

THE VOLCANO RABBIT *ROMEROLAGUS DIAZI*,
A PECULIAR LAGOMORPH

by

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1. Introduction

The order Lagomorpha includes rabbits, hares and pikas. Unlike pikas (Smith et al., 1990), rabbits and hares inhabit most of the earth's terrestrial ecosystems (Chapman & Flux, 1990), where they are often common and abundant. However, this does not hold true for all species. A large number of lagomorphs are rare, endangered or threatened, several of these being relict and endemic species with a restricted range. In addition, detailed documentation on the biology and ecology is scarce for the vast majority of such species.

The volcano rabbit *Romerolagus diazi* (Ferrari Pérez, 1893) is one of the best examples of these rare lagomorphs. The first collectors of this rabbit at the end of the 19th century pointed out its atypical characters (Merriam, 1897; Nelson, 1909). The morphological description of the rabbit given by early collectors expressed uncertainty as to whether it was a rodent (Herrera, 1897), a hare (Díaz, 1893), or a true rabbit (Miller, 1911). Since its first description a number of studies have been carried out on the biology and ecology of *Romerolagus*. Cervantes et al. (1990) and Velázquez et al. (in press) list most of these and provide an overview of the present knowledge of the rabbit species. However, not all the results of these studies have been published and many data are scattered in various specialized journals.

The objective of this paper is twofold: first, to review the atypical characters that make this species so peculiar, and second, to outline recent evidence which underscores the unique position of the volcano rabbit.

2. Atypical diagnostic characters

Volcano rabbits *Romerolagus diazi*, also known by the Mexican vernacular names of zacatuche and teporingo, are smaller (adult weight 350 g on average) than most other members of their family, the Leporidae (e.g., the European rabbit *Oryctolagus cuniculus* weighs on average 1400 g). They have short hind-feet, unusually small and rounded ears, and a tail so short as to be externally invisible (fig. 1). Unlike in most other lagomorphs, there is little difference in body size between males and females.

Many unique characters are found in their anatomy. The first lower premolar (p_3) is divided into two sections by two re-entrant folds rather than a single buccal re-entrant as in most leporids (Lyon, 1904). Their external auditory meatus is relatively larger than in other lagomorphs. In contrast to most rabbits and hares, they have a smaller than average sternum and the remainder of the presternum is long and nar-



Fig. 1. Adult male of *Romerolagus diazi* (Ferrari Pérez, 1893). Photograph taken in 1988 by A. Velázquez.

row. The manubrium (anterior presternum) is short and wide. The last two segments of the mesosternum are fused, the distal end of the humerus is small and flat, and the last three caudal vertebrae are rudimentary and turned upwards (Cervantes et al., 1990). The size of the spiny apophysis on the dorsal part of the thoracic vertebrae is relatively smaller than that of other rabbits. The ribs lack the distal expansion which is characteristic of jack-rabbits and hares (*Lepus* spp.) and the humerus is quite thin compared to that of most leporids, and is fused with the fibula over a longer surface than in most other rabbits. The short size of the hind-foot is basically due to the considerable basal width of the metatarsus compared with that of other leporids (Rojas, 1951). The external condylar process is the most developed of the Leporidae, and the pelvis is stronger curved than in any other rabbit (Lyon, 1904).

Unlike most leporids, the zacatuche's ventral pelage is soft, and there is no contrast in colour with the dorsal pelage (Corbet, 1982). The moulting process is also atypical compared with other leporids, or even with most mammals. This rabbit does not have a distinctive winter and summer pelage. The fur is moulted throughout the year in four stages: hair loss in random areas, disappearance of melanin, melanin deposition in the bare areas, and regrowth of the hair (Velázquez et al., in press).

The karyotype of *Romerolagus* ($2n = 48$, $FN = 78$) resembles that of hares and differs from that of rabbits (Van der Loo et al., 1979; Orlov & Bulatova, 1983). It has been argued that the volcano rabbit retains an ancestral karyotype, although its chromosome evolution must have ceased only at the end of the Pleistocene. In addition, unlike most

