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# Population dynamics of *Equus conversidens* (Perissodactyla, Equidae) from the late Pleistocene of Hidalgo (central Mexico): Comparison with extant and fossil equid populations

Alexis Pérez-Pérez <sup>a</sup>, Victor Manuel Bravo-Cuevas <sup>b</sup> , Philippe Fernandez <sup>c</sup>

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## Highlights

- Paleodemography of *Equus conversidens* is explored by life-tables and Lewis-Leslie matrices.
- Mortality pattern of *E. conversidens* is a prime-dominated profile.
- Hunting pressure by non-human predators is related to the mortality pattern.
- Predation and resource availability regulate population dynamics of *E. conversidens*.

## Abstract

The Mexican horse *Equus conversidens* is a representative member of the Quaternary North American megafauna. Systematics, phylogeny, and stable isotope ecology of this species are known in some detail, although information regarding population ecology is unexplored. Numerous fossil remains (isolated teeth, mandibles, skulls, and postcranial elements) of this horse have been collected from Pleistocene deposits that outcrop at southeastern Hidalgo, central Mexico. The available dental sample is suitable for recovering some aspects of its population dynamics. Our study compares life history traits of cohorts of *E. conversidens* from the state of Hidalgo to extant and Pleistocene species of equids from North America (United States and Canada), Europe (France), and Africa (Rwanda, Namibia). Life tables and age-structured models allow us to describe demographic parameters and mortality patterns. We highlight that *E. conversidens* was a typical K-strategist with high probability of surviving to adulthood with asymptotic growth rate ( $\lambda = 1.05$ ) indicating a population close to balance. Considering the mammalian associations from different habitats in southeastern Hidalgo and the flexible diet of *E. conversidens*, we suggest that ambush (*Panthera atrox*) and cursorial predators (*Canis dirus*) played a major role in the prime-dominated mortality pattern of this species. The presence of a woodland-grassland ecosystem that sustained a high diversity of herbivores and the occurrence of large-sized predators suggest that the population dynamics were regulated by resource availability and selective predation, as it occurs in populations of the extant plains zebra, *E. quagga*.



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Autoecology; Paleodemography; Equid cohorts; Mortality patterns; Leslie matrices

## 1. Introduction

Life tables and matrix population models are very efficient tools now widely applied in ecology to better understand the life history traits of plants and animal species (Fujiwara and Diaz-Lopez, 2017). In both cases, multiple cohorts are particularly well suited to interpret age structures through time (Fernandez et al., 2017).

Age-specific life tables were first applied in experimental biology to better understand invertebrate mortality patterns (e.g. Pearl and Miner, 1935). These models were then developed further, especially in many studies for wildlife management of large mammals (Caughley, 1966) or birds (Botkin and Miller, 1974). At the same time, matrix population models have been used to describe the evolution of multiple cohorts (projections in time, stationary *versus* unbalanced living populations) (Bernardelli, 1941; Lewis, 1942; Leslie 1945, 1948), followed more recently by the very well-known and impressive work of Caswell in the field of applied mathematical demography (2001).

Nevertheless, life table models have been poorly exploited in paleodemography except in a few studies involving large mammals (Kurtén, 1953; 1954a; 1954b; 1983; Van Valen, 1963; 1964; 1965; Voorhies, 1969; Reher 1970; 1973; 1974; Nimmo 1971; Hulbert, 1982; 1984; Koike and Oitaishi, 1985; 1987; Lyman, 1987; Turnbull and Martill, 1988; McDonald, 1996; Fernandez and Legendre, 2003; Muhlbachler, 2003; 2007; O'Sullivan J., 2005; Fernandez et al., 2006; Fernandez 2009; Prentiss et al., 2014), dinosaurs (Erickson et al. 2006, 2009; Steinsalz and Orzack, 2011), and small mammals (Korth and Evander, 1986; Bryant, 1991; Muhlbachler, 2012). In a similar way, age-structured Leslie models have received little interest in paleodemography although they have become a standard in population ecology (Fernandez and Boulbes, 2010; Monchot et al., 2012; Rodríguez-Gómez et al., 2014, 2016; Martín-González et al., 2016).

In this study we highlight the remarkable properties of life table demographic parameters (see below i.e.  $l_x$ ,  $s_x$ ,  $R_0$ ,  $r$ ,  $T_b$ , etc.) with Leslie matrix model projections considering an outstanding sample of different horse species from different ecological contexts and mammalian associations. Our *E. conversidens* sample consists of at least 50 individuals from the late Pleistocene of the state of Hidalgo. Here we compare it to the fossil cohorts of *Equus lambei* (Bluefish Caves, Canada) (Burke and Cinq-Mars, 1998), extant *Equus quagga* (Akagera, Rwanda) (Spinage, 1972), *Equus zebra* (Khomas Hocland, Namibia) (Joubert, 1974), *Equus caballus* (Pryor Mountain, Montana, United States) (Garrott and Taylor, 1990), *Equus hemionus* (Southern and Dzungaria Gobi, Mongolia) (Lkhagvasuren et al., 2017), and *Equus asinus* (Grand Canyon, Arizona, United States) (Ruffner and Carothers, 1982). In addition, key paleobiological contexts in France were selected for inter-specific age structures comparisons, such as the hyena den of Fouvent with its accumulation of *Equus germanicus*, and the Bau de l'Aubesier with its heavy anthropogenic hunting pressure on *Equus mosbachensis* (Fernandez and Legendre, 2003; Fernandez et al., 2006). Each of these populations offers an exceptional opportunity to provide detailed information about recent and fossil equids whose causes of death and demographic parameters are known.

In order to avoid biases resulting from different methodological approaches, individual ages for all fossil equids were obtained from polynomial equations whose parameters were estimated by bootstrapping starting from the dental height intervals of known age individuals (Fernandez and Legendre, 2003). Ternary diagrams and histograms are used to illustrate the age frequencies between equid populations in order to relate them to the two dominant theoretical types of mortality: attritional *vs.* catastrophic, which are usually considered key components in describing fossil age structures in the zooarchaeological literature.

Taken together, all of these aspects allow us to address issues that are central to our understanding of the Pleistocene *E. conversidens*: which demographic parameters are the most sensitive to the final state of the population from southeastern Hidalgo, central Mexico? And which human or non-human predators have affected the assemblage of *E. conversidens*?

## 2. Study area

The studied material comes from seven neighbor localities in southeastern Hidalgo known as Ventoquipa (HGO-9: 20°01' N - 98°20' W, 2289 m.a.s.l.); Barranca Piedras Negras (HGO-23: 20°03'03" N - 98°37'23" W, 2460 m.a.s.l.); Barranca del Berrendo (HGO-28: 20°01'20.7" N - 98°37'37.9" W, 2458 m.a.s.l.); Barranca San Agustín (HGO-29: 20°00'27.7" N - 98°37'59.9" W, 2467 m.a.s.l.); Jagüey Viejo (HGO-42: 20°02.311" N - 98°35.885" W, 2528 m.a.s.l.); Arroyo las Cajas



minimum of 1.75 km (between HGO-28 and HGO-29) (Fig. 1). In this area, there are Quaternary deposits that consist of clay, silt, and conglomeratic lenses set in a fluvial environment (Bravo-Cuevas, 2002) (Fig. 2). An important sample of fossil remains has been recovered from these sedimentary deposits. The record includes rodents, felids, dire wolves, ground sloths, giant armadillos, horses, llamas, pronghorns, deer, bison, mammoths, gomphotheres, and mastodons (Bravo-Cuevas, 2001, 2002; Bravo-Cuevas et al., 2009a, 2009b, 2011, 2012, 2013, 2015, 2016, 2017, 2020). The presence of material belonging to *Bison* and *Panthera atrox* is related to the Rancholabrean North American Land Mammal Age (NALMA) (Bell et al., 2004). The identification of *Bison antiquus* indicates that the maximum age of the fossil-bearing deposits is of about 60 ka (Bravo-Cuevas and Vázquez-Cortés, 2019), corresponding to the Wisconsin glaciation in North America.



