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Eomyids: happy old age or premature death? Reconstructing the life history of *Ligerimys* (Eomyidae, Rodentia, Mammalia)

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ABSTRACT
Mortality curves of extinct rodents can be reconstructed by using relative wear calculated from the amount of dentine exposed. MicroCT scanning of molars of the extinct Eomyid genus *Ligerimys* shows that this Wear Index increases gradually with wear; this means that wear classes can serve as a proxy for age and can therefore be used to reconstruct mortality curves. We reconstructed mortality curves of three species of *Ligerimys* from the late early Miocene of Spain. These curves show a similar trend, with decreasing numbers of molars as the amount of wear in each class increases. The curves show remarkable similarities to those of the wood mouse *Apodemus*. This suggests that *Ligerimys* was, like *Apodemus*, at the fast end of the fast-slow continuum, in other words r-selected, though not as extreme as some other rodents.

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Fast-slow continuum; Wear Index; Eomyidae; mortality curve; Miocene

Introduction

One of the aims of palaeobiology is to reconstruct how extinct animals lived. That task can be quite daunting. The vast majority of the fossil record of micromammals, for instance, consists only of isolated teeth. Yet, through functional morphology and comparison with living relatives, we can gain insight into the food preferences of extinct species (Lazzari et al. 2008; López-Torres et al. 2018). In addition, recently developed techniques like microwear or isotope analysis allow us to study the diet of rodents and insectivores in more detail (e.g., Silcox and Teaford 2002; Townsend and Croft 2008; Gomes Rodrigues et al. 2009; Firmat et al. 2010, 2011; Kimura et al. 2013; Oliver et al. 2014; Belmaker 2018; Menéndez et al. 2020).

An important aspect of the biology of species is their place in the fast-slow continuum, or, in older terms, whether it tends towards a more r-selected or K-selected life strategy (Oli 2004; Bielby et al. 2007; Dobson and Oli 2007). Species at the fast end of the continuum (r-selected) invest in a large number of offspring, few of which reach adulthood. By contrast, species at the slow end (K-selected) produce fewer offspring but with a higher chance of survival (McLain 1991). r-selected species are better equipped to survive in fluctuating environments and tend to have a wide niche. By contrast, K-selected species have a more limited niche and are more adapted to relatively stable environments, such as forests (Singh 2019). Of course, the underlying characteristics that determine the position of a species within the continuum (litter size, gestation period, age of sexual maturity) cannot be deduced from the fossil record, but a higher death rate of young individuals of r-selected species can be recognised in a higher percentage in the death assemblage. Freudenthal et al. (2002) used tooth wear stage as a measure for individual age to create mortality curves of what they still considered *Apodemus* (now *Apatodemus*) from the late Miocene of the Gargano Peninsula and compared them with those of extant *Apodemus*. Even though the amount of wear could not be linked to a specific age, their methodology provides a quantitative measure that is a significant improvement over mortality curves based on a series of distinct wear categories defined by wear surface morphology as used by Adamczewska-Andrzejewska (1973). Because of the strong similarity between the curves of the extant and the fossil populations, these authors concluded that the fossil population could be used as a reflection of a natural population. Given that the material from fossil localities not resulting from a single catastrophic event is accumulated over a longer period of time, it seems likely that death assemblages from these sites are not actually a natural population. However, unless a major shift in the life strategy of a species has occured, temporal averaging within a fossil site would have no effect on the distribution of age classes. As Freudenthal et al. (2002) indicated, a mixing of different ages within a karst fissure could have such an effect, but in that case we would also expect a certain amount of morphological change (e.g., Klietmann et al. 2014).

In this paper, we reconstruct mortality curves for various species of the Eomyid genus *Ligerimys*, based on localities from the Daroca-Calamocha area, which has yielded some of the richest eomyid assemblages in the world (Álvarez Sierra 1987). The occurrence of the genus in the area comprises its entire known stratigraphic range (Zones Z-C, MN 3 and 4; Van der Meulen et al. 2012). It includes a major change in the composition of rodent faunas in western Europe, as the glirid- and eomyid-dominated ‘Cricetid Vacuum’ (Zones Z-A, MN 3) came to an end when cricetids entered western Eurasia at the start of MN 4 (Daams and Freudenthal 1989). According to Van der Meulen and Daams (1992), the faunal turnover results from a change to more open landscapes and also comprises a change in the predominant life strategy of the rodent assemblages. The hamsters that would become dominant in the middle Miocene presumably have an r-selected strategy, whereas these authors considered glirids and eomyids generally as

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K-selected animals. Because eomyids are extinct, their presumed life strategy on the slow end of the continuum was based on the hypothesis that they were forest dwellers, and on their limited geographical and stratigraphic distributions. However, Van der Meulen and Daams (1992) noted that a species like *Ligerimys antiquus* has a larger geographical distribution than its congeners, which could suggest that it had a more opportunistic life strategy.

