

Evolutionary Biological Responses of Pikas (Lagomorpha, Mammalia) to Past Insular Ecosystems (Miocene-Holocene): A Key for the Management of Extant Species [†]

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Abstract: Fossil biotas provide an opportunity to explore eco-evolutionary adaptations to insular regimes not subjected to the anthropogenic perturbations. Historically, these studies have been biased towards large-sized taxa, and less efforts have been devoted to small ones. For this reason, the present study reviews the general and specific biological responses described in extinct insular ochotonids (Ochotonidae, Lagomorpha) from the Mediterranean Islands (Miocene-Holocene), given the last cutting-edge investigations. Parallel biological trends have been observed in these species, regarding an increase of adult body size, teeth modifications (e.g., higher hypsodonty), slow-gear lifestyle with new locomotion skills (related to digging, climbing or leaping), as well as a slow life history. Most of these features are also noticed in other extinct insular micromammals and large-sized species. Although a single ochotonid dwells in true insular environments at present, the future climate change will push them to inhabit top of mountains (ecological islands). The present paper provides useful baseline data (evolutionary history of the family, biological abilities or responses to insularity) for the design and implementation of innovative and effective management actions.

Keywords: conservation paleobiology; fossil record; island rule; life history; Mediterranean islands

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1. Introduction

Islands are regarded as natural laboratories and constitute a series of evolutionary repeatable and testable experiments [1]. Their mammalian dwellers are characterized by a set of distinguishing biological traits, which have evolved as predictable responses to the selective regimes of islands [2–6]. On one hand, the ‘island rule’ is defined as the biological trend for small mammals to evolve towards larger sizes (giants), whereas large-sized taxa evolve towards smaller morphotypes (dwarfs) [2–5]. Several authors have noticed that it is a more widespread trend than suspected initially, which is not solely limited to mammals. In this regard, other taxonomic groups, such as birds, reptiles or invertebrates, follow this ecogeographical rule (with few exceptions) [7,8]. On the other hand, the ‘island syndrome’ also states biological shifts in these taxa, regarding the demography, life history, behavior or morphology, when compared to mainland forerunners [6]. Ecologists have proposed three specific ecological factors as the main drivers of these biological parallel patterns: resource limitation, low predation and high intra-specific competition [4,5,9,10]. However, others have suggested alternative explanations based on the relative importance of the lower extrinsic mortality rate and limited resource availability on species life history [11]. Particularly, extinct insular endemics have aroused special interest, mainly because their biology and ecology were not perturbed by anthropogenic

actions [12]. In addition to size shifts, extinct insular endemics are characterized, in general, by changes in postcranial bones (proportions, length, robustness, articulation loss), dentition alterations (higher degree of hypsodonty, loss of premolars, more complex enamel pattern), as well as modifications in skull and brain (absence of pneumatization, short muzzles, brain and sense organs reduction) [13]. However, such results are biased (overrepresented by large mammals), and the eco-evolutionary adaptations of small mammals to insular regimes are relatively less known.

Lagomorpha is an evolutionary successful order of intermediate size, occurring in a wide range of habitats with a worldwide distribution. Ecologically, rabbits, hares and pikas play essential roles in ecosystems, representing the base of some predator-prey systems and supporting their communities (such as foxes, birds of prey or coyotes), impacting on hydrology and soil biology and modelling plant communities [14]. For this reason, lagomorphs were also common in extinct insular faunas. In Mediterranean Islands various lagomorph species have been identified (both ochotonids, O; and leporids, L): *Gymnesicolagus gelaberti* (O, but see Figure 1), *Hypolagus balearicus* (L), *Hypolagus peregrinus* (L), *Nuralagus rex* (L), *Paludotona etruria* (O, but see Figure 1), *Paludotona minor* (O, but see Figure 1), *Prolagus apricenicus* (O), *Prolagus figaro* (O), *Prolagus imperialis* (O), *Prolagus sardus* (O), and *Sardolagus obscurus* (L) (Figure 1) [15–24]. At date, these ochotonid species are the only ones recovered in extinct insular ecosystems. Currently a single ochotonid taxon (*Ochotona hyperborea*) inhabits true islands, but some others occur in ecological ones [25].