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Fig. 1. Index map of the study area in southeastern Hidalgo, central Mexico. The capital of the state, Pachuca city (large star) and the fossil localities are indicated. Localities: HGO-9, Ventoquiya; HGO-23, Barranca Piedras Negras; HGO-28, Barranca del Berrendo; HGO-29, Barranca San Agustín; HGO-42, Jagüey Viejo; HGO-46, Arroyo las Cajas; HGO-47, El Barrio.

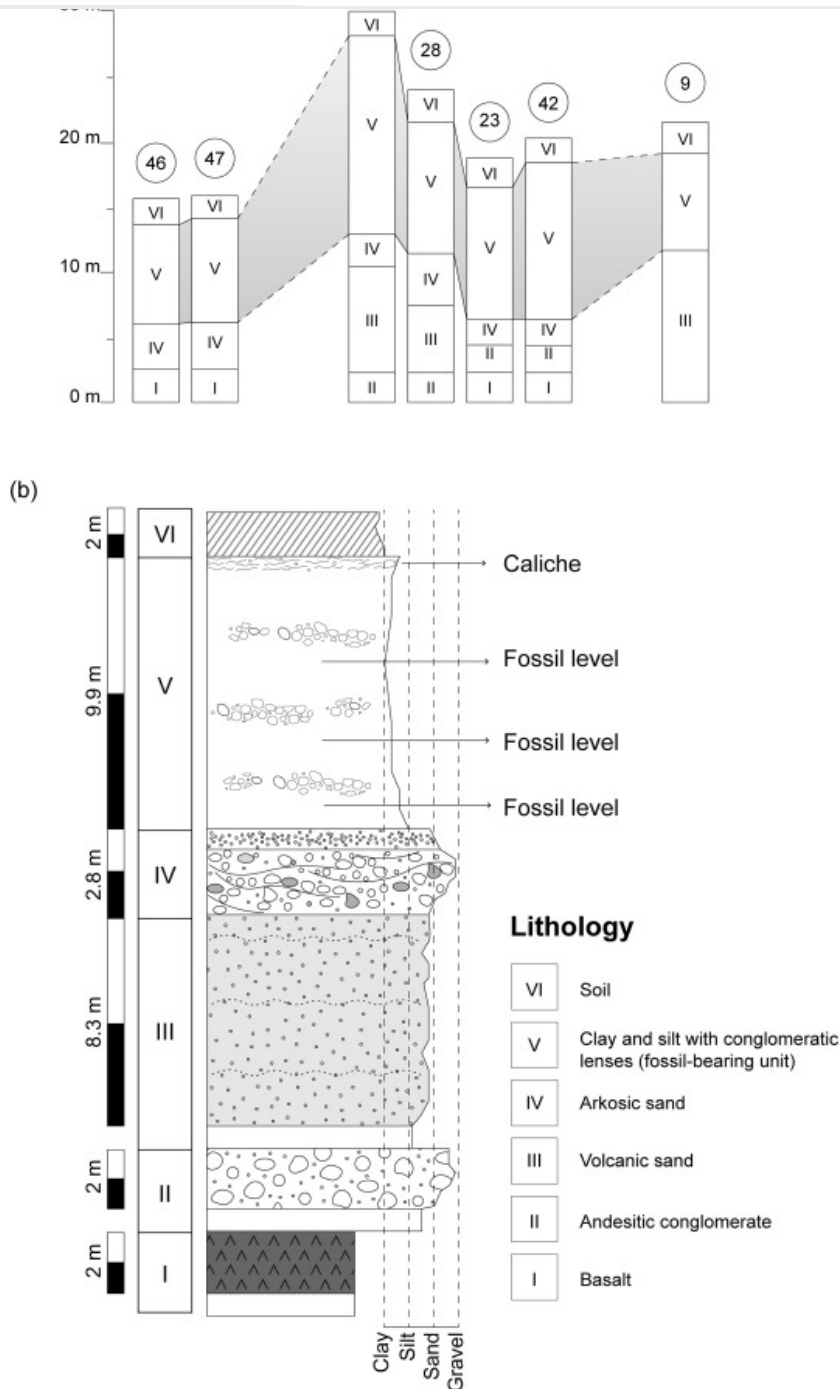

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Fig. 2. (a) Lithostratigraphic correlation of the fossil localities and (b) Generalized lithostratigraphy of the fossil localities. The localities are labeled as in Fig. 1.

### 3. Material and methods

#### 3.1. Dental fossil sample

The sample referable to *E. conversidens* considered here consists of 85 dental anatomical elements (Table 1). The fossil material includes two skulls with right and left P2-M3, one partial skull with right P2-M3, one left maxillary fragment with P2-M1, one right mandible fragment with p3-m3, one right mandible fragment with p2-m2, two left mandible fragments with p2-m3, five right mandible fragments with p2-m3, one right mandible fragment with p4-m3, two mandible fragments with right and left p2-m3, and 69 isolated cheek teeth (40 of the upper dentition and 29 of the lower



Table 1. Teeth specimens of *Equus conversidens* from Hidalgo. Upper/lower case for upper and lower dentition respectively (R, right; L, left).

Locality	Locality ID	Catalogue No.	Dental element	Crown height (mm)	Estimated age (years)
Ventoquipa	HGO-09	UAHMP-286	Rp4	58.1	7.43
Barranca Piedras Negras	HGO-23	UAHMP-179	RP3	71.6	5.99
		UAHMP-409	RM3	45.8	9.05
		UAHMP-181	Lp4	53.6	7.94
Barranca del Berrendo	HGO-28	UAHMP-941	RP2	38.7	9.42
		UAHMP-509	RP4	57.5	8.06
		UAHMP-905	RP3	67.0	6.74
		UAHMP-314	RP4	63.7	6.83
		UAHMP-319	LM1	43.3	9.97
		UAHMP-594	LM1	13.1	23.85
		UAHMP-901	LM1	34.7	12.47
		UAHMP-909	RM1	34.7	12.47
		UAHMP-316	LM2	66.6	6.69
		UAHMP-942	LM2	65.0	6.92
		UAHMP-356	LM3	61.3	7.36
		UAHMP-317	RM3	20.8	18.67
		UAHMP-939	RM3	60.8	7.40
		UAHMP-943	RM3	67.9	6.75
		UAHMP-215	Lp3	65.7	7.00
		UAHMP-353	Lp4	64.7	6.75
		UAHMP-4145	Rp4	50.2	8.40
		UAHMP-945	Lm1	44.0	8.26
		UAHMP-1916	Lp4	66.7	6.51
		UAHMP-403	Rm1	28.9	12.52
UAHMP-508	Rm1	78.7	4.49		
UAHMP-950	Rm1	19.4	17.51		
UAHMP-1915	Rm1	54.3	6.96		
UAHMP-4130	Rm1	20.0	17.14		
UAHMP-944	Lm2	74.8	5.97		
UAHMP-326	Rm3	38.7	11.16		
UAHMP-390	Rm3	65.3	6.63		
Barranca San Agustín	HGO-29	UAHMP-417	LP4	33.9	13.40
		UAHMP-415	LM1	47.4	9.06



