaeological layers corresponds at least to three time-deposits, so we retained the Time-specific model which enables to consider age-specific data as if cohorts were followed through time (Johnson, 1994). Furthermore, right and left elements of NISP suggest that animals died *in situ* with few post-depositional disturbances, allowing us to treat the sample as cohorts of same local population sharing the same shelter through time.

The entire set of age-specific demographic parameters of *H. refoffa* from Geula Cave were defined as follows:

- (x) refers either to age interval or age class (in months or any time interval). There is often confusion between them. According to Caswell (2001), the former begins at 0 and the latter at 1. Starting from this definition, we used the term “age class” when no upper limit is given as it is required for specific analysis (i.e., life table, life-cycle diagram, time-step projection). On the contrary we used “age interval” for interval of age with upper limit.
- (n_x) refers to the Minimum Number of Individuals (MNI), a method used for estimating the minimal number of individual animals of a given taxon represented in a bone assemblage, which involves counting of sided elements. MNI is usually calculated from the most abundant bone or tooth from either the left or right side of the animal (Poplin, 1976; Lyman, 2008: Table 2.4).
- (d_x) refers to the proportion of individuals of the whole cohort(s) dying at each age. It can be derived from the variable (l_x) series by:

$$d_x = (l_x - l_{x+1})$$

- (l_x) refers to survivorship that is to say the fraction of the cohort surviving during age interval x to $x+1$. The first value can be expressed per 1, 100 or 1000:

$$l_{x+1} = (l_x - d_x)$$

- (s_x) refers to age-specific survival rate. Proportion of individuals surviving from age x to age $x+1$:

$$s_x = l_{x+1}/l_x$$

- (m_x) refers to the average number of offspring for each age interval. Most demographic analyses of vertebrate populations have involved a female-dominant model, such that only demographic parameters of females are considered (see

Table 4 Minimum number of individuals (MNI) for *H. refossa* derived from lower teeth and fetal humeri for each age interval. MNI calculations for each age interval according to tooth eruption sequences: [0–5] = 15 (12 left + 3 undetermined) fetal humeri + 3 dP4; [5–8] = 5 right + 2 undetermined dP4; [8–18] = 3 left + 3 undetermined dP4; [18–30] = 5 left M/2; [30–48] = 10 left M/1; [48–144] = 12 left M/1. *: Preservation of left and right teeth according to the formula: $97.06 = \frac{[(85 + 80) \times 100]}{170}$ **. Given an interval of 5 months in first age class interval, the frequency density is: $0.062 = \frac{(31.03/5)}{100}$.

Age class (months)	Fetal bones		dP/4		P/4		M/1		M/2		M/3		NISP	%NISP	MNI	%MNI	Frequency density**
	Left	Right	L	R	L	R	L	R	L	R	L	R					
0–5	12	7	1	3			1	3					28	13.60	18	31.03	0.062
5–8			3	5	4		4	2	2	2	1	2	17	8.25	7	12.07	0.040
8–18			3	2	5		4	3	5	4	2	2	23	11.16	6	10.34	0.010
18–30						4	2	4	3	5	2	2	24	11.65	5	8.62	0.007
30–48						6	8	2	10	8	1	6	64	31.07	10	17.24	0.010
48–144						4	7	2	12	7	1	4	50	24.27	12	20.69	0.002
∑	12	7	5	7	10	9	15	6	31	23	2	17	206	100	58	100.0	

Total left teeth = 85.
 Total right teeth = 80.
 Total expected = 170.
 *Dental preservation (%) = 97.06.

Gaillard et al., 2003). This is a valid model as long as we can assume that males are not limiting reproductive output of the females, which is likely to be the case in most natural populations. Indeed male survival does not affect the growth rate nor the age structure of a given population. We therefore assumed a balanced sex-ratio at birth and inferred m_x from Van Aarde (1987), as half the number of offspring produced alive at birth by a female of age x .