By reconstructing the mortality curves of *Ligerimys* species from different parts of their stratigraphic range, we aim to investigate whether the younger species had changed their life strategy. We hypothesise that, faced with a change to a more open landscape and the competition of hamsters entering the area, *Ligerimys* may have seen a shift along the fast-slow continuum. Theoretically, this could either be a shift towards the fast end to be able to compete with the new immigrants or it could be a push further along the slow end of the spectrum. In either case, the strategy did not work and at the transition between Zones C and D (MN 4/MN 5), when the landscape opened even further, the genus went extinct (Van der Meulen et al. 2012).

Material and methods

Geographical and chronological setting

This study uses material from local biozones Z – Cb, (early Ramblian through to the early Aragonian; Daams et al. 1999) from the Daroca-Calamocha area in the provinces of Zaragoza and Teruel, which span a period of roughly 2.5 my. In addition, material from the locality of Buñol (early Aragonian, local biozone Ca; Daams and Freudenthal 1974) in the province of Valencia was studied for possible geographic variation of the same species.

Datasets

The dental elements studied here include the upper first molar (M1) and the upper second molar (M2). However, because it is extremely difficult to distinguish the lower first molars from the lower second ones (Álvarez Sierra 1987; Maridet et al. 2010), we decided to combine these in a single dataset, (m1-m2). This procedure thus resulted in three different datasets for each species.

The study focused on three species of *Ligerimys: Ligerimys ellipticus, L.* aff. *magnus* and *L. antiquus*. *Ligerimys ellipticus*, the longest persisting species in Spain, was chosen because of the large number of molars available to this study from both the Daroca-Calamocha area (the Vargas 1A locality, biozone Cb) and the more coastal Buñol locality (Biozone Ca).

One of the goals of this study was to monitor whether *Ligerimys* species living at different times had similar life strategies. Therefore, the other two species, *L.* aff. *magnus* and *L. antiquus*, were selected as representatives of *Ligerimys* from older local biozones. Large numbers of *Ligerimys* aff. *magnus* molars from the Rambler 3B locality (local biozone Z) in the Calatayud-Calamocha Basin were available for study. Two populations of *L. antiquus* from the Calatayud-Calamocha Basin, one from the Bañón 11A locality (local biozone A) and one from the Ramblar 1 locality (local biozone Z), were also studied though both sample sizes are small compared with those of *L. ellipticus* and *L.* aff. *magnus*. Nevertheless, as an early and widespread species, *L. antiquus* was considered an important part of this study.

In order to determine the relationship between wear and dentine surface, additional *L. antiquus* material from San Roque 4A (local biozone Z) and *L. ellipticus* from Vargas 4A (equivalent stratigraphic level to Vargas 1A but from a nearby sampling spot) was used. The use of specimens from other localities was due to the lack of completely unworn specimens of all the studied dental elements needed on any of the main samples except for Ramblar 3B.

Measuring occlusal wear in molars

The occlusal surfaces of all the first and second molars of the studied assemblages were photographed using a Leica MZ 16A microscope with a stacking camera. The magnetic lasso tool within Adobe Photoshop Extended CS5 was used to trace the areas where the dentine at the occlusal surface is exposed for each molar (see Figure 1), and then the number of pixels was recorded and added together in Microsoft Excel. The same procedure was used to trace the circumference of each molar and to record the number of pixels in the total surface area, i.e., dentine and enamel combined.

The Wear Index (WI) was determined by calculating the total area of dentine as a percentage of the total surface area of the molar (Freudenthal et al. 2002). In order to determine the relationship between wear and the dentine/total surface area in *Ligerimys* species, X-ray microtomography was used to virtually 'wear down' an unworn molar for each element of each species. As the wear surface is relatively flat in these species, we consider cross-sections parallel to the wear surface a good approximation of the actual dentine/enamel ratio at different heights of the molar. The molars were scanned using a Nikon XTH 160 X-ray microtomography equipment, at the Laboratory of non-destructive techniques of the Museo Nacional de Ciencias Naturales (MNCN-CSIC). The distance between the CT slices was 0.01 mm and digital segmentation of the molars was achieved using Avizo 2021.2 software.

Using manual segmentation, we were able to make a distinction between the enamel and the dentine, and with the Material Statistics module, we calculated the surface area of each of them (mm^2). The Wear Index of each slice was calculated by dividing the dentine area measured by the total area of the molar. We then plotted the Wear Index against the wear measured from the top of the each molar (in mm) in order to determine linearity and to be able to make a comparison between the different species included in the study (Figure 2). The graph represents the data up to those of the first slice in which enamel was only visible on the outside surface of the molar.