		UAHMP-491	LM1	59.6	7.12
		UAHMP-510	RM3	27.2	14.91
		UAHMP-492	Lp2	53.8	5.33
		UAHMP-512	Lp2	49.6	6.27
		UAHMP-418	Lp4	65.3	6.68
		UAHMP-932	Lm1	59.7	6.52
		UAHMP-504	Lm1	49.6	7.46
		UAHMP-387	Rm1	65.8	6.04
		UAHMP-4145	Lm2	56.0	8.36
		UAHMP-495	Rm2	41.3	10.62
		UAHMP-416	Lm3	64.8	6.70
		UAHMP-511	Lp3	Unworn	2.67
		UAHMP-4170	Rm1	Unworn	0.92
Barranca Jagüey Viejo	HGO-42	UAHMP-935	LP2	48.6	8.02
		UAHMP-902	RM1	37.3	11.63
		UAHMP-936	Lp4	28.3	15.47
		UAHMP-949	Rm1	71.2	5.53
		UAHMP903	Rm2	36.2	11.90
		UAHMP-937	Rm2	59.9	7.94
Las Cajas	HGO-46	UAHMP-1913	LP2	54.9	7.07
		UAHMP-1911	LM2	51.9	8.95
		UAHMP-1912	LM2	53.1	8.72
		UAHMP-507	Lp4	63.5	6.88
El Barrio	HGO-47	UAHMP-2706	RP2	37.3	9.65
		UAHMP-1125	RP3	50.1	9.13
		UAHMP-4014	RP3	44.8	10.03
		UAHMP-900	LP4	63.6	6.84
		UAHMP-1116	LP4	26.1	17.09
		UAHMP-2709	LP4	57.9	7.61
		UAHMP-2711	LP4	66.2	6.49
		UAHMP-1123	RP4	39.7	11.39
		UAHMP-1112	LM1	56.9	7.48
		UAHMP-4017	LM1	43.7	9.87
		UAHMP-1123	RM1	37.5	11.55
		UAHMP-2712	RM1	12.8	24.05
		UAHMP-4122	RM1	29.5	14.47
		UAHMP-4123	RM1	46.8	9.19
		UAHMP-4162	RM1	48.4	8.86



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UAHMP-A	RM1	24.3	16.93
UAHMP-1910	RM2	52.9	8.77
UAHMP-4019	RM2	53.7	8.63
UAHMP-2710	Lp3	18.6	18.26
UAHMP-4018	Lp4	30.9	14.10
UAHMP-2704	Rp4	60.6	7.18
UAHMP-B	Rp4	49.7	8.95
UAHMP-2704	Lm1	72.6	5.37
UAHMP-4120	Lm1	50.8	7.32
UAHMP-957	Rm1	57.3	6.71
UAHMP-1109	Rm1	34.9	10.37
UAHMP-2708	Lm3	25.3	15.87
UAHMP-4016	Lm3	71.3	5.48
UAHMP-4215	Lm3	55.5	8.10

### 3.2. The fossil cohorts of *E. conversidens* from Hidalgo

An ancient population or paleopopulation consists of different cohorts through time and retains the basic traits of an extant population (e.g., genetic flow, age structure, and interbreeding) (MacFadden, 2008; Fernandez et al., 2017). The time interval of a deposit should be considered to characterize a paleopopulation (Hunter, 1998). The mammalian association from Hidalgo represents a within-habitat assemblage set in a fluvial environment, time-averaging estimated limits range from decades to 100 kyrs (Behrensmeyer et al., 2000; Bravo-Cuevas et al., 2017). This time interval has been considered as a geological time duration that meets the assumption of multiple deposits corresponding to different cohort generations that interacted as an entire population (MacFadden, 2008).

MacFadden (1989) observed that intraspecific variation in dental characters in paleopopulations of fossil horses has coefficients of variation ( $V$ ) that range from about 4% to 10%, as it occurs in extant horse populations. In this regard, the coefficients of variation related to the anteroposterior length (7.55%) and transverse width (5.59%) of the first upper molars of *E. conversidens* from the state of Hidalgo are less than 10% (Table 2). Consequently, the fossil collection has been treated as a natural assemblage of horses of the same species that shared the same area (southeastern Hidalgo) at the same geological time-interval (late Pleistocene).

Table 2. Coefficient of variation ( $CV$ ) in the anteroposterior length (APL) and transverse width (TW) of M1s of *Equus conversidens* from the late Pleistocene of southeastern Hidalgo, central Mexico (measurements in mm).

Locality	ID	APL	TW
HGO-28	UAHMP-319	22.29	22.6
HGO-28	UAHMP-594	20.89	24.22
HGO-28	UAHMP-901	21.76	24.65
HGO-28	UAHMP-509	24.2	24.22
HGO-29	UAHMP-415	22.86	23.33
HGO-29	UAHMP-491	24.07	23.91
HGO-42	UAHMP-902	24.05	25.57



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HGO-47	UAHMP-1112	23.35	24.11
HGO-47	UAHMP-4017	22.18	22.98
HGO-47	UAHMP-1123	25.66	25.33
HGO-47	UAHMP-2712	20.35	27.44
HGO-47	UAHMP-4122	21.85	23.55
HGO-47	UAHMP-4123	24.92	25.18
HGO-47	UAHMP-4162	26.31	26.97
HGO-47	UAHMP-1116	21.7	23.87
CV		7.55	5.59

### 3.3. Estimation of the number of individuals

Teeth are often the best anatomical elements to estimate the number of individuals in fossil assemblages because they are better preserved than bones and represent diagnostic material for the identification of species (Lyman, 1994). The sample of *E. conversidens* from Hidalgo consists of isolated teeth, mandibles, skulls, and postcranial remains, dental elements being the most abundant (Bravo-Cuevas et al., 2011). For comparative purposes, we used two indices: Minimum Number of Individuals (MNI) (Badgley, 1986) and the total Number of Identified Specimens (NISP) (Lyman, 2008). Assuming multiples cohorts in the seven localities from central Mexico, the total MNI was summed between each one of them and calculated considering the most abundant tooth from one side of the body (left or right). Partial or complete dental series set in skulls or mandibles were counted as one individual for NISP.

When fossil deposits are produced or modified by either humans, carnivores or natural processes such as those caused by micro-organisms, we have to estimate the potential taphonomic biases. Here, we calculated the proportion between left and right teeth according the method of Brain (1981) in order to evaluate dental preservation and potential disturbances of the assemblage.

Finally, together the MNI, NISP and the dental preservation of *E. conversidens* were compared with middle and upper Pleistocene *Equus* populations from France (Table 3).

Table 3. Comparison of the minimum number of individuals (MNI) and the total number of identified specimens (NISP), the frequencies of right and left teeth, and the degree of differential preservation (following Brain, 1981) of the horse population of *Equus conversidens* from the late Pleistocene of southeastern Hidalgo, central Mexico, and selected populations of Pleistocene *Equus* from France (data from Fernandez et al., 2006: Table 3, p. 180).

	MNI	NISP	Left teeth (LT)	Right teeth (RT)	Total expected	Differential preservation (Dp*)
<b>Hidalgo</b>	50	85	50	39	100	89.00%
<b>Bau del'Aubesier</b>	49	353	186	167	372	94.89%
<b>Fouvent</b>	54	464	353	326	706	96.17%
<b>Combe-Grenal</b>	67	396	173	218	436	89.67%

\*

$$Dp = (LT + RT) * 100 / \text{Total expected teeth.}$$

### 3.4. Individual age and age intervals estimation

We took into account isolated teeth and cheek teeth set in the maxilla or the mandible. We used the method of Fernandez and Legendre (2003), which uses crown height to assign each tooth (i.e., P2/p2, M3/m3 ...) to a particular age interval.



coefficients.