- ($l_x m_x$) refers to the average number of offspring produced by individuals in each age interval, which is simply the product of l_x and m_x
- (R_0) refers to the net reproductive rate and corresponds to the average number of offspring produced by an individual during its lifetime and is also interpreted as a population stability index. $R_0 < 1$ indicates the members of the cohorts that are not replacing themselves such that the population is in decline. $R_0 > 1$ denotes an increasing population while $R_0 = 1$ means a stable and perfectly stationary population. This index corresponds to the sum of fecundity rates in all age intervals. Summed across all ages, this is also the average lifetime reproduction:

$$R_0 = \sum l_x m_x$$

The use of matrix models to describe the demography of animal populations was first developed by Bernardelli (1941) followed by Lewis (1942) and Leslie (1945, 1966). Leslie matrices also provide a means of identifying critical life-history stages and serve as an aid

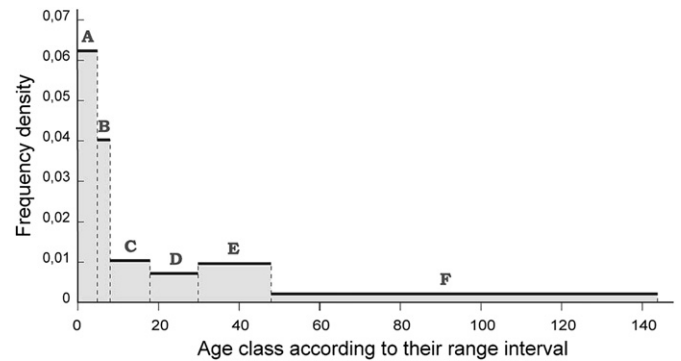


Fig. 3. Histograms (mortality profiles) of age-dependent wear classes of *H. refossa* from Geula. Data derived from Table 4.

Table 5 Life table of *H. refossa* from Geula constructed from raw data. See details of calculation in text. (n_x) Age class (in months). (n_x) Minimum Number of Individual in each age class. (d_x) Fraction of the whole cohort dying during the age class x to $x+1$. (l_x) Proportion of individuals surviving from the start of the first age class. (s_x) Age-specific survival rate. (m_x) Average number of offspring for each age class. ($l_x m_x$) Fecundity rate in each age class. (R_0) Net reproductive rate.

Age class (x) months	n_x	d_x	l_x	s_x	m_x^a	$l_x m_x$
0	–	0.000	1.000	0.690	0.000	0.000
5	18	0.310	0.690	0.825	0.000	0.000
8	7	0.121	0.569	0.818	0.250	0.142
18	6	0.103	0.466	0.815	0.563	0.262
30	5	0.086	0.379	0.545	0.693	0.263
48	10	0.172	0.207	0.000	0.693	0.143
144	12	0.207	0.000	0.000	0.693	0.000
$R_0 = \sum l_x m_x$						0.811
$\sum n_x$	58					

^a Calculated from van Aarde (1987: Table 1).

Table 6
Standardized life table of *H. refossa* from Geula with regular interval (1 year) in each age class considering a longevity of 12 years.

Age class (x) year	l_x	s_x	m_x^a	$l_x m_x$
0	1.000	0.525	0.000	0.000
1	0.525	0.800	0.250	0.131
2	0.420	0.737	0.563	0.236
3	0.310	0.667	0.693	0.215
4	0.206	0.667	0.693	0.143
5	0.138	0.667	0.693	0.095
6	0.092	0.667	0.693	0.064
7	0.061	0.667	0.693	0.042
8	0.041	0.667	0.693	0.028
9	0.027	0.667	0.693	0.019
10	0.018	0.667	0.693	0.013
11	0.012	0.667	0.693	0.008
12	0.008	0.667	0.693	0.006
$R_0 = \sum l_x m_x$				1.001

^a Calculated from van Aarde (1987: Table 1). Calculations for s_x detailed in Appendix.

for animal management. Stable age distributions are not required for population projections. Leslie matrices have become a standard in population ecology and have been extensively discussed in reference books (Caswell, 2001; Keyfitz and Caswell, 2005). In this study we used the simplest matrix projection model (Lewis–Leslie) as presented here:

$$\begin{pmatrix} f_0 & f_1 & f_2 & \dots & f_{12} \\ S_0 & 0 & 0 & \dots & 0 \\ 0 & S_1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & S_{11} & 0 \end{pmatrix} * \begin{pmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_{12}(t) \\ n(t) \end{pmatrix} = \begin{pmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_{12}(t+1) \\ n(t+1) \end{pmatrix}$$

The state of the population is described as a vector $n(t)$, whose entries $n_i(t)$ give the numbers of individuals in each age interval.

