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COMPARING THE BODY MASS VARIATIONS IN ENDEMIC INSULAR SPECIES OF THE GENUS *PROLAGUS* (OCHOTONIDAE, LAGOMORPHA) IN THE PLEISTOCENE OF SARDINIA (ITALY)

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Abstract. *Prolagus figaro* and *P. sardus* are part of an endemic insular anagenetic lineage that populated Sardinia since the earliest Late Pliocene to Holocene. BM of some populations of these two species was calculated using regression models. The best BM proxies for *Prolagus* are: femur length, zeugopod measurements and distal humerus diameter. The anagenetic lineage shows a BM increase of ca 20% from the populations of *P. figaro* (398-436 g) to *P. sardus* (504-525 g). The trend shown by the size of lower third premolar, even if not directly comparable with BM, is opposite (ca -30% at the transition *P. figaro-P. sardus*). Compared to *P.* cf. *calpensis*, a continental species of similar age, BM of *P. figaro* is ca +25%. The comparison with the insular endemic *P. apricenicus* evidenced differences in BM range and timespan required to attain it, due to the different size and palaeogeographical situation of the islands. Insular endemic *Prolagus* follow the small mammal pattern of Island Rule. Mein's (1983) biphasic model seems applicable to the evolution of *P. figaro*. A tachytelic phase followed by a bradytelic one seems to characterize also the appearance of *P. sardus*, at least for dental traits, a process probably triggered by important variations of abiotic and biotic traits of the environment, as indicated by the turnover that marks the onset of the Dragonara subcomplex. The prediction of life history traits and other biological attributes of Sardinian *Prolagus* using BM should be considered with caution due to the complexity of ecological selective regimes of Sardinia.

INTRODUCTION

Body size is a fundamental trait in the biology and ecology of species as it shows tight correlation with several physiological, behavioral, morphological, ecological and life history attributes (Peters 1983; Calder 1984). The best proxy for quantifying the BS of individuals is their body mass or weight (Gingerich et al. 1982). Thus, predicting the BM of fossil species is of critical significance for knowing their biology as well as for understanding and quantifying their adaptations to habitats (Palombo 2009a). For most of mammalian taxa, the allometric relationships among BM and bone/dental measurements of extant relative species allow the development of regression models to estimate the average weight of extinct ones (Damuth & MacFadden 1990; see Palombo 2009a: tab. 1 for a synopsis).

In spite of the abundance, diversity and ubiquity of fossil lagomorphs (leporids and ochotonids), models for estimating the BMs of species belonging to this order were developed very recently. Quintana Cardona (2005) and Quintana et al. (2011) provided the first models for leporids. Subsequently, expanding the database of Quintana Cardona (2005) and adding measurements of extant ochotonids, Moncunill-Solé et al. (2015) developed general and specific equations for estimating the BM of lagomorphs based on a multiproxy approach (teeth, cranial and postcranial measurements). BM estimation models for lagomorphs are going to enhance data about palaeocommunity structures and their palaeoenvironmental interpretations.

In view of the potential of this field, we decided to study the BM of the insular endemic ochotonids of the Pleistocene of Sardinia (Italy): *Prolagus figaro* and *Prolagus sardus*. *Prolagus figaro* is known from the latest Pliocene/earliest Pleistocene to the late Early Pleistocene of Sardinia (Capo Figari/

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		Femora	Tibiae	Humeri
Species	Fissure filling	N	N	N
		(coding)	(coding)	(coding)
Prolagus figaro	X3	10	6	14
		(SSN/X3/fe/1–10)	(SSN/X3/ti/1–6)	(SSN/X3/hu/1–14)
	IVm	5	–	–
		(SSN/IVm/fe/1–5)		
	X4	13	11	–
		(SSN/X4/fe/1–13)	(SSN/X4/ti/1–11)	
Prolagus sardus	XIr	74	42	60
		(SSN/XIr/fe/1–74)	(SSN/XIr/ti/1–42)	(SSN/XIr/hu/1–60)
	VI6	20	9	49
		(SSN/VI6/fe/1–20)	(SSN/VI6/ti/1–9)	(SSN/VI6/hu/1–49)

Tab. 1 - Fossil material used for performing the study.

Orosei 1 subcomplex of the *Nesogoral* FC- Orosei 2 subcomplex of the *Microtus* (*Tyrrhenicola*) FC; Palombo 2009b). *Prolagus sardus* is reported since the Middle Pleistocene (Dragonara subcomplex of the *Microtus* (*Tyrrhenicola*) FC; Palombo 2009b) until historical epoch in Sardinia and also in Corsica (Vigne & Valladas 1996; Wilkens 2004). We aim to:

1) Evaluate the BM trend of *Prolagus* in an insular habitat from an evolutionary point of view, as the two species of *Prolagus* from Sardinia are part of an anagenetic evolutionary lineage (Angelone et al. 2015).

2) Assess the response of fossil ochotonid species to insular regimes (Island Rule) (see Palombo 2009a and references therein for an update of the debate about this subject) as there are not extant relatives living on islands.

3) Provide data to increase the scarce biological knowledge of Sardinian *Prolagus*.