The crown height (in mm) was measured using a digital caliper (range 0–150 mm, resolution 0.01 mm, accuracy 0.003 mm, and was taken from the separation of the roots, straight to the occlusal surface along the mesostyle and the ectostylid in the upper and lower cheek teeth respectively. We estimate the measurement uncertainty following the methodology of JCGM (2008), recording a set of 30 measurements of crown height on the same tooth (UAHMP-941). The measurand value is  $\pm 0.0005$ .

The median (1), minimum and maximum (2) age (in years) for each tooth were estimated from the following equations (from Fernandez and Legendre, 2003: Table 5, pp. 1583; Fernandez et al., 2006: Table 2, pp. 180):

$$Age = a_0 + a_1H + a_2H^2 + a_3H^3 \quad (1)$$

$$Age = (a_0 + a_1H + a_2H^2 + a_3H^3) \pm 2E \quad (2)$$

In these equations,  $a_0$  = slope;  $a_1$ ,  $a_2$ ,  $a_3$  = intercept;  $H$  = crown height, and  $E$  = mean prediction error. Estimation of the age distribution of each tooth in appropriate age intervals is detailed in the step-by-step procedure of Fernandez (2009: Fig. 1, pp. 7). In this study, we also compared the age distributions derived from the MNI on the one hand, and the NISP on the other hand using a Kolmogorov-Smirnov non-parametric test and Spearman's rank-order correlation coefficient (Klein and Cruz-Urbe, 1984; Vasileiadou et al., 2007) (Table 4).

Table 4. Comparison of age distribution derived from the minimum number of individuals (MNI) and the total number of identified specimens (NISP) indices, using a Kolmogorov-Smirnov test ( $K-S = 0.735$ ,  $p > 0.10$ ) and Spearman's rank correlation coefficient ( $r_s = 0.881$ ,  $p > 0.01$ ).

Age interval	MNI	NISP
0–3	1.70	1.75
3–6	7.82	10.39
6–9	26.37	37.74
9–12	6.23	17.68
12–15	3.12	7.07
15–18	3.02	6.23
18–21	0.73	2.14
21–24	1.00	2.00
Number of individuals	50	85

Table 5. Life tables of *E. conversidens* (age intervals of three years) using the minimum number of individuals (MNI) and the number of identified specimens (NISP) indices. Demographic parameters described as it is indicated in the method.

	x	$n_x$	$d_x$	$l_x$	$s_x$
MNI	0	0.00	0.000	100.000	0.966
	3	1.70	3.399	96.601	0.838
	6	7.82	15.643	80.958	0.348
	9	26.37	52.749	28.210	0.558

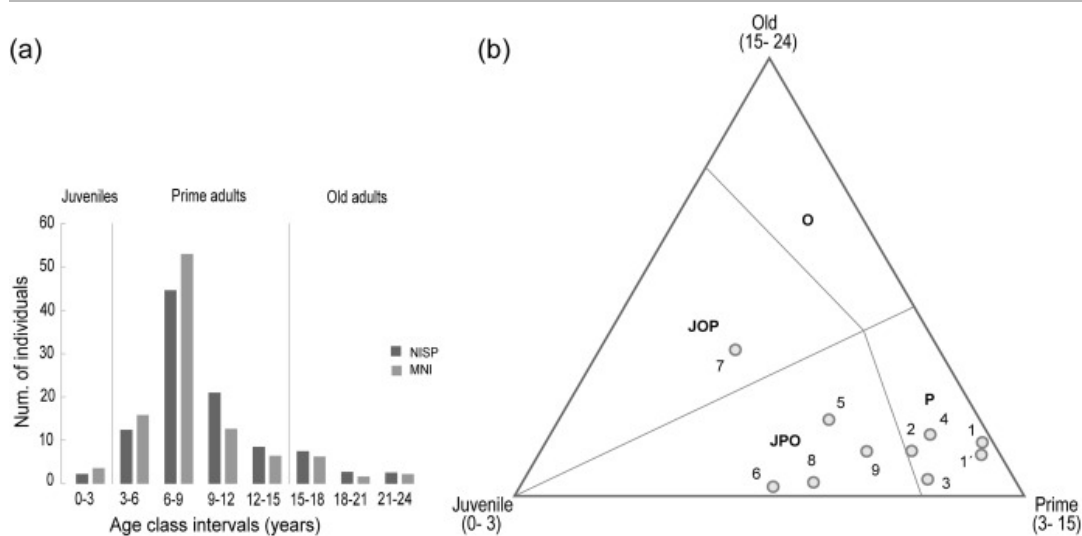
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	12	6.23	12.469	15.740	0.604
	15	3.12	6.235	9.505	0.364
	18	3.02	6.043	3.462	0.578
	21	0.73	1.462	2.000	0.000
	24	1.00	2.000	0.000	0.000
<b>NISP</b>	0	0.00	0.000	100.000	0.979
	3	1.75	2.059	97.941	0.875
	6	10.39	12.225	85.717	0.482
	9	37.74	44.406	41.311	0.497
	12	17.68	20.798	20.512	0.595
	15	7.07	8.312	12.200	0.399
	18	6.23	7.330	4.870	0.483
	21	2.14	2.518	2.353	0.000
	24	2.00	2.353	0.000	0.000

### 3.5. Mortality patterns

We established the age structure of the population of *E. conversidens* with both histograms and ternary diagrams, as they are the most common tools to compare mortality profiles (Stiner, 1991, 1994; Steele, 2005; Steele and Weaver, 2002; Discamps and Costamagno, 2015). MNI and NISP indices were used in histograms where each bar represents the number of individuals that died in each age interval (Fig. 3a). To show the mortality patterns of equids proposed by Discamps and Costamagno, we rebuilt the limits of the areas of the ternary diagram. In the present study, three age categories were retained as with the extant plains zebra *E. quagga* from the Serengeti (Grange et al., 2004: p. 526):

- 1) Juveniles (J) = non-reproductive individuals with an age of 0–3 years (year 3 ending at 36 months).
- 2) Prime adults (Pa) = individuals with an age of 3–15 years (year 3 beginning at 37 months), including potentially reproductive individuals like young adults and adults.
- 3) Old adults (Oa) = individuals with an age greater than 15 years.



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extinct and extant *Equus*. Horse populations: 1, *E. conversidens* (NISP); 1', *E. conversidens* (MNI); 2, *E. lambei*; 3, *E. mosbachensis*; 4, *E. germanicus*; 5, *E. quagga*; 6, *E. zebra*; 7, *E. caballus*; 8, *E. asinus*; 9, *E. hemionus*.

The fraction of Potential Ecological Longevity (PEL) of the population of *Equus conversidens* from Hidalgo was estimated assuming a PEL of about 24 years, corresponding to the oldest individuals (UAHMP-594:  $23.85 \pm 0.38$  years and UAHMP-2712:  $24.05 \pm 0.389$ ), which is comparable to that of the extant *E. quagga* (Spinage, 1972). The PEL was used for the graphical demarcation between the zones in the ternary diagram, considering the following areas: Juveniles-Prime-Old (JPO), Juveniles-Old-Prime (JOP), Prime (P), and Old (O) (sensu nomenclature of Discamp and Costamagno, 2015). The fraction of PEL to each age category is as follows: Juveniles = 12.5%, Prime adults = 50%, and Old adults = 37.5% (Discamp and Costamagno, 2015).

Finally, the mortality pattern of *E. conversidens* from Hidalgo was compared with selected Pleistocene and extant populations of *Equus*.