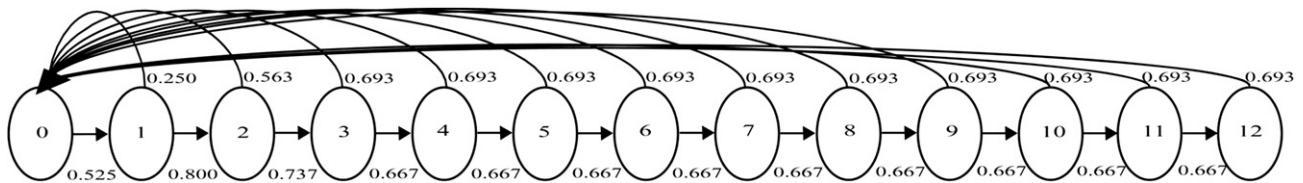


Fig. 4. Life-cycle diagram of *H. refossa* from Geula. Age classes (in years) are in circles. Arcs represent age-specific fertility rates m_x and arrows are age-specific survival probabilities s_x . Data derived from Table 6.

Table 7
Projection matrix and vital statistics of *H. refossa* from Geula. Data m_x (first line of the matrix) and s_x (plotted on the sub-diagonal) entered in the matrix are from Table 6 (see also details of calculation in the text).

0.000	0.250	0.563	0.693	0.693	0.693	0.693	0.693	0.693	0.693	0.693	0.693	0.693
0.525	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.800	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.737	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.667

Asymptotic growth rate $\lambda = 1.002$.
Exponential growth rate $r = 0.002$.
Mean length generation $Tb = 4.78$.

Therefore $n(t+1) = An(t)$. Then matrix A is constructed with age-specific fecundity (f_0, f_1, \dots) corresponding to the values of m_x in its first row, and the diagonal below contains the probability of survival from one age to the next with age-specific survival (S_1, S_2) corresponding to the values of s_x . The projection of the matrix, with the initial population $n(t)$ which is a vector whose elements are n_x individuals gives a new vector $n(t+1)$. This specifies the new number of individuals in each age interval at the next succeeding census of the projection interval.

5. Results

Since taphonomic processes affect fossil assemblages and may cause an over or under estimation of some age intervals, we evaluated the degree of dental preservation using Brain’s method, by comparing the proportion of left and right teeth (Brain, 1981). The results indicate a high degree of dental preservation (97%) showing that the remains were well preserved after their original deposition. Table 4 presents the MNI in each of the six age intervals and shows a clear L-shaped structure (Fig. 3).

In Table 5, the calculations from the life table indicate a declining population ($R_0 = 0.811$) but the value results from the unequal age intervals. Consequently, we derived a standardized life table (Table 6) with regular intervals and constant survival beyond 3 years of age as supported by Van Aarde (1987: Fig. 2) (see Caughley, 1977 for a full treatment of standardization). The age structure indicates a net reproductive rate of 1 (i.e., $R_0 = 1$), which perfectly characterizes a stationary population.

To build our matrix projection, as a first step, we drew a life-cycle diagram, starting from the data displayed in Table 6 (see the detail of calculations in Appendix). In Fig. 4, age intervals are located in circles. The arcs represent the average number of offspring for each age interval (m_x), and the arrows indicate survival rates (s_x) from age x to age $x+1$. Data were entered into a pre-breeding Leslie matrix (Caswell, 2001) and we used the software PopTools, developed by Hood (2008), to perform the calculations.