We then assigned the calculated Wear Indices in each eomyid sample to a wear class following the previously used procedure of defining 10 classes of WI with 10% intervals following Gurnell and Knee (1984) and Freudenthal et al. (2002). In this way, the least worn molars were assigned

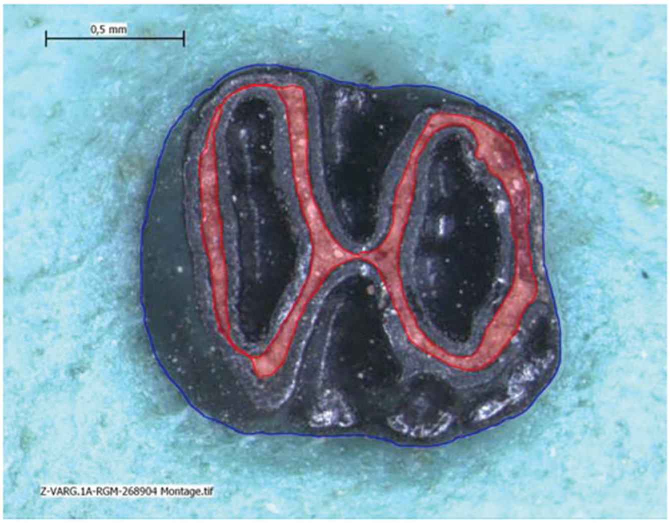

Figure 1. Photograph showing the dentine (red) and the occlusal surface (blue line indicates the perimeter) of a lower m1-m2 of *Ligerimys ellipticus* from the Vargas 1A locality (RGM 268904). In this example, the dentine represents 18.85% of surface area and is assigned Wear Class 2.