### 3.6. Population dynamics: life tables and Leslie matrices

A static or time-specific life table model was constructed based on vertical or cross-sectional analysis (i.e., Caughley, 1977; Dodd and Stanton, 1990). This model is suitable for the analysis of the *E. conversidens* population because it considers individuals of all ages belonging to different cohorts and multiple diachronic deposits over time (Fernandez et al., 2017). In this regard, two assumptions must be taken into account:

- (1) time-specific life tables are female-dominated models. However, it is widely accepted that male survival does not affect the population growth rate of most natural mammalian populations (Caswell and Weeks, 1986; Lindström and Kokko, 1998). This implies a balanced sex-ratio at birth (1:1) and a fecundity rate that is half the number of offspring produced alive at birth by a female of a given age.
- (2) it is assumed that the migration processes did not influence the age structure of the studied population (Caughley, 1977).

The life table parameters used here are defined below (see also Fernandez et al., 2017).

- ( $x$ ) refers indiscriminately either to “age interval” or “age class”. Nevertheless, strictly speaking the former begins at 0 and the latter at 1 (Caswell, 2001). In this study the standardization of one-year age intervals was derived from the  $s_x$  values following the procedure of Fernandez and Boulbes (2010: p. 801).
- ( $n_x$ ) is the number of individuals in each age interval. It is derived either starting from the MNI or from the NISP (see calculation above).
- ( $d_x$ ) refers to the proportion of individuals of the whole cohort(s) dying in each age interval. It can be estimated as follows:

$$d_x = (n_x / \sum n_x) * 100 \text{ or by } d_x = (l_x / l_{x+1})$$

- ( $l_x$ ) is the cumulated survivorship and corresponds to the fraction of a cohort that survives to an age  $x$ . The first value can be expressed per 1, 100, or 1000 and subsequent values are estimated as:

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

In a standardized life table with regular pooled age-class intervals where  $d_x$  is not available, the algebraic relation with  $s_x$  calculates the proportion:

$$l_{x+1} = (s_x * l_x)$$

- ( $s_x$ ) refers to the age-specific survival rate. The rate of individuals that survived from age  $x$  to  $x+1$ :

$$s_x = \frac{l_{x+1}}{l_x}$$

- ( $m_x$ ) refers to the fecundity rate. This variable is defined as the average number of descendants per age interval.



half the number of offspring alive at birth produced by a female in each age class, assuming a balanced sexual ratio between males and females of 1:1.

The fecundity of *E. conversidens* from Hidalgo is derived from the age-dependent birth and survival patterns observed in females of the extant plains zebra *E. quagga* (Rubenstein and Nuñez, 2009: table 8.2, p. 206), considering their close phylogenetic relationships (Barrón-Ortiz et al., 2019). To obtain a more accurate approximation in the fecundity rate, we assumed that as in *E. quagga*, females with an age from 17 to 21 years decreased their fecundity by 6.49% (Grange et al., 2004), whereas females over 21 years show low survivorship expectancy by having commonly a null fecundity (Spinage, 1972; Smuts, 1976).

- $(l_x m_x)$  refers to the contribution of a given age interval to the population reproduction as the product of  $l_x$  and  $m_x$ .
- $(R_0)$  refers to the net reproductive rate of a fossil cohort that is calculated as follows:

$$R_0 = \sum l_x m_x$$

In this regard, if  $R_0 < 1$  indicates that population is declining whereas if  $R_0 > 1$  indicates an increasing population and  $R_0 = 1$  means a perfect stationary population (Monchot et al., 2012; Martín-González et al., 2016).

Since the pioneer articles of Leslie (1945, 1948), the so-called Leslie matrices have become a standard in population ecology with the impressive book of Caswell (2001). A projection matrix reveals whether the age structure of the different cohorts is related to a stationary population at any particular time. It gives both the picture of the initial fossil sample and the projection in time of the entire population to characterize its viability of a population. Here we used the simplest matrix projection model known as Lewis-Leslie:

$$\begin{bmatrix} m_0 & m_1 & m_2 & \dots & m_{24} \\ S_0 & 0 & 0 & \dots & 0 \\ 0 & S_1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 \\ 0 & 0 & 0 & S_{23} & 0 \\ A \end{bmatrix} * \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_{24}(t) \\ n(t) \end{bmatrix} = \begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_{24}(t+1) \\ n(t+1) \end{bmatrix}$$

Matrix  $A$  contains the age-specific fecundity rates ( $m_0, m_1 \dots$ ) as in the life tables. The diagonal contains the age-specific survival rates ( $s_0, s_1 \dots$ ) that corresponds to the values of  $s_x$ . The vector  $n(t)$  is obtained from the  $l_x$ , as the fraction of the total number of individuals in one-year intervals, whereas the vector  $n(t+1)$  is the new number of individuals in each age interval at the next succeeding census of the projected population [ $An(t) = n(t+1)$ ] (see details in Fernandez et al., 2017). The population projection of *E. conversidens* was performed using the software PopTools version 3.0.6 (Hood, 2008).

We first entered the age-specific survival ( $s_x$ ) and the fecundity data ( $m_x$ ) of the horse's population into our pre-breeding matrix as it is the basic model used for mammals (see Caswell, 2001). The projection returns the asymptotic growth rate ( $\lambda$ ), the exponential growth rate ( $r$ ), and the mean generation time ( $T_b$ ) that corresponds to the mean age of a female giving birth in a reproductive event (Leslie, 1966). In this regard, decreasing populations are characterized by having  $\lambda$  less than 1 and negative values for  $r$ . On the contrary, increasing populations have values greater than 1 for  $\lambda$  and positive values for  $r$ . In ideal conditions stationary populations have  $\lambda = 1$  and  $r = 0$  values (Lemos-Espinal et al., 2005; Fernandez et al., 2017).

Mammalian populations often show early fluctuations in the asymptotic growth rate, which is known as transient dynamics. In this regard, the damping ratio ( $\rho = \frac{\lambda_1}{|\lambda_2|}$ ) describes how fast the transient dynamics is stabilized after perturbation around the asymptotic growth rate regardless of population structure (Fernandez et al., 2017). We calculated the damping ratio using the software R Studio vr. 1.1.463, package popdemo (RStudio Team, 2015; Stott, 2018).

We also performed a disturbance analysis using the PopTool software (Hood, 2008), to explore the elasticity of the asymptotic growth rate related to changes in survival and fertility rates (see details in Caswell, 1978). The elasticity of the *E. conversidens* population from Hidalgo was compared and plotted with that of selected Pleistocene and extant *Equus* populations using ternary diagrams (Oli, 2004). We considered here: (1) elasticity of the survival of juveniles [ $e(S_j)$ ], which is the sum of the elasticity values of individuals from 0 to 3 years; (2) elasticity of adult survival [ $e(S_a)$ ], which is



The population dynamics and elasticities of *E. conversidens* were compared to the following equid populations: *E. lambei* from the Bluefish Caves, Wisconsinian of Yukon, Canada; in France *E. germanicus* from Fouvent, Oxygene Isotopic Stage 3; *E. mosbachensis* from Bau de l'Aubesier, Oxygene Isotopic Stage 7–6; and the extant populations of the plains zebra *E. quagga* from Akagera, Rwanda; and the mountain zebra *E. zebra* from Khomas Hochland, Namibia (Spinage, 1972; Joubert, 1974; Burke and Cinq-Mars, 1998; Fernandez and Legendre, 2003; Fernandez et al., 2006; Fourvel et al., 2014, 2015) (Supplementary Data).