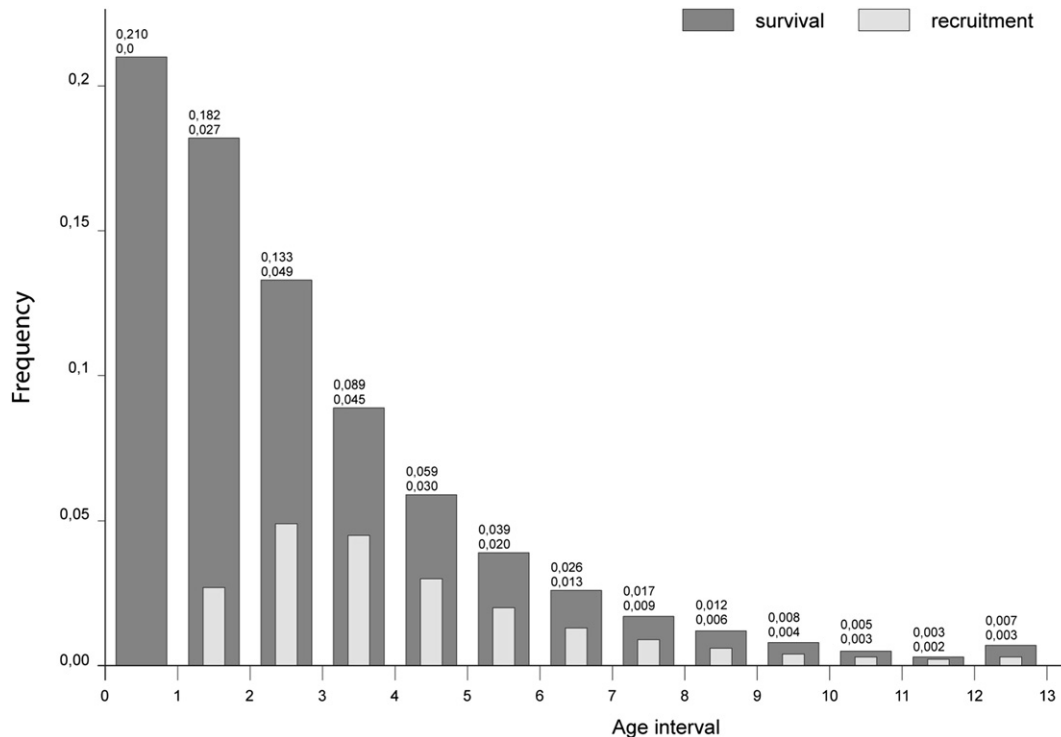


Fig. 5. Elasticity values for recruitment and survival stages of *H. refossa* from Geula. Data derived from Table 9.

population very quickly becomes stationary starting from the fifth projection interval $t_{(5)}$ and λ converges towards a constant and definitive value at $t_{(24)}$.

To better understand our results we investigated elasticity, which has become standard practice in demographic analysis since the works of Demetrius (1969) and Keyfitz (1971). Elasticity generates noise in measuring the proportional change of λ and identifies which vital rates (e.g., survival and recruitment) are more likely to influence overall changes in population size (Caswell, 1978, 2001; De Kroon et al., 1986). Elasticity values of *H. refossa* are available in Table 9 and clearly show that a given change in adult survival would have a greater effect on λ . For example, as shown in Fig. 5, for an age interval 0–1, the elasticity indicates that a 1% increase in adult survival leads to increase the lambda by 0.210% that is to say that it has a greater impact on the population growth rate than the same proportional change in any other vital rate.

6. Conclusion

By combining the two approaches of life tables and Leslie matrices, we characterized the demographic parameters for an archaeological population of *H. refossa*. We believe that we have shown the potential of such powerful tools in comparison with attritional and catastrophic model that are usually employed to describe mortality profiles and to infer behavior in paleobiological contexts. We demonstrated that the population of *H. refossa* from Geula Cave was not in decline nor shrinking but was stationary, as shown by the exponential rate of increase $r = 0.002$ and projections in time with $\lambda = 1.002$. Stable populations of vertebrates usually fluctuate with r around a mean of zero (if so $\lambda = 1$). If environmental conditions become more favorable for instance, due to an increase in the amount of food available, or a low density implying negligible competition, a population will usually increase, with a rise of fecundity as well as a decline in

mortality (Caughley and Sinclair, 1994). Elasticity analysis pointed out the critical parameter that would make the strongest contribution to variation in population growth for *H. refossa*. At Geula Cave, it appears to have been adult survivorship that was the most critical parameter in the life history of *H. refossa*. This is also the case in modern populations of large herbivores (Gaillard et al., 1998).