ABBREVIATIONS

BM: body mass; BS: body size; CMd1: Capo Mannu D1; IC: interval of confidence; FC: faunal complex; FL: femur length; FTDd: distal femoral transversal diameter; FTDp: proximal femoral transversal diameter; HAPDd: distal humeral anteroposterior diameter;

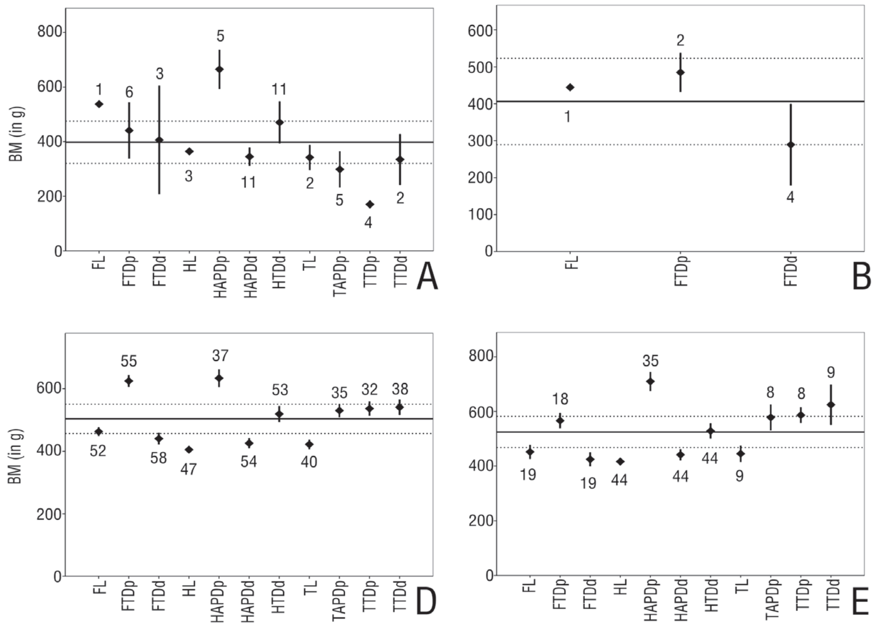

Fig. 1 - BM predictions (Y axis, in g) for *Prolagus figaro* and *P. sardus* calculated on the basis of different postcranial measurements (X axis). BM average (black line), confidence interval (dotted lines) and number of individuals are shown. A) *Prolagus figaro*, fissure infilling X3; B) *P. figaro,* fissure infilling IVm; C) *P. figaro*, fissure infilling X4; D) *Prolagus sardus*, fissure infilling XIr and E) *P. sardus*, fissure infilling VIb.

		BM *Prolagus figaro*						**BM *Prolagus sardus***			
		X3		**IVm**		**X4**		**XIr**		**VI6**	
Measurement	**Equation**	**x̄** **(IC)**	**N**	**x̄** **(IC)**	**N**	**x̄** **(IC)**	**N**	**x̄** **(IC)**	**N**	**x̄** **(IC)**	**N**
FL	logBM=−1.11+2.229logFL	537.57	1	444.74	1	−	−	463.09	52	452.12	19
								(448.98-477.20)		(426.38−477.85)	
FTDp	logBM=0.498+2.217logFTDp	441.19	6	484.96	4	474.51	10	624.91	55	566.28	18
		(337.88-544.51)		(432.23-537.69)		(423.18-525.84)		(605.96-643.86)		(538.47-594.08)	
FTDd	logBM=0.318+2.481logFTDd	406.21	3	289.40	2	306.13	3	440.50	58	424.84	19
		(207.12-605.30)		(178.91-399.90)		(251.76-360.51)		(421.79-459.21)		(398.98-450.70)	
HL	logBM=−1.221+2.418logHL	364.47	3	−	−	−	−	633.99	47	416.71	44
		(360.73-368.22)						(605.66-662.33)		(403.42-430.00)	
HAPDp	logBM=0.916+1.769logHAPDp	665.15	5	−	−	−	−	633.99	37	709.82	35
		(593.75-736.56)						(605.66-662.33)		(675.19-744.15)	
HAPDd	logBM=1.354+1.769logHAPDd	345.03	11	−	−	−	−	425.75	54	441.69	44
		(311.26-378.80)						(409.64-441.87)		(421.16-462.25)	
HTDd	logBM=1.053+1.513logHTDd	470.57	11	−	−	−	−	519.21	53	528.79	44
		(393.39-547.74)						(493.6-544.77)		(501.34-556.24)	
TL	logBM=−1.271+2.254logTL	342.28	2	−	−	−	−	422.18	40	445.57	9
		(296.52-388.03)						(407.09-437.27)		(415.82-475.32)	
TAPDp	logBM=0.599+2.265logTAPDp	298.77	5	−	−	545.27	6	530.28	35	578.26	8
		(233.38-364.16)				(454.86-635.69)		(509.28-551.47)		(530.81-625.71)	
TTDp	logBM=0.219++2.577logTTDp	170.50	4	−	−	400.62	6	536.58	32	586.70	8
		(155.93-185.06)				(312.36-488.68)		(513.18-559.98)		(558.05-615.35)	
TTDd	logBM=0.461+2.584logTTDd	334.94	2	−	−	452.19	5	540.94	38	624.73	9
		(241.77-428.12)				(353.44-550.93)		(516.22-565.66)		(551.11-698.36)	
Arithmetic Mean		397.88		406.37		435.74		503.86		525.05	
		(320.68-475.08)		(289.50-523.23)		(357.59-513.90)		(456.89-550.83)		(468.12-581.97)	
Weighted Average		402.34		423.34		453.326		520.83		512.40	

Tab. 2 - BM predictions (in g) for the populations of *Prolagus figaro* and *P. sardus* analyzed in this paper. Last two rows, highlighted in gray, show the arithmetic mean of BM calculated for each site, and their weighted average.