## 4. Results and discussion

### 4.1. Population size

The estimated number of individuals in the sample of *E. conversidens* is 50 and 85 from MNI and NISP indices respectively. Classical works on population dynamics of ancient populations have shown that sample sizes between 30 and 40 individuals are suitable for interpreting important demographic features (see Kurtén, 1953; 1954a; 1954b). Lyman (1987) also demonstrated that about 30 individuals are necessary if 10 age classes are used but this critical assumption is often overlooked in zooarchaeological literature. In fact, optimal MNI depends on both the standard deviation of individual age and mean prediction error for each tooth category that will condition the width of the interval age classes, as well as their number (see details in Fernandez et al., 2017, Fig. 1, p. 480). The dental preservation of *E. conversidens* calculated from Brain (1981) is comparable to that of Combe-Grenal and is somewhat lower in comparison to the Pleistocene French sites of the Bau de l'Aubesier and Fouvent (Table 3). This suggests limited taphonomical biases for dental material between different deposits of our sample.

The Kolmogorov-Smirnov test indicates non-significant differences between MNI or NISP indices in the age distribution of *E. conversidens* ( $K-S = 0.74$ ;  $p > 0.10$ ) and the Spearman's rank correlation coefficient indicates a positive correlation between the estimated age distributions ( $r_s = 0.881$ ,  $p > 0.01$ ) (Table 4, Fig. 3a). It is not surprising that NISP and MNI both suggest the same age distribution, because it has been demonstrated that they were not independent of one another (see detailed discussions in Grayson, 1979, 1984; Lyman, 2008).

### 4.2. Mortality profiles

The mortality profiles of *E. conversidens* show a right asymmetry and a leptokurtic distribution. These profiles do not fit the basic attritional (U-shaped) and catastrophic (L-shaped) mortality patterns. The observed patterns are more similar to the stalking-model proposed by Levine (1983: Fig. 4.8, p. 31) (Fig. 3a). Hunting mainly of prime adults with a bell-shaped distribution produces this pattern (Levine, 1983). Even if the dental preservation of our sample is quite good, this kind of distribution has also often been documented in North American bison kill sites. Herds of animals were killed and their mortality pattern is usually attributed to poor preservation of the less ossified bones and teeth of youngsters (e.g., Munson, 2000; Munson and Garniewicz, 2003; Munson and Mearns, 2003).

The prime adults of the age interval 6–9 years represent 52.75% (MNI) and 44.41% (NISP), whereas the juveniles and old adults of the age intervals 0–3 years and 21–24 years respectively represent each less than 10% of individuals for both indices (Fig. 3a). The high percentage of prime adult individuals in comparison to individuals of other age classes may be the result of an accumulation over time where predation played an important role (Levine, 1983). Other horse populations showing this pattern have been related to the influence of human and/or non-human predators, including the population of *E. lambei* from Bluefish Caves, late Pleistocene of Canada (humans and large-sized predators, such as wolf, bear, and lion) (Burke and Cinq-Mars, 1998); the population of *E. mosbachensis* (Level I) from Bau de l'Aubesier, Upper Pleistocene of southern France (selective hunting by Neanderthals) (Fernandez and Legendre, 2003); and the paleopopulation of *E. germanicus* from Fouvent, Upper Pleistocene of eastern France (hyena den) (Fernandez et al., 2006).

The predominance of young adults and mature adults indicates a prime-dominated mortality pattern (Stiner, 1990; Kahlke and Gaudzinski, 2005; Bai et al., 2011). This pattern is consistent with the location of the population of *E. conversidens* in the ternary diagram, within the Prime adult area (P) (Fig. 3b). The comparison with selected populations of fossil and extant *Equus* shows that *E. lambei*, *E. mosbachensis*, and *E. germanicus* also fall within the Prime adult area (P) whereas *E. quagga*, *E. zebra*, *E. asinus*, and *E. hemionus* are located within the Juveniles-Prime-Old area (JPO). Only





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A prime-dominated mortality pattern has been interpreted to reflect selective hunting strategies by humans (Stiner, 1990, 1991, 1994; Driver and Maxwell, 2013); however, there is an ecologically complementary influence by non-human predators (Marín et al., 2017). This mortality pattern has been observed in large ungulates, including several Pleistocene horse populations (e.g., Levine, 1983; Fernandez and Legendre, 2006; Marín et al., 2017).

The studied sample does not show anthropic traces, and direct (e.g., bone remains) or indirect evidence (e.g., stone tools or bone surface modifications) of humans in southeastern Hidalgo during the late Pleistocene is not reported. However, the mammalian fauna from the late Pleistocene of southeastern Hidalgo includes large-sized predators, such as dire wolf *Canis dirus* and American lion *Panthera atrox* (Bravo-Cuevas et al., 2009, 2016). *Equus conversidens* represented a suitable prey for these predators (Bravo-Cuevas et al., 2016). Given this, the mortality profile of *E. conversidens* from Hidalgo probably was the result of the influence of these predators, providing high return rates to these carnivores (Stephens and Krebs, 1986).

#### 4.3. Life tables and Leslie matrices

Table 5, Table 6 indicate the vital statics of the population of *Equus conversidens* from Hidalgo.

Table 6. Standardized life tables of *E. conversidens* (age intervals of one year) using the minimum number of individuals (MNI) and the number of identified specimens (NISP) indices. Demographic parameters described as it is indicated in the method.

	x	$l_x$	$s_x$	$m_x$	$l_x m_x$
<b>MNI</b>	0	1.000	0.989	0.000	0.000
	1	0.989	0.989	0.000	0.000
	2	0.977	0.989	0.000	0.000
	3	0.966	0.943	0.105	0.101
	4	0.911	0.943	0.105	0.096
	5	0.859	0.943	0.105	0.090
	6	0.810	0.704	0.340	0.275
	7	0.570	0.704	0.340	0.194
	8	0.401	0.704	0.340	0.136
	9	0.282	0.823	0.340	0.096
	10	0.232	0.823	0.340	0.079
	11	0.191	0.823	0.460	0.088
	12	0.157	0.845	0.460	0.072
	13	0.133	0.845	0.460	0.061
	14	0.112	0.845	0.460	0.052
	15	0.095	0.714	0.460	0.044
	16	0.068	0.714	0.460	0.031
	17	0.048	0.714	0.430	0.021
	18	0.035	0.833	0.430	0.015
	19	0.029	0.833	0.430	0.012
	20	0.024	0.833	0.430	0.010

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	21	0.020	0.833	0.430	0.009
	22	0.017	0.833	0.000	0.000
	23	0.014	0.833	0.000	0.000
	24	0.012	0.833	0.000	0.000
				$R_0 =$	1.48
<b>NISP</b>	0	1.000	0.993	0.000	0.000
	1	0.993	0.993	0.000	0.000
	2	0.986	0.993	0.000	0.000
	3	0.979	0.957	0.105	0.103
	4	0.937	0.957	0.105	0.098
	5	0.896	0.957	0.105	0.094
	6	0.857	0.784	0.340	0.291
	7	0.672	0.784	0.340	0.228
	8	0.527	0.784	0.340	0.179
	9	0.413	0.792	0.340	0.140
	10	0.327	0.792	0.340	0.111
	11	0.259	0.792	0.460	0.119
	12	0.205	0.841	0.460	0.094
	13	0.173	0.841	0.460	0.079
	14	0.145	0.841	0.460	0.067
	15	0.122	0.736	0.460	0.056
	16	0.090	0.736	0.460	0.041
	17	0.066	0.736	0.430	0.028
	18	0.049	0.785	0.430	0.021
	19	0.038	0.785	0.430	0.016
	20	0.030	0.785	0.430	0.013
	21	0.024	0.785	0.430	0.010
	22	0.018	0.785	0.000	0.000
	23	0.014	0.785	0.000	0.000
	24	0.011	0.785	0.000	0.000
				$R_0 =$	1.79

The net reproductive rate ( $R_0$ ) was 1.48 and 1.79 using MNI and NISP indices respectively (Table 6), suggesting an increasing population. The observed  $R_0$  in all selected populations of *Equus* varies from 1.44 to 1.87, except for *E. zebra* that showed a value of 0.40 (Table 7).  $R_0 > 1$  indicates an increasing population (Monchot et al., 2012; Martín-González et al., 2016).