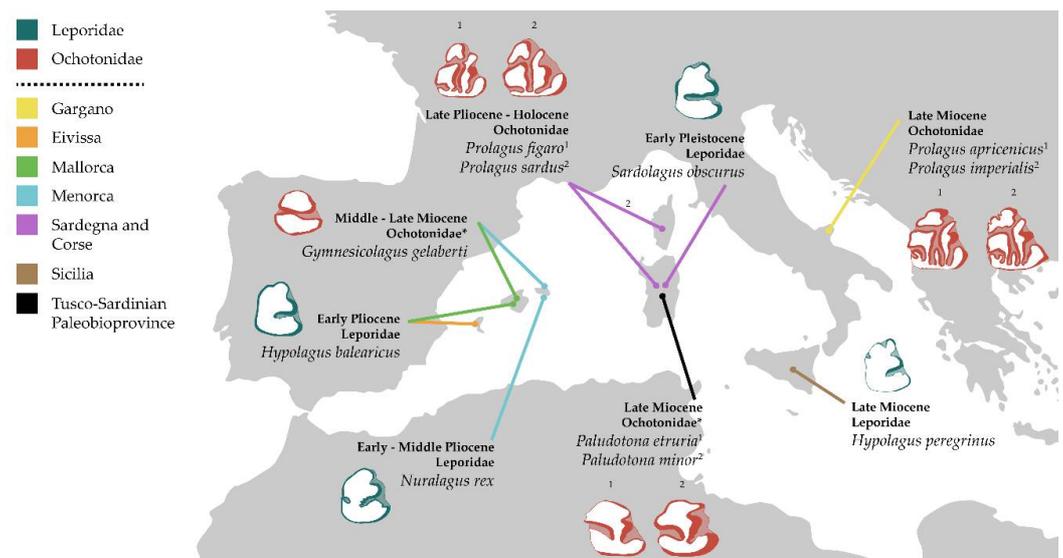


Figure 1. Distribution of extinct lagomorphs in the Mediterranean Islands. Geographic location, geologic age, taxonomic details (family and species), as well as illustration of right p3 (no scale) are provided for each taxa. * Although *Gymnesicolagus* and *Paludotona* are considered to be ochotonids in the present paper, some recent studies identify them as stem-lagomorphs [23,26].

Considering the above background, the present paper has the main objective of reviewing the eco-evolutionary adaptations of extinct ochotonids (Lagomorpha, Ochotonidae) to insular regimes. The results will contribute to: (1) enhancing the paleobiological knowledge of past lagomorphs, and (2) understanding the biological responses of small mammals to insular ecosystems. Moreover, the exposed conclusions may give clues to address the management and conservation of extant ochotonids, which will be largely affected by climate change according to species distribution models.

2. Experiments

The present research is a review of the paleobiological data derived from previous investigations and studies in the extinct ochotonid taxa that dwelled in insular ecosystems. To this end, the data was gathered accurately from peer-reviewed published papers carried out by several authors [18,23,27–38], as well as from very recent unpublished results. Taxonomic details (species and family), geographic distribution and geologic age of the assessed ochotonids are provided in Figure 1. Paleobiological information of insular leporids or micromammalian taxa (rodents and soricids) was also gathered for comparative purposes [13,37]. With the same objective, material of extant lagomorph species (housed at the Hungarian Natural History Museum) was also assessed. 100% stacked bar plots (showing relative percentages) have been used to compare evo-evolutionary adaptations between insular ochotonids and other micromammalian groups.

3. Results

The paleobiological data of Mediterranean extinct ochotonids is summarized in Table 1.

Table 1. Eco-evolutionary adaptations described in extinct ochotonids from the Mediterranean Islands (Miocene-Holocene). Abbreviations: $\hat{\uparrow}$: high; $\hat{\downarrow}$: low; $>$: increase; $?$: unknown; $\hat{\downarrow}$: doubtful.