HAPDp: proximal humeral anteroposterior diameter; HL: humerus length; HTDd: distal humeral transversal diameter; Lp3: length of the third premolar; N: sample size; SSN: Soprintendenza dei Beni Archeologici per le Provincie di Sassari e Nuoro, sede di Nuoro; TAPDp: proximal tibia anteroposterior diameter; TL: tibia length; TTDd: distal tibia transversal diameter; TTDp: proximal tibia transversal diameter; $\bar{x}$: arithmetic mean; $\bar{x}_w$: weighted mean.

MATERIAL

The samples of *P. figaro* and *P. sardus* come from the Monte Tuttavista karstic complex (E Sardinia; Abbazzi et al. 2004) (Tab. 1). Remains of *P. figaro* come from infillings X3, IVm and X4, pertaining to the Capo Figari/Orosei 1 subcomplex of the *Nesogoral* FC-Orosei 2 subcomplex of the *Microtus* (*Tyrrhenicola*) FC (latest Pliocene/earliest Pleistocene to the late Early Pleistocene; Palombo 2009b). In this context, notice that Palombo (2009b) gave a different relative temporal arrangement of the aforementioned infillings (IVm-X4-X3). Remains of *P. sardus* have been sampled from infillings XIr and VI6, included in the Dragonara subcomplex of the *Microtus* (*Tyrrhenicola*) FC (Middle and Late Pleistocene; Palombo 2009b). Infillings XIr and VI6 were accumulated in a quite short time and their palaeontological contents are taxonomically homogeneous (see Angelone et al. 2008 for discussion). Preliminary analysis of *Prolagus* remains and literature data based on other taxa (Angelone et al. 2009; Palombo 2009b and references therein) pointed out that X3, IVm and X4 also are taxonomically homogeneous infillings. The fossil material is curated at the SSN.

METHODS

The skeletal maturation indicates the complete cessation of longitudinal growth and, consequently, the moment when animals achieve the final BS which is maintained until their death (Peters 1983). Thus, BM estimations of *Prolagus* species were only carried out on individuals that have already attained skeletal maturity (fused epiphyses). Specimens with unfused or broken epiphyses were not considered. *Ochotona*, the extant relative of *Prolagus*, shows a minimal sexual dimorphism (Smith 1988; Nowak 1999). For this reason, we did not assume BM differences between sexes in our fossil sample.

For undertaking the BM estimations, we followed the methodology described and illustrated by Moncunill-Solé et al. (2015: fig. 1). The following measurements were taken on postcranial remains: 1) FL, FTDd and FTDp on femora; 2) HL, HAPDp, HAPDd and HTDd on humeri; and 3) TL, TAPDp, TTDp and TTDd on tibiae. Moncunill-Solé et al. (2015) observed that burrower species of *Ochotona* and leporids show significant differences in the allometric models of the humerus, but not in other skeletal elements (femur and tibia). Although *Ochotona* is the closest relative of *Prolagus*, we preferred to use a general regression model for humeri (i.e. models that include data of leporids and *Ochotona*) because the locomotion of the species of *Prolagus* is not well known. The equations are shown

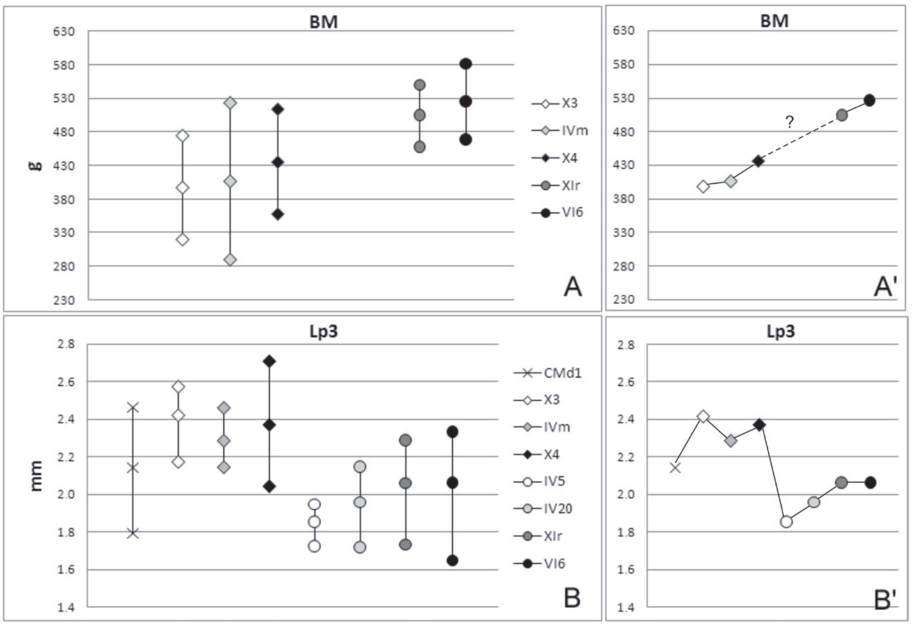

Fig. 2 - BM range A) and Lp3 range B) showing max, average and min values of *Prolagus* aff. *figaro* (cross, CMd1), *P. figaro* (diamonds, X3, IVm, X4) and *P. sardus* (circles, IV5, IV20, XIr, VI6), with detail of average values and trends of BM (A') and Lp3 (B').