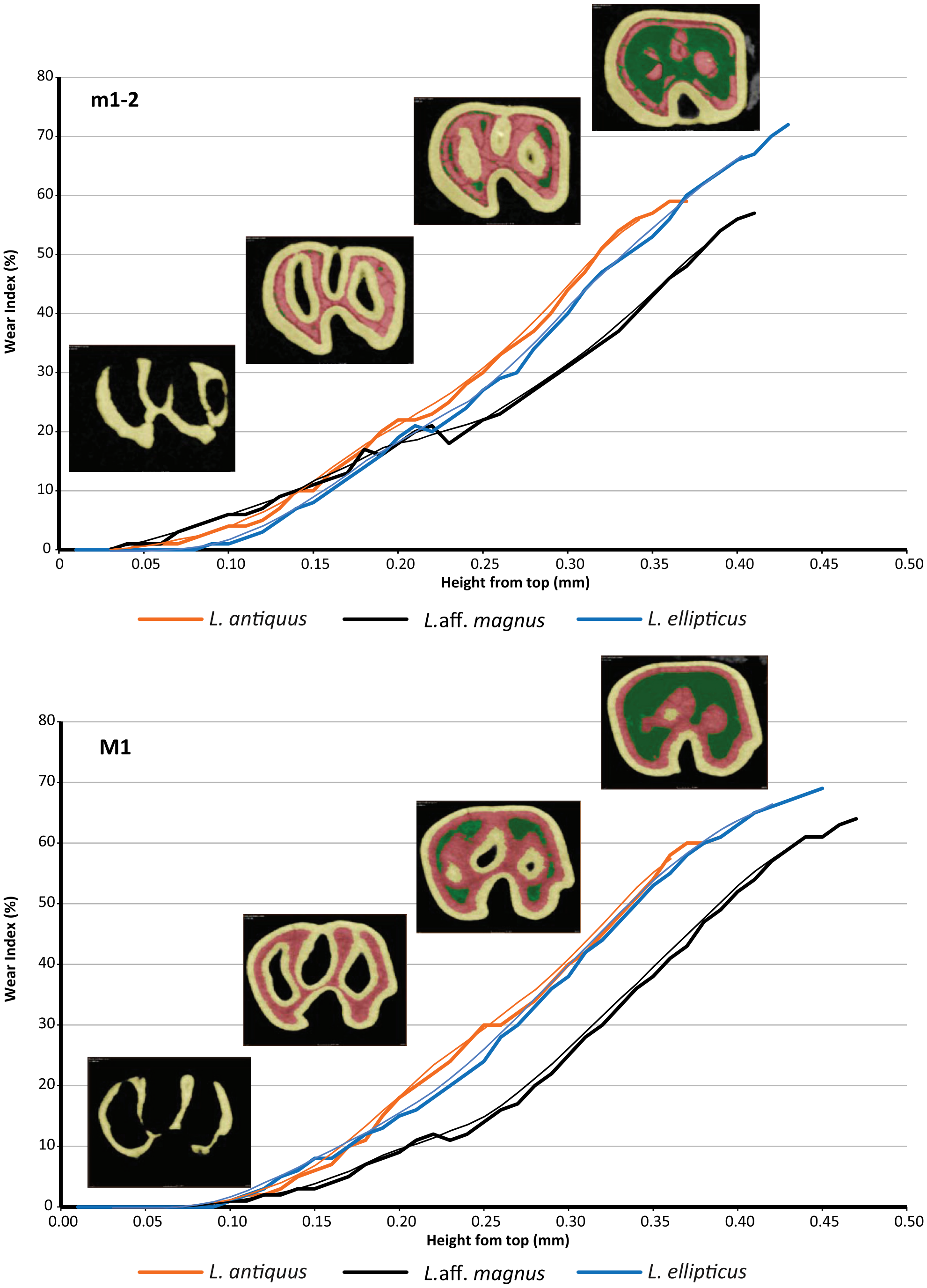

Figure 2. Line graphs showing the Wear Index against the 'virtual wear' measured from the top (in mm) for upper and lower molars of *L. ellipticus (VR4A 390, VR4A 710)*, *L.* aff *magnus (RA3B 167, RA3B 394)* and *L. antiquus (SR4A 1027, SR4A 1093)* from the Daroca-Calamocha Basin. In m1-2, images show four different wear stages of *L. antiquus*, from slightly to heavily worn. In M1, the images represent four different wear stages of *L. ellipticus*. Yellow areas indicate enamel, pink dentine and green missing dentine or pulp cavity. Thin lines represent moving average trend lines of 6 period.

to Wear Class 1 since the amount of dentine revealed fell into the 0% to 10% of the total surface area category. Molars with slightly more revealed dentine, i.e., 10% to 20% of the total surface area, were assigned to Wear Class 2 (see Figure 1); and so on.

The wear classes of every fossil eomyid sample were then plotted against the number of individuals in each wear class as a percentage of the total number of individuals in the sample. We decided to use percentage total as opposed to the absolute number of individuals in order to facilitate a better comparison of species with widely differing sample sizes.

We then reconstructed individual curves for the M1, M2 and m1-2 for each species and each locality, so that we could directly compare the three separate age distribution curves based on different molar elements (Figure 3).