Species	Body Mass (g)	Dental Features	Locomotion	Life History
<i>Gymnesicolagus gelaberti</i>	$\hat{\downarrow}$ 5400	Hypselodonty and hypsodonty ¹	?	?
<i>Paludotona minor</i>	?	Hypselodonty, hypsodonty, and $>$ masticatory area	?	?
<i>Paludotona etruria</i>	?	Hypselodonty, hypsodonty, and $>$ masticatory area	?	?
<i>Prolagus apricenicus</i>	150–250	Hypselodonty, $\hat{\downarrow}$ hypsodonty, $\hat{\uparrow}$ enamel pattern, and $>$ premolar area	Non-cursorial, jumping skills	Slow
<i>Prolagus imperialis</i>	500–750	Hypselodonty, $\hat{\downarrow}$ hypsodonty, $\hat{\uparrow}$ enamel pattern, and $>$ premolar area	Non-cursorial, jumping skills	?
<i>Prolagus figaro</i>	398–436	Hypselodonty, $\hat{\downarrow}$ hypsodonty, $\hat{\uparrow}$ enamel pattern, $>$ premolar area, and megadontia	?	?
<i>Prolagus sardus</i>	504–525	Hypselodonty, $\hat{\uparrow}$ hypsodonty, $\hat{\downarrow}$ enamel pattern, $>$ premolar area ² , and megadontia	Non-cursorial, jumping and digging skills	$\hat{\downarrow}$ Slow

¹ This trait is not observed in all teeth. ² To a lesser degree than other *Prolagus* species.

3.1. Body Mass

The body mass of extant pikas ranges between 70–250 g, whereas leporids are much heavier (from half a kilo to nearly 5 kg) [34]. Extinct insular *Prolagus* (~150–750 g, depending on the species) and *G. gelaberti* (5400 g) were larger than extant ochotonids (Table 1) [30,33–35]. At present, the weights of *Paludotona* species have not been estimated, but their teeth dimensions suggest a smaller size than *P. imperialis* [23]. The degree of body size shift of insular species is assessed by means of S_i (=mass of insular population/mass of mainland forerunners) [37]. The strong modifications experienced by insular species prevent, in most of the cases, to determine certainly the direct ancestor of these taxa, but several approximations have been done using contemporary continental relatives [37,38]. Following the ‘island rule’, these results indicate a shift towards larger morphotypes ($S_i \sim 2.27\text{--}35.82$). In extant insular leporids, the ‘island rule’ is quite complex

and a clear pattern is not observed. Some taxa have evolved towards a large size (S_i max. ~ 1.5 – 1.6), whereas others have become dwarfs (S_i min. ~ 0.4 – 0.5) [5].

3.2. Dental Features

Several modifications have been identified in the dentition of insular ochotonids, regarding hypselodonty (ever-growing teeth), hypsodonty (high crowned teeth), complexity of enamel pattern, and increase of occlusal surface area (cited as masticatory area, premolar area and/or megadontia) (Table 1). *Gymnesicolagus gelaberti* has a hypselodont dentition, with some hypsodont upper teeth (although this latter feature has not been assessed quantitatively) [18,30]. The taxon also shows a short snout and a short mandibular diastema, as well as it lacks m_3 . These have been considered archaic traits, suggesting that they are not related to insular regimes [30]. The hypselodont dentition of *Paludotona* species has higher crown teeth (lacking a quantitative assessment too). Although this genus also shows some archaic features, an increase of the masticatory surface is noted as a response to insular regimes [16,23]. Regarding *Prolagus* species, all of them are characterized by an hypselodont dentition. Some taxa (*P. apricenicus*, *P. imperialis*, and *P. figaro*) have low hypsodonty combined with a high complexity of the enamel pattern, whereas, on the other hand, *P. sardus* shows the opposite traits (high hypsodont dentition with a poor complex enamel pattern). An increase of premolar area is noticed in all the taxa, but to a lesser degree in *P. sardus* [28]. Sardinian *Prolagus* are also characterized by megadontia (an increase of the occlusal area of postcanine dentition relative to body mass).