in Tab. 2. Once the regression models were applied, we eliminated outliers due to their potential for skewing the distributions. We followed the criterion of Tukey (1977): outliers (Y) were considered when $Y < (Q1-1.5IQR)$ or $Y > (Q3+1.5IQR)$ (where Q1 is the 25th percentile, Q3 is the 75th percentile, and IQR the interquartile range (Q3−Q1)) (Quinn & Keough 2002). For each specific measurement, it was calculated an arithmetic mean ($\bar{x}$) and a confidence interval (IC) [$\bar{x}\pm((\sigma/\sqrt{N})Z_{\alpha}/2)$]. Based on the BM of each measurement, we performed an arithmetic average ($\bar{x}$) and a weighted average ($\bar{x}_W$) [$(X_1W_1+X_2W_2+\ldots+X_NW_N)/(W_1+W_2+\ldots+W_N)$].

In order to compare the different populations of *Prolagus* and analyze the BM variation, we performed ANOVA analyses and post hoc tests (Tukey HSD) ($\alpha = 0.05$) using the IBM SPSS Statistics 19 software.

RESULTS

The results of BM estimations (means, IC, N) are shown in Tab. 2 and are represented in Fig. 1.

For *P. figaro*, we estimate a weight of 397.88 g (320.68-475.08) in fissure filling X3, of 406.37 g (289.50-523.23) in IVm and of 435.74 g (357.59-513.90) in X4. For *P. sardus* the results are greater, 503.86 g (456.89-550.83) in fissure filling XIr and 525.05 g (468.12-581.97) in VI6. We do not observe significant differences between $\bar{x}$ and $\bar{x}_W$ (their difference is ca 10-20 g) and the latter falls perfectly in the IC of the former (Tab. 2). Statistically, there are only significant differences ($p < 0.05$) between the oldest population of *P. figaro* (X3) and the youngest of *P. sardus* (VI6).

When the BM estimations of each measurement are assessed, a similar pattern could be observed comparing the populations with the largest N (VI6 and XIr) (Fig. 1). The variables FTDp and HAPDp estimate a BM far above the arithmetic mean (between 100-200 g greater), especially in VI6 population. The other variables fall next or inside the IC of the arithmetic mean (specially FL, TAPDp, TTDp, TTDd and HTDd). Analyzing the results of the other populations (X3, IVm and X4), we observe more heterogeneous patterns. This may be consequence of: 1) few measurements taken in postcranial bones (3 in IVm and 5 in X4) and 2) small N (ranging from 1 to 11 individuals in X3). However, in this latter population (X3), it is already evident a large value of BM when HAPDp measurement is used, but not in FTDp.

DISCUSSION

BM of Sardinian *Prolagus*: trends and best estimators. Based on dental morphology, a relative temporal arrangement of the studied fissure has been attempted. Preliminary results suggested the relative chronological arrangement X3-IVm-X4 (from older to younger) of populations of *P. figaro* (Angelone et al. 2009). In the case of populations of *P. sardus*, infilling XIr is older than VI6 on the basis of a morphological cline (Angelone et al. 2008). In view of this and the BM results, the three selected populations of *P. figaro* show a total weight increase of ca 10% from the oldest fissure filling (X3) to the youngest (X4) (see Tab. 2, Fig. 1 and 2A). The BM of the oldest population of *P.*

sardus here analyzed (XIr) is ca 15% greater than the youngest of *P. figaro* (X4). The average BMs of the two populations of *P. sardus* selected for this study show a very slight difference (average BM of VI6 is about 4% larger). Finally, the total increase among the oldest (X3) to the youngest populations (VI6) of Sardinian *Prolagus* is of 32% (statistically significant, $p < 0.05$). Thus, we can affirm that Sardinian *Prolagus* increased its BM (average) throughout the Pleistocene.

The best BM estimator for an extinct species not only depends on the accuracy of the model (statistical values), but also on a subjective judgment of the results of predictions (Reynolds 2002). According to the fissure infilling with highest sample (XIr) (Fig. 1d), hindlimb bones seem to be the better BM estimators for *Prolagus* species (as shown also in Moncunill-Solé et al. 2015), particularly FL, TAPDp, TTDp and TTDd. However, HTDd also gives adjusted estimations. All these measurements predicted BM that fall inside the IC of the arithmetic mean and, consequently, we can consider them good proxies for the estimation of BM in the genus *Prolagus*. However, N must be taken into due account. For example, the BM predicted by FL (N=1) in X3 population is far above the arithmetic mean. It is recommendable to work with the largest sample possible in order to better represent the biological variability of the species and, thus, obtain more realistic values. The measurements regarded as the best BM estimators are surprising for two facts. Firstly, zeugopods (tibiae), which are involved in the locomotion and lifestyle of the animal, normally predict worse the BM of mammals (Scott 1990). Secondly, the lengths of long bones are also considered as less accurate than diameters or perimeters (Scott 1990). However, in the case of lagomorphs, the models that use length or zeugopodial measurements are as reliable (coefficient of determination or average absolute per cent prediction) as those that use other postcranial elements, in contrast to other mammalian orders (see also Moncunill-Solé et al. 2015).