According to Van Aarde (1987), feral cape porcupine usually live in extended family groups where each group is comprised of at least one adult male, one adult reproducing female and a varying number of siblings. High juvenile survival rates during the early stages of life at Geula can be explained by parents who protected offspring against intruders and who accompanied them during foraging excursions for the first few months of life. In the cave, the remains of fetal bones in all the layers testify to the presence of many pregnant porcupine females, which occupied the site alternatively with hyenas and humans. We suggest that these predators did not affect porcupine age structure, as indicated by estimates of the demographic parameters we provided. Geula Cave was therefore a shelter for different cohorts of porcupines with limited scavenging or hunting by hyenas or man. The recent overview of numerous Late Pleistocene localities in Germany clearly indicates that different species of *Hystrix* used hyena dens and recycled their accumulated bone rubbish. It appears that bone fragments of spotted hyenas prey found in the caves were a special and easy way to obtain a source of calcium (Diedrich, 2009). From this point of view, the very often association between porcupine and hyena such as in Geula Cave will have to be explored in terms of paleoecological interactions and sympatry.

This contribution to mammalian paleodemography represents a further step in the growing collaboration between paleontologists, zooarcheologists and ecologists in studying life history dynamics in different fossil contexts.

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Appendix A. Example of the calculation for the survival values (s_x) in Table 6

Starting from the survival values of Table 5, $S_{0-5} = 0.690$ and $S_{5-8} = 0.825$ thus we easily get $S_{0-8} = 0.690 \times 0.825 = 0.56925$. We also know $S_{8-18} = 0.818$ and we have to consider an interval of 10 to get $\sqrt[10]{0.818} = 0.9801112$ so that $S_{8-12} = (0.9801112)^4 = 0.9227869$. Thus in Table 6 we find $S_{0-1 \text{ year}} = 0.56925 \times 0.9227869 = \mathbf{0.525}$.

Starting from the Table 5 values, $S_{8-18} = 0.818$ and we have to consider an interval of 10 to get $\sqrt[10]{0.818} = 0.9801112$ so that $S_{12-18} = (0.9801112)^6 = 0.8864456$. We also know $S_{18-30} = 0.815$ and we have to consider an interval of 12 to get $\sqrt[12]{0.815} = 0.9830972$ so that $S_{18-24} = (0.9830972)^6 = 0.9027734$. Thus in Table 6 we find $S_{1-2 \text{ years}} = 0.8864456 \times 0.9027734 = \mathbf{0.800}$.

Starting from the Table 5 values, $S_{18-30} = 0.815$ and we have to consider an interval of 12 to get $\sqrt[12]{0.815} = 0.9830972$ so that $S_{24-30} = (0.9830972)^6 = 0.9027734$. We also know $S_{30-48} = 0.545$ and we have to consider an interval of 18 to get $\sqrt[18]{0.545} = 0.9668417$ so that $S_{30-36} = (0.9668417)^6 = 0.816831$. Thus in Table 6 we find $S_{2-3 \text{ years}} = 0.9027734 \times 0.816831 = \mathbf{0.737}$.

Starting from the Table 5 values, $S_{30-48} = 0.545$ and we have to consider an interval of 18 to get $\sqrt[18]{0.545} = 0.9668417$ so that $S_{36-48} = (0.9668417)^{12} = 0.667213$ which represents in Table 6 the survival of $S_{3-4 \text{ years}} = \mathbf{0.667}$. This value is used for animals between the ages of 3 and 12 years because we assume a constant survival rate beyond 30 months of age as mentioned in the text.

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