3.3. Locomotion

In general, the lifestyle of extinct insular ochotonids has been little studied (Table 1). The postcranium of the Garganic ochotonids (*P. apricenicus* and *P. imperialis*) is similar to that of extant talus pikas. Such resemblance suggest jumping skills and a reduction of cursoriality in these extinct taxa [35]. On the other hand, *P. sardus* has more upright position of the head and a greater range of movements than extant relatives. Their postcranial morphology also lacks cursorial skills, but shows adaptations to jumping, digging and climbing [27].

3.4. Life History

The life history of extinct species is studied by means of histological analyses of bones. As it is an invasive technique, this has only been carried out in *P. apricenicus* so far. A minimum longevity of 7 years is suggested for this species, what means a long life relative to its body size. For this reason, specialists describe that this species moved towards the slow-end of the ‘fast-slow continuum’ of the life history variation [34]. In addition, paleopathological incidence can also shed light on the species life history. In the present case, several abnormal conditions have been identified in *P. sardus*, although the incidence of pathologies in mainland taxa is very low. As pathologies are more frequent in species with a longer life, this high incidence in the insular taxon could be interpreted as an extended life relative to mainland forerunners [35,36].

4. Discussion

4.1. Eco-Evolutionary Adaptations of Small Mammals to Islands: Comparisons and Drivers

Ochotonids show clear eco-evolutionary responses to insular regimes [35]. However, when they are compared to other small insular taxa, the patterns are not so homogenous (Figure 2) [13]. Comparatively, extinct ochotonids are the small mammals from Mediterranean area that have been best paleobiologically described. This contrasts with soricids for which neither locomotor nor life history studies have been carried out at date.

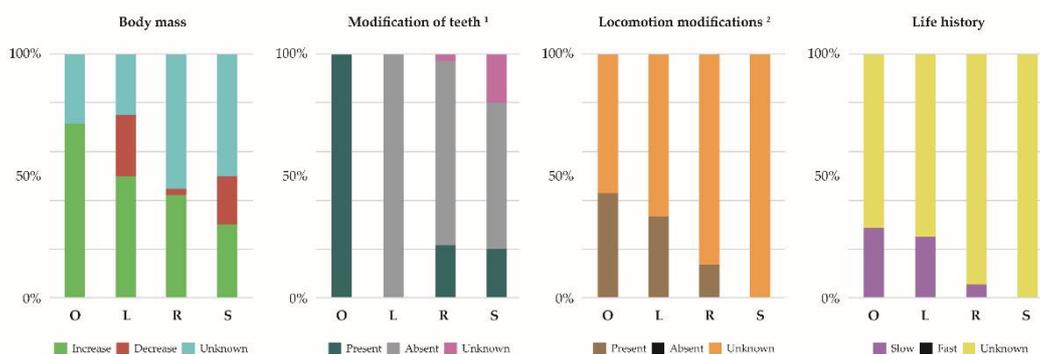


Figure 2. Comparison of the eco-evolutionary adaptations described in the most important micromammalian taxa from Mediterranean Islands (Miocene-Holocene): O, ochotonids (N = 7); L, leporids (N = 4); R, rodents (N = 37); and S, soricids (N = 10). Data was obtained from present study and previous publications [13]. ¹ Hypsodonty, enamel pattern complexity, masticatory surface and/or tooth loss. ² Non-cursorial locomotion, with fossorial, jumping and/or climbing skills.

Generally speaking, extinct small mammals experience an increase of body mass following the ‘island rule’ (Figure 2). Although they show a huge size, in most of the cases this value has not been compared to the size of their direct ancestors [13,39]. Therefore, these results should be taken with caution. In some cases it is documented that small species do not follow the ‘island rule’, showing a similar size than their forerunners (e.g., *Mus minotaurus* from Crete), or even becoming dwarves [40]. According to Palkovacs [11], body size modifications of insular endemics depend on the extent to which low extrinsic mortality and limitation of resources affect to their life history. Small mammals, generally, are more affected by the lower extrinsic mortality, driving to an increase of age at maturity and a larger size. However, in such island where micromammals experience a strong resource limitation, these selective pressures will trigger a dwarf morphotype.