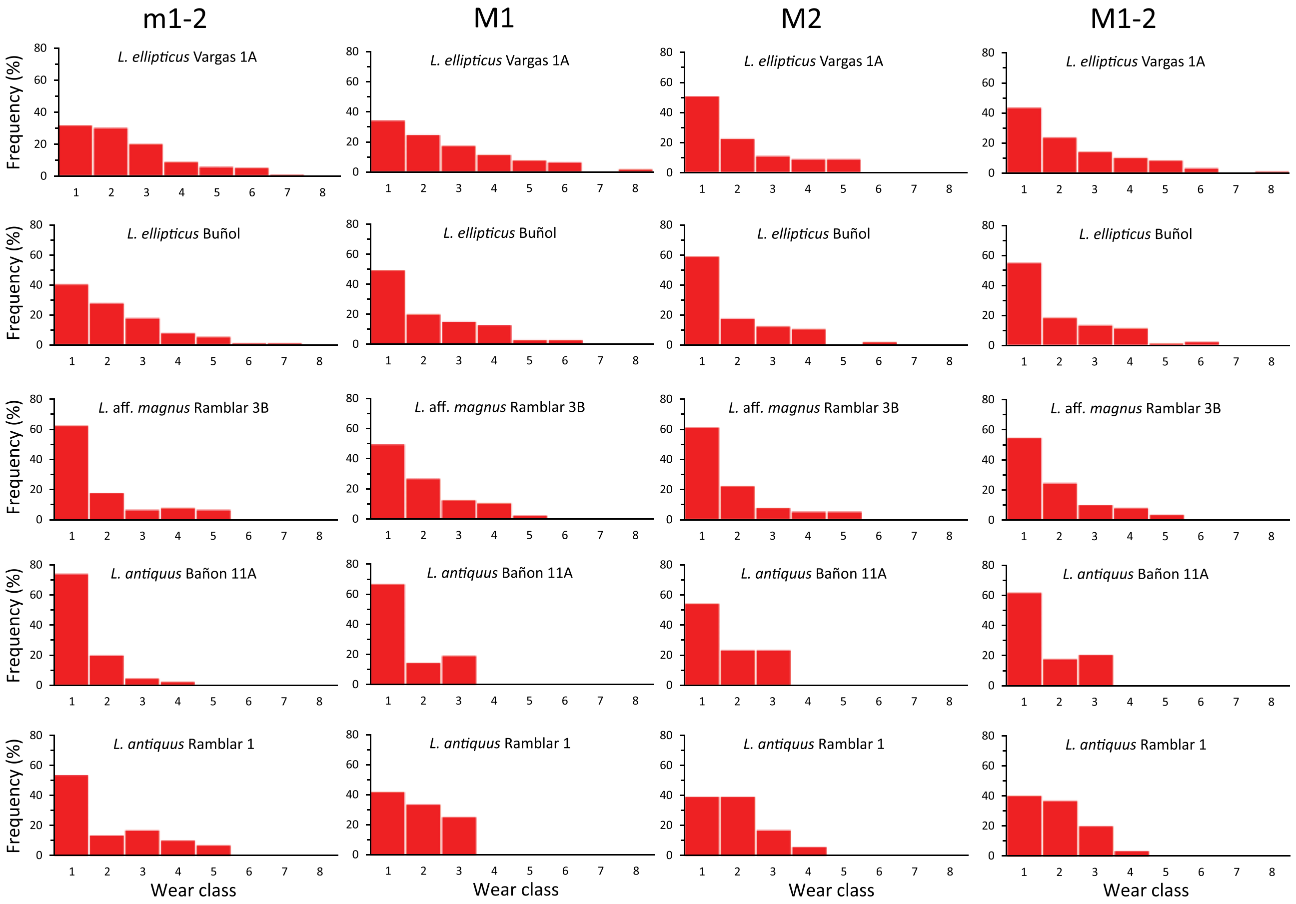

Figure 3. Distribution of Wear index of the different elements and species of eomyids from the Daroca-Calamocha area and Buñol.

Storage

The studied assemblages are stored in the Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid (Ramblar 3B, San Roque 4A and Vargas4A), Naturalis Biodiversity Center, Leiden (Ramblar 1, Bañon 11A, Vargas 1A) and Utrecht University (Buñol).

Results

It should be noted that wear simulated by using X-ray tomography shows an almost linear relation between height and enamel/dentine ratio suggesting a progressive linear increase for Wear Index (WI). It also adds weight to the idea that Wear Index can be used as a reliable proxy for age determination (Figure 2). Also, important to note is the fact that the three species used in this study show very similarly shaped curves, suggesting that age categories based on wear are likely to be similar for all the species used in this study, making it possible to compare age distributions directly.

Table 1 shows the frequencies of the different wear classes for each species sample and dental element. The wear class histograms for the different species and the various elements show remarkable similarities (Figure 3). The first wear class is consistently the best represented, after which the numbers drop significantly. The wear class distribution becomes more even between the higher wear categories. The results also show that wear class 1 of M1 is proportionally lower than that of M2. That is what we will expect because, as the M2 erupts later than the M1, it will always tend to show less wear than the M1. The results for *Ligerimys antiquus* are slightly more erratic, but this is almost certainly due to the small sample size of the assemblages of this species.

Despite general similarities, we have also tested whether there are differences in wear distributions among different samples and elements. Table 2 shows the results on Kruskal–Wallis non-parametric test, calculated with IBM SPSS statistics v. 28, for comparison of Wear Index distribution of the different dental elements from each locality and also for Wear Index distribution for the same dental element from different localities. Table 2 also includes the pairwise comparison of dental elements and localities in case the results of the Kruskal–Wallis test indicate significant differences. Comparisons among the different dental elements for each eomyid sample indicate that most of the species studied show no significant differences between them. Only *L. ellipticus* from Vargas 1A show significant differences. The pairwise comparison indicates that the differences are in the distribution of wear index of the M2 compared to those of M1 and m1-2, although when adjusted by the Bonferroni correction for multiple tests, the results become non-significant. Results comparing calculated Wear Index distributions for each dental element among the various eomyid samples indicate that there is a highly significant difference in wear class distribution of the m1-2 and a significant difference on M1 and M1-2. The pairwise comparisons show that there are significant differences between *L. ellipticus* and the other two species for the m1-2, M1 and M1-2, although mostly for the Vargas 1A sample.