Taking into consideration quantitative results, HAPDp measurement overestimates in all populations the BM in *Prolagus* and could not be considered a reliable proxy. FTDp does not show a clear pattern, being far above in the case of XIr population (those with the largest N), but not in others (X3, IVm, X4, VI6). The BM overestimation observed when HAPDp is used for prediction is indicative that this measurement does not only represent the BM of the species but also other biological attributes, such as locomotion or phylogeny. Samuels & Valkenburgh (2008) described some skeletal specializations of rodents depending on their locomotion style. For example, a broad and robust distal humerus is indicative of fossorial or semifossorial habits. We encourage the scientific community to perform new studies that analyze the locomotion, biomechanics and skeletal proportions of *Prolagus* species in comparison with its extant relatives (*Ochotona* spp.). This will increase the biological knowledge of *Prolagus* and might help us to discard those measures that are correlated with their locomotion or phylogeny for predicting BM.

BM and teeth size: the case of Sardinian *Prolagus*. It is interesting to compare the trends of BM vs Lp3 in the *P. figaro* – *P. sardus* lineage. We take into consideration p3 because it is the most reliable tooth position for specific identification in lagomorphs. As shown in Fig. 2b, average Lp3 increases (ca 13%) when the oldest population of *P. figaro* (X3) is compared to *P.* aff. *figaro* from CMd1 site, the "founder" of the Sardinian lineage. Lp3 of *P. figaro* shows a maximum oscillation of 6% in the considered populations. A drastic drop of Lp3 (almost 30%) is recorded between *P. figaro* (X4) and the oldest studied population of *P. sardus* (IV5). After IV5, Lp3 values of *P. sardus* increase slightly through time (total increase of ca 11% in the studied populations) following an asymptotic pattern (see also Angelone et al. 2008). When we analyzed the BM variation, the first thing that we observe is that its record is more incomplete than for teeth: BM estimations are not available for *P.* aff. *figaro* and older populations of *P. sardus* (Fig. 2a). Moreover, we have to take into due account that BM values have been obtained after complex data treatment, whereas Lp3 are raw data. Nevertheless, it is evident that BM and Lp3 of Sardinian *Prolagus* follow quite different trends. The differences are not so evident among populations of *P. figaro*: average BM increases of ca 10%, whereas average Lp3 fluctuates of ca 6%. Evident discrepancies can be noticed with the appearance of *P. sardus*. Average Lp3 drops of ca 30% between youngest *P. figaro* (X4) and oldest *P. sardus* (IV5). Then, Lp3 average increases through time in *P. sardus* attesting to a value of 2.06 mm (VI6) which is ca 15% smaller than in X4. Lacking data relative to older infillings (IV5 and IV20), we can only state that younger ones (XIr and VI6) show a higher BM average (ca 15-20%) than *P. figaro* (X4). Hypothesizing a dramatic BM decrease between *P. figaro* and *P. sardus* followed by an explosive increase to exceed *P. figaro* BM values is not realistic. The most parsimonious hypothesis is that BM followed a general increase trend through the transition *P. figaro-P. sardus* and throughout the evolution of *P. sardus*, countertrending Lp3 drastic drop observed at the transition *P. figaro* – *P. sardus*.

The fact that p3 dimensional trend shows evident discrepancies with BM pattern inferred through postcranial elements casts doubts about the usage of p3 as a proxy for BM estimation in insular endemic *Prolagus*. Compared to continental species of *Prolagus*, insular endemic species show a noticeable enlargement of the size of p3 vs the size of molariform elements of the lower tooth row (see Angelone 2005: fig. 6 for a qualitative comparison) probably due to a reassessment in jaw mechanics. At any rate, the reliability of teeth as BM proxies has been questioned also in studies that took into consideration a continental species of *Prolagus* as well as a wider selection of fossil lagomorphs case studies (Moncunill-Solé et al. 2015). They prefer models based on postcranial bones, as directly related to weight bearing.

Timing and patterns of BM variations in Sardinian *Prolagus*. Mein (1983) illustrated a biphasic pattern of evolution on islands consisting in a first tachytelic step in which the immigrant species undergoes sudden morpho-dimensional changes corresponding to its entrance to insular selective regimes and a second step in which the taxon undergoes a relatively long bradytelic phase. Millien (2006) further corroborated and "quantified" Mein's rule. According to some authors (Sondaar 1977; Alcover et al. 1981; Lister 1989, 1996), the tachytelic stage is a change in the "evolutionary direction" (sensu Sondaar 1977; e.g. BS shift or low gear locomotion) whereas the bradytelic one is a further continuation of the existing "direction of the change" (ib., e.g. harvesting saving by increase of hypsodonty, changes in dentognathic feeding apparatus, or developing traits for searching fallback resources). Evans et al. (2012) estimated a minimum of 4000 years for small mammals to become giants (ca 16000 generations).