Table 7. Comparison of the net reproductive rate ( $R_0$ ), mean generational time ( $T_b$ ), exponential growth rate ( $r$ ), growth rate ( $\lambda$ ), and damping ratio ( $\rho$ ) of the population of *Equus conversidens* from Hidalgo and selected populations of extinct





Population	$R_0$	$T_b$	$r$	$\lambda$	$\rho$
A	1.48, 1.79	9.21, 9.41	0.04, 0.06	1.04, 1.06	1.21, 1.24
B	1.66	9.08	0.07	1.07	1.21
C	1.44	6.86	0.05	1.05	1.36
D	1.87	7.53	0.08	1.08	1.29
E	1.78	10.31	0.06	1.05	1.21
F	0.40	8.40	-0.11	0.89	1.37

The mean generation time ( $T_b$ ) of the population of *E. conversidens* is 9.21 and 9.41 using the MNI and NISP indices respectively, indicating that females produced an average of 1.63 descendants in about 9.31 years. This pattern of an increasing population is also observed in *E. lambei*, *E. mosbachensis*, *E. quagga*, and *E. germanicus*, although the latter population should be related to rapid population growth because females produced 1.87 descendants in about 7.53 years. By contrast, the population of *E. zebra* is related to a declining population, considering that females produced 0.40 descendants in about 8.4 years (Table 7).

The exponential growth rate ( $r$ ) related to the population growth of *E. conversidens* is 0.04 (MNI) and 0.06 (NISP) which is very close to other selected species where  $r$  is about 0.06; only *E. zebra* has an  $r = -0.11$  indicating that the number of individuals in the population decreased by 11% each year (Table 7).

The asymptotic growth rate ( $\lambda$ ) of *E. conversidens* and the other selected horse populations is  $> 1$ , except for *E. zebra* where  $\lambda$  is  $< 1$  (Table 7). The average asymptotic growth rate for the species considered (excluding *E. zebra*) is 1.06. In this regard, when  $\lambda = 1$  suggests perfect stability and a non-impacted population (Fernandez et al., 2017). Ransom et al. (2016: pp.76) reported average  $\lambda$  of 1.12 for populations of wild and feral equids, Gaillard et al. (2000: pp. 370) indicated values of  $\lambda$  ranging from 1.25 to 1.35 related to maximum annual population growth rates in extant equids, and Fernandez et al. (2017: pp. 488) reported values ranging from 1.21 to 1.26 in extant populations of wild equids that all evolve in optimal conditions. The values of  $\lambda$  for the population of *E. conversidens* (MNI: 1.04, NISP: 1.06) from Hidalgo are somewhat lower than those observed in some populations of extant wild horses, although similar to the populations of *E. lambei* ( $\lambda = 1.07$ ), *E. mosbachensis* ( $\lambda = 1.05$ ), and *E. germanicus* ( $\lambda = 1.08$ ) (Table 7).

Some populations of *E. caballus* and *Equus ferus przewalskii* inhabited areas without significant pressure from predators, presenting somewhat high survival rates in all age class intervals (Ransom et al., 2016). By contrast, the populations of *E. lambei*, *E. mosbachensis*, and *E. germanicus* are related to the selective influence of diverse predators with a preference for adult individuals (Burke and Cinq-Mars, 1998; Fernandez and Legendre, 2003; Fernandez et al., 2006). This could have occurred in the population of *Equus conversidens* from Hidalgo, which is in agreement with the observed prime-dominated mortality pattern.

The analysis of population dynamics of *E. conversidens* from Hidalgo suggests a relatively stable increasing population with slow growth ( $\lambda = 1.05$ ,  $T_b = 9.31$ ). Similar population dynamics are observed in stable populations of the modern plains zebra *E. quagga* from Serengeti, Tanzania ( $\lambda = 1.01$ ,  $T_b = 8.24$ ) (Grange et al., 2004), and different to that of declining populations of the same species from Hwange, Zimbabwe related to intensive predation ( $\lambda = 0.094$ ,  $T_b = 12.58$ ) (Grange et al., 2015).

The damping ratio ( $\rho$ ) of the population of *E. conversidens* is about 1.22 (Table 7). A damping ratio greater than 1 indicates a population that stabilized around the  $\lambda$  somewhat rapidly after perturbations regardless of population structure (Fernandez et al., 2017). Here this parameter is slightly greater than 1 for all the species considered, suggesting the convergence to stable size distribution was not so rapid. According to their values of  $\rho$ , a similar pattern should be expected for the populations of *E. conversidens*, *E. lambei*, and *E. quagga* and to a lesser extent with *E. germanicus* (Table 7).


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both indicate an increasing population; a similar pattern is observed in the populations of *E. mosbachensis* and *E. quagga*. Furthermore, *E. germanicus* has the fastest population growth, which is consistent with its highest values of net reproductive rate, exponential growth rate, and growth rate among the populations compared (Fig. 4, Table 7). By contrast, *E. zebra* is the only species that shows a negative growth curve reflecting a declining population (Fig. 4).

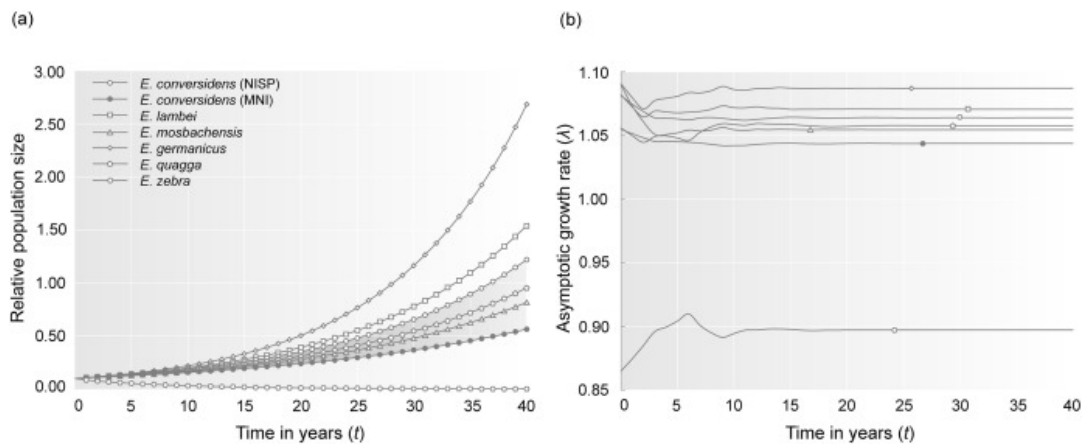

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Fig. 4. (a) Projection of the population growth and (b) transient dynamics of *Equus conversidens* from the late Pleistocene of Hidalgo and selected populations of extinct and extant *Equus*.