Looking at Figure 3, the significant difference in the distribution of the lower molars results from a less frequent first wear class in *L. ellipticus* compared to the other species. In the upper molar, the differences could be also due to the more even distribution shown by *L. ellipticus* from Vargas 1A. The surprising lack of significant differences on the wear index distribution in the different dental elements from Ramblar 1 and the other assemblages is probably

Table 1. Distribution of Wear Indexes among wear classes on several *Ligerimys* species from the Daroca-Calamocha Basin by dental element. N = number of specimens.

m1-2	*L. ellipticus*				*L. aff. magnus*		*L. antiquus*			
Wear Class	Vargas 1A		Buñol		Ramblar 3B		Bañon 11A		Ramblar 1	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
1	59	31.2	49	40.1	49	62.0	34	73.9	16	53.3
2	56	29.6	33	27.5	14	17.7	9	19.6	4	13.3
3	37	19.6	21	17.5	5	6.3	2	4.3	5	16.7
4	16	8.4	9	7.5	6	7.6	1	2.1	3	10.0
5	10	5.3	6	5.0	5	6.3			2	6.7
6	9	4.8	1	0.8						
7	1	0.5	1	0.8						
Total N	188		120		79		46		30	

M1	*L. ellipticus*				*L. aff. magnus*		*L. antiquus*			
Wear Class	Vargas 1A		Buñol		Ramblar 3B		Bañon 11A		Ramblar 1	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
1	28	33.7	20	48.7	24	49.0	14	66.7	5	41.7
2	20	24.1	8	19.5	13	26.5	3	14.3	4	33.3
3	14	16.9	6	14.6	6	12.2	4	19.0	3	25.0
4	9	10.8	5	12.2	5	10.2				
5	6	7.2	1	2.4	1	2.0				
6	5	6.0	1	2.4						
7										
8	1	1.2								
Total N	83		41		49		21		12	

M2	*L. ellipticus*				*L. aff. magnus*		*L. antiquus*			
Wear Class	Vargas 1A		Buñol		Ramblar 3B		Bañon 11A		Ramblar 1	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
1	48	50.5	34	58.6	25	60.9	7	53.8	7	38.9
2	21	22.1	10	17.2	9	21.9	3	23.1	7	38.9
3	10	10.5	7	12.1	3	7.3	3	23.1	3	16.7
4	8	8.4	6	10.3	2	4.9			1	5.6
5	8	8.4			2	4.9				
6			1	1.7						
Total N	95		58		41		13		18	

M1-2	*L. ellipticus*				*L. aff. magnus*		*L. antiquus*			
Wear Class	Vargas 1A		Buñol		Ramblar 3B		Bañon 11A		Ramblar 1	
	N	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
1	76	42.7	54	54.5	49	54.4	21	61.8	12	40.0
2	41	23.0	18	18.2	22	24.4	6	17.6	11	36.7
3	24	13.5	13	13.1	9	10.0	7	20.6	6	20.0
4	17	9.6	11	11.1	7	7.8			1	3.3
5	14	7.9	1	1.0	3	3.3				
6	5	2.8	2	2.0						
7										
8	1	0.6								
Total N	178		99		90		34		30	

related to the small sample size for that species. Surprisingly, M2 considered independently does not show significant differences in wear distribution among the samples of eomyid studied. The comparison of both samples of *L. ellipticus* indicates the absence of significant differences between wear class distributions.

The general trend in our diagrams is in line with the wear class distribution for *Apodemus* and *Apatodemus* as reconstructed by Freudenthal et al. (2002). In line with these authors, we interpret our wear histograms as a good reflection of the mortality curve for our species.

Discussion

As noted here, there is a linear relation between height and enamel/dentine ratio. This does not imply that wear is relatively constant over time. In the early stages of wear, the effective chewing surface is relatively small, which will lead to a more rapid decrease in crown height. Adamczewska-Andrzejewska (1973,fig. 8) showed that of the six wear stages in *Apodemus*, stages one-three represented the first three months of life.

The survivorship curves for the various species of *Ligerimys* are very similar, suggesting that all of these species held a similar position in the fast-slow continuum. Van der Meulen and Daams (1992) have suggested that *L. antiquus* was possibly more r-selected based on its wide distribution. It is indeed notable that the species had a pan-European distribution whereas its contemporary congeners showed a much more restricted distribution. This species may have been more generalised in its ecological requirements but our results do not support a life strategy very different from the other, more specialised species of *Ligerimys*, such as *L.* aff. *magnus*. Our results indicate that *L. ellipticus* may have had a more K-selected strategy than the other species analysed, as would be expected for a more specialised species like *L. ellipticus*. However, this result is not reflected in the upper second molar curves and therefore has to

Table 2. Results of the Independent-Samples Kruskal–Wallis for homogeneity between wear indexes of dental elements by locality and between localities of eomyids from the Daroca-Calamocha Basin by dental element. d.f. = degrees of freedom; Sign. = signification; Adj. sign. = Adjusted signification by the Bonferroni correction for multiple tests. * = significant at 95% ** = significant at 99%.