If we apply Mein's model to Sardinian *Prolagus* lineage, the first phase should have taken place during or short after the Early/Late Pliocene boundary (age of the CMd1 fossil assemblage). Indeed, *P.* aff. *figaro* from CMd1 shows very slight morphological modifications due to endemism, evidence of its very recent arrival from mainland (Angelone et al. 2015). The Lp3 of *P.* aff. *figaro* is comparable to the values of populations of continental Italy from MN16 (absence record for MN15; Angelone et al. 2015) and is between 7-13% smaller than *P. figaro*. There is no record of the possible changes of BM occurred in the 1 Ma that separate CMd1 and the oldest populations of *P. figaro* from Monte Tuttavista. We have not enough data to clearly recognize the tachytelic stage of Mein's model in *P.* aff. *figaro-P. figaro* and to verify/quantify the dimensional changes and the time span needed to produce them. The populations of *P. figaro* here analyzed should cover a time span of ca 0.3-0.4 Ma (inferred from Palombo 2009b: fig 2). In this time span, slight weight fluctuations have been observed, which may correspond to the bradytelic phase of Mein's model.

The appearance of *P. sardus* (closely related to *P. figaro* and not an immigrant from mainland; Angelone et al. 2015) occurred during the transition from the Orosei 2 subcomplex to the Dragonara subcomplex (ca 0.8-0.7 Ma; inferred from Palombo 2009b: fig 2). This transition is characterized by the highest species turnover recorded in the Quaternary of Sardinia (Palombo 2009b). Leaving aside the reason of this dramatic change (see next section), it seems to have triggered a new biphasic evolutionary phenomenon which follows Mein's model too. In general the phyletic lineages of Sardinian small mammals underwent outright (geologically speaking), an abrupt and noticeable increase in dental size (Abbazzi et al. 2004). Contrarily *Prolagus*, as stated above, experienced a drastic Lp3 decrease. The absence of data from IV5 and IV20 fissure fillings does not allow us to quantify changes in BM. Teeth size and morphology in early populations of *P. sardus* underwent an evolution comparable to Mein's model first phase. The slight, asymptotic growth of *P. sardus* Lp3 and postcranial measurements (Angelone et al. 2008), that in our data covers the interval between ca 0.6-0.4 Ma (inferred from Palombo 2009b: fig. 2), parallelizes Mein's model second phase. Indeed, Mein's rule focuses on the first stages of colonization of the island, making reference to the biological adaptation of the species to the new selective regimes. However later on, changes can also take place consequence of the variation in the environment. Abiotic changes (climatic, topographic, among others) and variations of biotic traits (e.g. levels of predation, intra- and interspecific competition), both have a significant role to drive evolution (Alcover et al. 1981; Brockhurst et al. 2014). Our data seem to indicate that Mein's model can be applied several times to a taxon during its evolution of an island, if significant ecological changes occur (e.g. climatic changes or variation in levels of selective regimes). The study of other mammalian lineages of the Pleistocene of Sardinia or other islands may provide more case studies to support this hypothesis.

Driving factors in the evolution of Sardinian *Prolagus*: some hypotheses. The sea level low stand at the Early/Late Pliocene transition allowed the migration of *P. sorbinii* from Italian mainland towards Sardinia (Angelone & Kotsakis 2001; Angelone et al. 2015). Insular selective regimes triggered the morpho-dimensional changes in the immigrant that led to *P. figaro*. *Prolagus figaro* survived until the end of the Orosei 2 subcomplex. The appearance of *Prolagus sardus* marks the onset of the Dragonara subcomplex, characterized by a complete turnover in the small mammals' component of Sardinian fauna (except for *Talpa*): the leporid and the glirid *Tyrrhenoglis* did not survive the transition; the insectivore *Nesiotites* and the rodents *Tyrrhenicola* and *Rhagamys*, descendants of taxa already present in the Orosei 2 subcomplex, underwent evident modifications of teeth morphology and a noticeable increase of teeth size probably coupled with a BS increase (Abbazzi et al. 2004); the ochotonid *Prolagus* underwent a decrease of Lp3 but an increase of BM.

The ancestors of the small mammal genera which survived into the Dragonara subcomplex were present and already showed endemic traits since the Orosei 2 subcomplex (i.e. *Tyrrhenicola*) or at least since the Capo Figari/Orosei 1 subcomplex. The competition among small mammal species as driving factor of the turnover between the Orosei 2/Dragonara subcomplexes can be ruled out and the extinction of glirids and of the leporid is not likely to have triggered a competition to occupy its niche in taxa with such a wide range of ecological requirements, and the arrival of *Tyrrhenicola* already occurred earlier. The arrival of the canid *Cynotherium* (once regarded as a specialized *Prolagus* hunter, and recently considered a small-prey hunter, possibly also birds, without evident specialization in *Prolagus* hunting; Malatesta 1970; Lyras et al. 2006, 2010) occurred at the onset of the Orosei 2 subcomplex without triggering any sudden, evident change in small mammals, least of all in *Prolagus*, which increases its BM throughout Pleistocene. This fact apparently contradicts van der Geer et al. (2013) who noticed that the BS increase in insular small mammals that occurs following colonization or first appearance, ceases or is reversed after the arrival of mammalian predators or competitors. Probably the impact of a new predator was not so catastrophic because, contrarily to other islands, several carnivores were already present in Sardinia prior to *Cynotherium* (i.e. *Chasmaporthetes*, *Mustela* and *Pannonictis*; the latter also coexisted with *Cynotherium* for a while). In fact, due to its large area, Sardinia had selective regimes more similar to mainland than other Mediterranean islands. It could support the presence of terrestrial predators and had not a strong resource limitation as small islands (Heaney 1978, 1984). Thus, we can not affirm that the arrival of *Cynotherium sardoum* increased the extrinsic mortality of Sardinian pikas.