The fluctuations of the asymptotic growth rate ( $\lambda$ ) suggest that the population of *E. conversidens* stabilized at the projection time  $t_{27}$  and  $t_{31}$  derived from the MNI and NISP indices respectively. The projection from the MNI shows that the lambda values decreased from the time  $t_0$  ( $\lambda = 1.055$ ) to  $t_9$  ( $\lambda = 1.042$ ), indicating fluctuations in the age structure during this time interval and the slower population growth; other minor fluctuations should occur before reaching stabilization at  $t_{27}$ . The projection from the NISP shows that the lambda values decreased from the time  $t_0$  ( $\lambda = 1.081$ ) to  $t_6$  ( $\lambda = 1.062$ ), indicating major fluctuations during this time interval and reaching stabilization at  $t_{31}$  where the population experienced faster and constant growth (Fig. 4b). Both projections suggest fluctuations in the age structure related to juvenile (0–3 years) and young-adults (3–6 years) age classes, occurring when the population experienced slower growth. Usually, these early fluctuations in the projection of a population are related to the initial conditions of the demographic parameters in the age structure (Fernandez et al., 2017).

The projection curve of *E. conversidens* is very similar to that of *E. germanicus* ( $t_{26}$ ), *E. quagga* ( $t_{29}$ ), and *E. lambei* ( $t_{31}$ ), whereas the population of *E. mosbachensis* converge to stable size more rapidly ( $t_{17}$ ) (Fig. 4a). All of these fluctuations are consistent with the observed damping ratios for each species.

The elasticity values derived from all species are shown in the ternary diagram of Fig. 5. It indicates that survival, compared to fertility, is the most important demographic parameter in the population growth. It has been observed that survival is an important demographic pattern in the population growth of ungulates (Gaillard et al., 2000; Oli, 2004; Funston and Mills, 2006). In the ternary diagram, the population of *E. conversidens* and the selected horse populations occupy a plot space with average elasticity values of fecundity lesser than 0.20 ( $e(F) = 0.12$ ) and average elasticity values of survival greater than 0.80 ( $e(S_j) = 0.46$ ;  $e(S_a) = 0.42$ ). These values are related to populations with slow life histories (Oli, 2004).

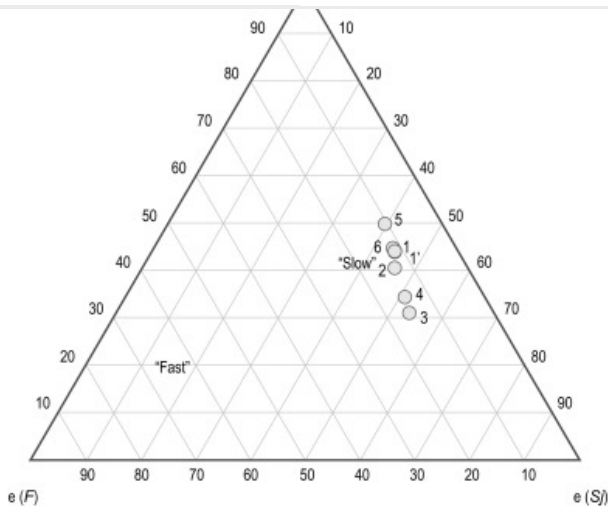

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Fig. 5. Ternary diagram of elasticity values of *Equus conversidens* from the late Pleistocene of Hidalgo and selected populations of extinct and extant *Equus*.  $e(F)$ , fecundity;  $e(Sj)$ , survivorship of juvenile individuals (0–3 years);  $e(Sa)$ , survivorship of adults ( $\geq 4$  years). Horse populations: 1, *E. conversidens* (NISP); 1', *E. conversidens* (MNI); 2, *E. lambei*; 3, *E. mosbachensis*; 4, *E. germanicus*; 5, *E. quagga*; 6, *E. zebra*.

The demographic models of *E. conversidens* derived from MNI and NISP indices suggest that the survival of prime individuals ( $>3$  years) is more important for population growth, as with *E. quagga* and *E. zebra*. The survival of juveniles (0–3 years of age) for *E. lambei*, *E. mosbachensis* and *E. germanicus* is somewhat more important for population growth. Finally, we observed that all the populations considered in this study fall within the “slow” area of the ternary diagram, which also reflects the theory of *fast-slow continuum life stories* (see review [Oli, 2004](#)). Our results are clearly related to the life history of large mammals characterized by late maturity, long lifespan, high survival and fecundity rates as well as higher  $\lambda$  in comparison with the “fast model”. By the same token, and despite the concerns regarding the adequacy of the r-K selection theory ([Stearns, 1992](#) but see [Boyce, 1984](#)), the demographic parameters of all species studied here allow us to classify them as K-strategists in stable ecosystems ([Pianka, 1970](#)).

#### 4.4. Ecological considerations

The extant plains zebra *Equus quagga* has a similar body size (ca. 300 kg) and is the closest relative species of *E. conversidens* ([Alberdi et al., 1995](#); [Barron-Ortiz et al., 2019](#)), being a suitable model for comparison purposes. Several studies have shown that population dynamics of *E. quagga* is related to multiple factors, including seasonality, predation, environmental conditions, and/or resource availability ([Mohelman, 2002](#); [Georgiadis et al., 2003](#); [Grange et al., 2004, 2015](#); [Funston and Mills, 2006](#); [Owen-Smith, 2008](#); [Rubenstein, 2010](#); [Ransom et al., 2016](#); [Kiffner et al., 2017](#)).

Isotopic ecology and palynological studies indicate that savanna-like habitats with flood plains and channels were present in southeastern Hidalgo during the late Pleistocene ([Bravo-Cuevas et al., 2017](#); [Pineda-Maldonado, 2017](#)). This woodland-grassland ecosystem sustained a high diversity of large mammalian herbivores, providing a suitable environment characterized by diverse food plant resources ([Bravo-Cuevas et al., 2017](#)). Considering their flexible feeding strategies, observed through mesowear and stable isotope analyses, individuals of *E. conversidens* were able to exploit the available food resources in different habitats ([Bravo-Cuevas et al., 2011, 2017](#)).

We propose that the influence of ambush (American lion) and cursorial social predators (dire wolf) are related to the mortality profile of the population of *E. conversidens*. Other ungulates that represented potential prey of these large carnivores have been reported at southeastern Hidalgo, including llamas, camels, deer, antelopes, and bison ([Bravo-Cuevas et al., 2016](#)). In this regard, populations of *E. quagga* experience different intensities of predation ([Georgiadis et al., 2003](#); [Owen-Smith, 2008](#); [Funston and Mills, 2006](#)), although it is not a limiting factor of population growth if there is an abundance of large preys ([Funston and Mills, 2006](#)).



slightly (Bowler et al., 2014).

## 5. Conclusion

The current ecological standard tools such as life tables (time-specific model) and Lewis-Leslie matrices, are very efficient to derive paleodemographic parameters from the late Pleistocene cohorts of *E. conversidens* from Hidalgo. We compared this species to a sample of modern equids (*E. asinus*, *E. zebra*, *E. hemionus*, *E. caballus*) and fossil species (*E. mosbachensis*, *E. germanicus*, *E. lambei*) from different habitats. The mortality pattern of *E. conversidens* is a prime-dominated profile sometimes associated to hunting pressure or density-mediated destruction of faunal remains. We propose that the influence of natural predators produced this pattern, considering the association of large-sized predators, such as the dire wolf (*Canis dirus*) and the American lion (*Panthera atrox*), at southeastern Hidalgo during the latter half of the Pleistocene. By the same token, it is proposed that population dynamics of *E. conversidens* from Hidalgo were regulated by predation and resource availability as it occurs in the extant plains zebra, *E. quagga*.

## Authors contribution

Alexis Pérez-Pérez: Conceptualization, Methodology, analysis, writing. Victor Manuel Bravo-Cuevas: Conceptualization, writing, editing. Philippe Fernandez: Conceptualization, Methodology, writing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

The following is the Supplementary data to this article:

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Multimedia component 1.

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