Independent-Samples Kruskal-Wallis Test comparing Wear index of dental elements by locality

L. ellipticus				*L.* aff. *magnus*		*L. antiquus*			
Vargas 1A		Buñol		Ramblar 3B		Bañon 11A		Ramblar 1	
Test Statistic	**Sign.**	**Test Statistic**	**Sign.**	**Test Statistic**	**Sign.**	**Test Statistic**	**Sign.**	**Test Statistic**	**Sign.**
8.64	0.34*	3.21	0.36	2.03	0.57	1.05	0.79	0.004	1

Pairwise Comparisons of Dental elements	**Vargas 1A**		
	Std. Test Statistic	Sign.	Adj. Sign.[a]
M2 _ M1-2	1.242	0.214	1.000
M2 _ m 1–2	−2.607	0.009**	0.055
M2 _ M1	2.252	0.024*	0.146
M1-2 _ m 1–2	−1.630	0.103	0.618
M1-2 _ M1	−1.358	0.174	1
m 1–2 _ M1	0.074	0.941	1

Independent-Samples Kruskal-Wallis Test comparing Wear index of localities by dental element

m1-2			**M1**			**M2**			**M1-2**		
Test Statistic	d.f	Sign.	**Test Statistic**	d.f	Sign.	**Test Statistic**	d.f	Sign.	**Test Statistic**	d.f	Sign.
35.81	4	<0.001**	12.42	4	0.014*	4.49	4	0.343	13.04	4	0.011*

Pairwise Comparisons of Locality	**m1-2**			**M1-2**			**M1**		
	Std. Test Statistic	**Sign.**	**Adj. Sign.**	**Std. Test Statistic**	**Sign.**	**Adj. Sign.**	**Std. Test Statistic**	**Sign.**	**Adj. Sign.**
BA11A-RA3B	−1.931	0.053	0.534	−1.171	0.242	1.000	−1.629	0.103	1.000
BA11A-RA1	−2.485	0.013*	0.130	−1.763	0.078	0.779	−1.369	0.171	1.000
BA11A-Buñol	−3.736	<0.001**	0.002**	−1.806	0.071	0.709	−2.068	0.039*	0.386
BA11A-VR1A	−5.343	<0.001**	<0.001**	−3.029	0.002**	0.025*	−3.287	0.001**	0.010**
RA3B-RA1	1.049	0.294	1.000	0.976	0.329	1.000	0.218	0.827	1.000
RA3B-Buñol	1.999	0.046*	0.456	0.847	0.397	1.000	0.615	0.539	1.000
RA3B-VR1A	−3.884	<0.001**	0.001**	−2.561	0.010**	0.104	−2.097	0.036*	0.360
RA1-Buñol	.317	0.751	1.000	−0.396	0.692	1.000	0.182	0.856	1.000
RA1-VR1A	−1.506	0.132	1.000	−0.636	0.525	1.000	−0.996	0.319	1.000
Buñol-VR1A	−1.980	0.048*	0.478	−1.659	0.097	0.972	−1.298	0.194	1.000

be interpreted with the utmost caution, even though other dental elements show highly significant differences in Wear Index distributions. Since the age distribution histograms for the lower molars have been produced by combining undifferentiated m1 and m2, there is also a possibility that differences in the lower molars are due to the different proportions of m1 and m2 in each sample, with m1s showing, on average, a more advanced wear stage than m2s, as has been observed on the upper molars (Figure 3). The absence of significant differences in the survival distribution between the two populations of *L. ellipticus* indicates that the different local environmental conditions between those two areas did not affect the mortality of this species.

The similarity of the wear class histograms with the one that Freudenthal et al. (2002) reconstructed for the extant species *Apodemus sylvaticus* is striking. These authors classified the mortality curve of *Apodemus* as a Pearl's II curve, which has a relatively constant mortality rate, i.e., log-transformation of the data reveals a linear relationship. We also found this same relationship in our curves, although, as Freudenthal et al. (2002) pointed out, deviations may occur at the lower end of the curve, where one molar fewer or more makes a substantial difference to the results. Freudenthal et al. (2002) interpreted this as a population in which there is no preference for mortality of juvenile or senior individuals. Again we need to bear in mind that individual wear classes may not represent equally distributed age classes: earlier wear classes represent shorter periods within the life-cycle, perhaps reflecting a higher mortality rate among the very young and inexperienced. The similarity between the eomyid curves and that of *Apodemus*, however striking, does not automatically imply that *Ligerimys* occupied a similar environment as the wood mouse. Nevertheless, it fits well with the presumed environmental preference for Eomyidae as forest dwellers as indicated by previous authors.