The most important cause of the turnover at the onset of the Dragonara subcomplex, and thus the trigger of the transition *P. figaro-P. sardus* is likely to be climate change, in particular those related to the mid-Pleistocene Transition. Even after Middle Pleistocene, the evolution of *P. sardus* seem related to climate changes and to consequent specific modifications of the environment. Preliminary data by Boldrini & Palombo (2010) suggested a correlation between limb length and temperature in *P. sardus*. Effects of climate on BS have been highlighted in insular endemic fossil vertebrates of the Mediterranean by van der Geer et al. (2013), according to whom BS fluctuates over time linked to climatic oscillation. Also Millien & Damuth (2004) noticed the influence of geographical climatic gradients and climatic change through time on fossil endemic insular species.

Regarding the extinction of Sardinian *Prolagus*, it probably occurred less than 2000 years ago, in the Roman period, between the arrival of *Rattus rattus* and the present time (Vigne 1982). Authors do not agree on the importance of men's influence (directly by predation and indirectly by introduction of alien predators, competitors, parasites, infectious diseases, modification of the landscape by agricultural activities, among others) to the extinction of *Prolagus*.

Insular endemic lagomorphs and the Island Rule. Radical morpho-dimensional adaptations are observed in insular endemic organisms. In mammals, apart from modifications in dental, cranial and limbs morphology and relative proportions, it is observed a BS trend coined as Island Rule (Foster 1964; Van Valen 1973): in general small-sized mammals considerably increase their size, whereas large-sized mammals show an opposite trend. This ecogeographic rule is also observed in insular endemic fossil mammals. In the Neogene-Quaternary of Mediterranean islands and palaeoislands, insular gigantism and dwarfism have been the subject of several studies and debates (from the pioneer general studies, e.g. Vaufrey 1929; Thaler 1973; Sondaar 1977; Azzaroli 1982; to the most recent reviews, e.g. van der Geer et al. 2010; Lomolino et al. 2013 and references therein).

Lagomorphs are usually considered as small mammals together with rodents and insectivores. Although they have a larger size than the average of the small mammals, this order is far from reaching the size of the great majority of large mammals (e.g. elephants, rhinos, etc.). Their medium or intermediate BM undertakes a key position in ecosystems (Valverde 1964) and compromises their response (adaptation) to island environments (Island Rule). Actually in extant endemic insular leporids the BM trend reported in literature is variable, but mostly directed towards a reduction of the size (Foster 1963, 1964; Lawlor 1982; Palacios & Fernández 1992; Tomida & Otsuka 1993). In the case of ochotonids, no extant species are present on islands and their trend is unknown.

When we deal with insular endemic fossil lagomorphs, it is not easy to determine their actual BM and its relative variation compared to the continental ancestor. This is consequence of two facts: 1) mainly most remains consist in teeth, whose size, at least in lagomorphs, does not directly reflect BM (see above and Moncunill-Solé et al. 2015); and 2) the supposed ancestor is often unknown or wrongly identified (e.g. *P. sardus* from *P. michauxi* and *Gymnesicolagus gelaberti* from *P. crusafonti* in Lomolino et al. 2013 and van der Geer et al. 2013). A reliable BS estimation is available for an insular endemic fossil leporid, *Nuralagus rex* (Pliocene of Menorca, Spain), which BM has been calculated in 8 kg (Moncunill-Solé et al. 2015, who reconsidered the BM estimation of 12 kg by Quintana et al. 2011). Even if not quantifiable, the size increase with respect to its supposed continental ancestor, the relatively small-sized genus *Alilepus*, should have been quite remarkable.

For *Prolagus* species it is not possible to quantify exactly the relative BM increase of insular endemic vs their mainland ancestors. In the case of Sardinian *Prolagus*, this is due to the lack of studies of postcranial remains of *P. sorbinii*, whereas in the case of Apulian *Prolagus*, their continental ancestor is not known yet (Angelone 2007; Angelone & Čermák 2015; Angelone et al. 2015). Nevertheless, we can have a gauge of the BM difference between endemic insular *Prolagus* and continental species taking into consideration the only available BM datum of a continental *Prolagus*, i.e. the BM of *P.* cf. *calpensis* from the Late Pliocene of Spain, estimated in ca 320 g (based on average of femurs and tibiae; Moncunill-Solé et al. 2015). Thus, *P. figaro* from Monte Tuttavista X3 had a noticeably larger BM (ca 25%) than an almost coeval western European mainland *Prolagus*. One among the oldest known populations of *P. apricenicus* (Cava Fina F1; BM = ca 282 g; Moncunill-Solé et al. in press) had a BM ca 13% smaller than *P.* cf. *calpensis*, not because it decreased its size in an insular domain, but probably because the continental ancestor of Apulian *Prolagus* was a pre-Messinian, medium-sized species (see Angelone 2007; Angelone & Čermák 2015). Later populations of *P. apricenicus*, weighing ca 601 g (Moncunill-Solé et al. 2015), almost doubled the BM of *P.* cf. *calpensis*.