All insular species of ochotonids show modifications of their dentitions, what contrasts with observations in leporids (Figure 2). In rodents and soricids the % of teeth modifications is rather small. These discrepancies could be consequence of the fact that teeth have only been examined by taxonomical purposes, and some features (e.g., hypsodonty index) have been neither considered nor quantified. However, the shifts documented in ochotonids and some other taxa are also identified in large-sized endemics [13]. These have been related to a more abrasive diet triggered by the arid resource-limited place where they dwell [28,41]. However, such features also increase the longevity of the teeth, and might respond to other biological and ecological stressors (e.g., extended life) [23].

Little is known about the locomotion and life history of small-sized endemics (Figure 2). The few studies show that they evolved towards a slow-gear locomotion with digging, leaping and/or climbing skills. The absence of carnivorous predators, the strong limitation of resources and the orography of Mediterranean Islands were the main drivers of such traits [42]. In these conditions, selection favors a more stable and resistant skeleton, which allowed them to explore different environments and establish in new ecological niches [43,44] and to search underground resources when limitations are very strict [13,42]. In relation to life history, small-sized endemics moved towards the slow-end of the life-history continuum, as consequence of the low extrinsic mortality that occurs in insular regimes [11]. In this regard, according to this hypothesis, *Hypnomys onicensis* shows similar growth rate but a more extended life than extant relatives [45]. In the case of large-mammals, they also evolved towards a slower life history [13].

4.2. Past Insular Ochotonids: A Key for the Management of Extant Species

The recent modelizations of the coming climate change and its consequences on extant ecosystems and biotas suggest that more than two-thirds of lagomorph species will be affected [46]. Specially, ochotonids will be profound impacted, experiencing marked range declines, and will be forced to move towards high-altitude areas. In some cases,

these new climatic conditions will finally push species to extinction [46]. On the other hand, most of leporids will migrate to maintain their current ecological niche towards high latitudinal regions as consequence of their larger sizes [46]. Knowing the ecological and biological variables of extant ochotonids (e.g., adult body size or litter size), as well as understanding how these species respond to environmental changes at evolutionary level, are essential keys for design effective mitigation measures and conservation protocols.

The conservation paleobiology tries to use long-term paleobiological data of past species to know their evolutionary responses to environmental changes, and to address the conservation and management of extant species [47]. In this regard, the present study provides baseline data describing how ochotonids responded to insularity in the past. As discussed above, climate change will contract the range of pikas, and most of them will be restricted in ecological islands (top-mountain regions) [48]. This ecological isolation will prevent them to move to nearby regions, and will increase their susceptibility to decline [46]. Results highlight the successful adaptation of ochotonids to insular regimes, even showing some long-lasting lineages. Moreover, all groups showed very similar predictable responses, including dental morphology, locomotor attributes, body size and life history (Table 1, Figure 2). These features will have to be carefully reviewed to face with the management of extant threatened ochotonids, allowing to identify suitable candidates or to evaluate assisted relocations for some of them. In this regard, *Ochotona princeps* is very resilient in front of warmer conditions, changing its foraging tactics and adjustment its activity cycle. However, their isolated populations have been removed due to their limited dispersion [48].

5. Conclusions

The present paper reviews the eco-evolutionary adaptations of past ochotonids to insular regimes (Miocene-Holocene, Mediterranean Islands). All examined species responded with similar biological shifts. Besides increasing their adult body size, they also experienced changes in teeth, lifestyle and life history. This set of adaptations have also been identified in other micromammalian taxa from insular habitats. The present study provides baseline data that might be useful for conservation purposes. As consequence of climate change, extant pikas will be threatened and will be restricted to small regions (ecological islands). Knowing which are the eco-evolutionary responses of ochotonids to these ecological stressors (insularity) could be decisive in the design of effective management.

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