Menendez et al. (2017) reconstructed mortality profiles based on wear for the hamsters *Megacricetodon collongensis* and *Democricetodon larteti* from the middle Miocene locality of Somosaguas. Their curves were based on the methodology of Freudenthal et al. (2002), but included all molars, rather than just the m3. The basic shape of the curves is the same as in our study, with an ever decreasing number of individuals in the higher wear classes. However, the first two wear classes of these hamsters comprise the vast majority of the specimens, with an enormous drop between the wear class below 10% and the 10%–20%, suggesting a very high mortality rate in juveniles. The authors attributed this high mortality to a prolonged catastrophic event. However, there is no need to assume such an event as high predation among juveniles is common for species, which are strongly associated with the fast end of the fast-slow continuum. Van der Meulen and Daams (1992) had already pointed out that the harsh environments of the middle Aragonian favoured r-selected taxa including these hamsters. In the steeper curves, the hamsters seem to be positioned more at the fast end of the fast-slow continuum than the eomyids. However, in order to corroborate these suggestions, we would need to confirm that the hamsters also show a linear relationship between the amount of wear and the enamel-dentine ratio.

The main reason for Menendez et al. (2017) to assume a catastrophic event is that the mortality curves did not show the attritional model common to many mammals. When mortality is highest among the very young and very old, individuals in the prime of their life stand a larger chance of survival and so the mortality curve will be U-shaped. This type of curve was found by Vasileiadou et al. (2007) in their study on the theridomyids from the late Eocene of the Isle of Wight. These authors made a composite curve based on the amount of wear of the DP4 and M3. As the DP and M3 are not functional at the same time and there were no unworn (= unerupted) M3s in the sample, it is clear that the least worn M3s represent an older age category than the most worn DP4s and so the two can be combined for an overall age profile.

The attritional profile for the theridomyids places them nearer to the slow end of the fast-slow continuum than either the eomyids or the hamsters. In fact, the profile shows a remarkable resemblance to that of the ground squirrel *Spermophilus columbianus*. Neuhaus and Pelletier (2001) found that mortality rates were highest among the very young, followed by the four-year olds. Females in particular could live for nine years or more.

All in all, a picture arises of *Ligerimys* as being more towards the fast end of the fast-slow continuum than larger rodents, which is to be expected. As small rodents, the different *Ligerimys* species were prone to high predation and we would therefore expect a rather short life-span in the wild. In *Apodemus*, the most advanced wear stages are reached well within a year (Adamczewska-Andrzejewska 1973, fig. 8) and we can assume that this would not be much different in *Ligerimys*. Nevertheless, mortality rates in the eomyid were not as high as in the hamsters *Democricetodon* and *Megacricetodon*.

Conclusions

Wear categories, expressed in terms of a wear index and based on the dentine/enamel ratio, provide a useful tool for reconstructing mortality curves in extinct rodents. However, one needs to be aware of how the WI changes with wear. Simulated wear using microCT scanning showed that, in the case of the eomyid genus *Ligerimys*, there is a linear relationship between wear and the dentine/enamel ratio. Therefore, wear categories can be used as a proxy for age groups, although not necessarily age groups of comparable length.

The mortality curves of the three *Ligerimys* species studied are very similar, suggesting that, even during the vast palaeoenvironmental changes around the end of the early Miocene, each species had a similar life strategy. The curves show a decline in the numbers of individuals towards the 'older' wear categories, a pattern consistent with continuous predation throughout life. In this respect, the curves show a remarkable similarity to those of the wood mouse *Apodemus* and the insular murine *Apatodemus*, which was previously included in that genus. By contrast, the curves differ greatly from that of the ground squirrel *Spermophilus*, which shows an attritional pattern with increased mortality both in the very young and the old individuals. This seems to place *Ligerimys* at the fast end of the fast-slow continuum. However, comparison with the mortality curves of the hamsters *Megacricetodon* and *Democricetodon* show that the latter two have an even higher mortality rate and should therefore be considered even more r-selected. A lower mortality among juveniles in *L. ellipticus* suggests that the youngest species had a trend towards more K-selected, in line with its more specialised dentition.

Traditionally, eomyids are considered to be forest dwellers. The striking resemblance of the mortality curves with those of *Apodemus* would fit with that presumed habitat for these extinct rodents, but any conclusions based solely on life history must be drawn with the utmost caution. It is clear, however, that the hamsters that dominated the middle Aragonian faunas of Spain were on an even faster track in the fast-slow continuum, which helped them cope with the harsher environments of that period. Ultimately, loss of habitat and increased competition spelled the end for *Ligerimys* at the end of the early Aragonian.

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