The known average BM range of both Sardinian species of *Prolagus* (397.88-525.05 g; a BM of 800 g for Mesolithic *P. sardus* inferred by Sondaar & van der Geer (2000) on a qualitative basis has to be verified) is smaller than the populations of *P. apricenicus*, whose BM range is ca 280-600 g (Moncunill-Solé et al. 2015, in press). The other Apulian species, *P. imperialis*, is traditionally considered gigantic, because it has the largest p3. However, our analyses and results make clear that dental remains do not directly reflect actual BM, and sometimes even countertrend postcranial-based results. Pending a study of postcranial remains of *P. imperialis*, we refrain to make inferences about its BM.

Millien (2011) argued that in smaller islands the evolutionary rate is higher. This possibly explains the explosive BM increase of *P. apricenicus*, confined to a very limited, fragmented area, in contrast to the *P. figaro*-*P. sardus* trend, which lived in a larger island.

In general, the scanty available quantitative data indicate that both fossil leporids and ochotonids follow the small mammal Island Rule pattern. They underwent a BM increase which extent is highly variable, though. This trend is not in line with the variable response observed in extant insular endemic leporids (see above).

BM and life history of insular endemic *Prolagus*. In the last twenty years, several researches have been focused on the life history of insular fossil species, principally addressed to dwarfism (Bromage et al. 2002; Raia et al. 2003; Raia & Meiri 2006; Köhler 2010; Kubo et al. 2011; Marín-Moratalla et al. 2011; Jordana et al. 2012, 2013; van der Geer et al. 2014) although, newly, investigations regarding gigantism have been performed (Moncunill-Solé et al. in press; Orlandi-Oliveras et al. in press). BM scales with several traits of the life history of species such as life span, fecundity, age at maturity, among others (Blueweiss et al. 1978; Peters 1983; Calder 1984). For this reason, at first sight, we could think in predicting some of these life history traits for *P. figaro* and *P. sardus* using the BM results of our analysis. However, Moncunill-Solé et al. (in press) analyzed the histology and BM of one of the Apulian insular endemic species of *Prolagus* (*P. apricenicus*) and suggested that it had a slower life history than expected from its BS. Histologically, the longevity is estimated of at least 7 years for *P. apricenicus* from F1 fissure filling contrasting with the 4.5 years expected from its BS (around 300 g). The selective regimes of insular habitats (low levels of extrinsic mortality and resource limitation) are the most probable triggers of this shift (Palkovacs 2003). This is also observed in extant ochotonids (*Ochotona* spp.) that dwell in rocky habitats which are subjected to a low average yearly mortality. They show a slower life history (later age at maturity and longer longevity) than the species of *Ochotona* that live in meadows, although both groups do not have steep differences in BM (Smith 1988).

Taking in consideration of the aforementioned, extant and extinct relative species that dwell in habitats with low levels of extrinsic mortality show a slower life history than expected from their BS. In the case of *P. figaro* and *P. sardus* the levels of extrinsic mortality may not be as low as in the case of *P. apricenicus* from Gargano consequence of the presence of predators. However, the ecological selective regimes of Sardinia would not be like the mainland's one. For this reason, the prediction of life history traits and other biological attributes using the estimated BM should be considered with caution. Probably, we would underestimate the values of these traits. The absence of histological data of extant and extinct ochotonids encourages the studies focused on this field in order to improve the biological knowledge of insular and mainland lagomorphs.

CONCLUSIONS

BMs were estimated for *P. figaro* from X3 (397.88 g), IVm (406.37 g) and X4 (435.74 g); and for *P. sardus* from XIr (503.86) and VI6 (525.05 g). These results allow us to state a significant increase of BM of the species *Prolagus* from Sardinia throughout the Pleistocene. The best measurements for determining the BM of *Prolagus* are FL, TAPDp, TTDp, TTDd and HTDd. In contrast, HAPDp and FTDp appear to be unreliable proxies. The BM increase opposes to the pattern of the Lp3, which shows a drastic drop at the transition between *P. figaro* and *P. sardus*. This is due to the fact that teeth are not weight-bearing elements, and thus, their use as BM proxies is not recommended. However, when the teeth dimensions are taken into account, the biphasic Mein's model (tachytelic and bradytelic stages) may be observed twice. This cannot be confirmed with BM estimations due to the absence of postcranial elements in some key sites as CMd1 (*P.* aff. *figaro*) and IV5 (oldest known population of *P. sardus*). The entrance of *Cynotherium* and the presence of other species of carnivores during the Pleistocene seem to not have influence on the pattern of adaption to insular ecological regimes of *Prolagus*.

Currently, the absence of ochotonids on islands does not allow us to know the adaptions of this group to insular ecological regimes (Island Rule). In the fossil record, the two species of *Prolagus* studied in our research and one of the two endemic insular Apulian species (*P. apricenicus*) suggest a gigantism pattern for ochotonids. However, this latter species shows a more explosive increase of BM perhaps as a result that it dwelled in a smaller, fragmented area. It is observed in extant and extinct species that the environments with a lower extrinsic mortality can promote a lower life history (e.g. greater longevity than that expected for its BM). Thus, the estimations of life history traits taking into account the BM results of our research should be considered with caution.

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