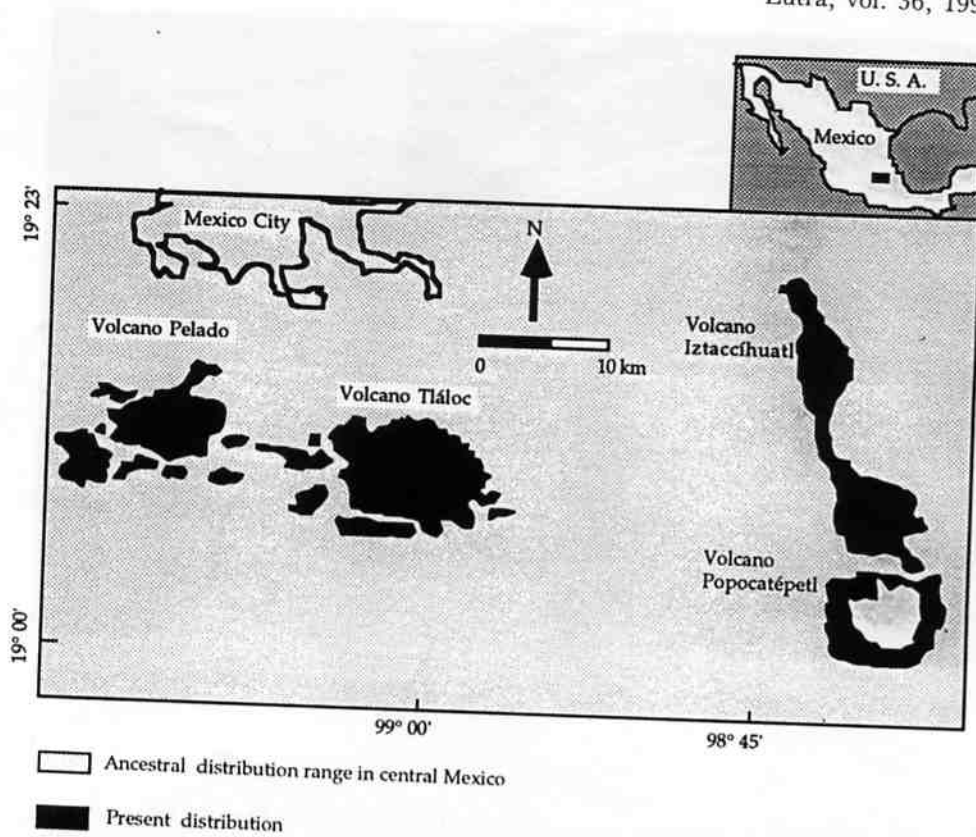


Fig. 2. Ancient (c. 18,000 years ago) and present geographic distribution ranges of *Romerolagus diazi* in Central Mexico. The former covers the entire area in the frame whereas the latter is only 360 km² (source: Velázquez, 1993a).

lagomorphs, the volcano rabbit retains an ancestral genetic polymorphism (Cervantes et al., 1990).

This set of atypical morphological features, including the rudimentary fusion of vertebrae, peculiar dental pattern and ancestral genetic characteristics recalls the primitive status of the volcano rabbit (Hibbard, 1963). It is also worth mentioning the great variety of specific ecto- and endoparasites of *Romerolagus* such as nematodes (*Boreostrongylus romerolagi*, *Dermatoxys romerolagi* and *Lamothiella romerolagi*; Cervantes et al., 1990), cestodes (*Anoplocephaloides romerolagi*; Kamiya et al., 1979), fleas (*Cediopsylla tepolita* and *Hoplopsyllus pectinatus*; Barrera, 1966) and mites (*Cheyletiella mexicana* and *Ch. parasitovorax*; Uchikawa & Suzuki, 1979). *Ch. mexicana* is host-specific and the occurrence of these two mites on one host species is unique, because otherwise species of *Cheyletiella* exclude each other. To summarize briefly, *Romerolagus diazi* is a relict species which is characterized by its ancestral morphological features and primitive parasites.

3. Distribution

In the last decade a number of studies have thoroughly documented the actual geographic distribution of the volcano rabbit (e.g., López-Forment & Cervantes, 1981; Hoth et al., 1987; Velázquez et al., 1991). These studies agree that the distribution area has been undergoing a continuous process of shrinking and fragmentation from both natural and human-induced causes (Velázquez, 1993a). To illustrate this, the likely range of the volcano rabbit 18,000 years ago (potential distribution) and the present range in central Mexico are given in fig. 2. The former potential distribution can be elucidated by shifting the borders of the vegetation types occurring in the species' present range 800 m downwards. This 800 m interval was calculated based on the prevailing temperature at that time, which may have been 5-6 °C lower than at present (Ohngemach & Straka, 1983). The former potential distribution shown in fig. 2 covers the whole area within the frame, whereas the present range only covers 360 km² (Velázquez, 1993a). In addition, the present range is fragmented into 16 patches (Velázquez et al., 1991). The volcano rabbit's present distribution in central Mexico is only about 10% of what it could have been 18,000 years ago. Moreover, the areas currently occupied by the rabbit may be considered relict Holocene habitats. Unfortunately, no fossil evidence has been found to confirm the postulated former distribution of this rabbit. The likely causes determining the present distribution are explained in the following paragraphs.

4. Ecology

In contrast to the prevalence of synecological studies, research on the autecology of the volcano rabbit lags behind. Few studies and casual field observations are the only sources of information from which details on the species' population dynamics, home range, reproductive success, food requirements, predation and competition have to be inferred (Velázquez et al., in press).

Recent studies have shown that the abundance of volcano rabbits varies significantly among vegetation communities (Velázquez, 1993b). Subalpine bunchgrass *Festuca tolucensis* and pine *Pinus hartwegii* communities (subalpine bunchgrassland-pine communities) are the habitats with highest rabbit densities. Groups of five to seven volcano rabbits have been observed in these communities (Cervantes et al., 1990). Here, volcano rabbits give birth in the grass (Velázquez et al., in press), whereas in rocky terrain, where bunchgrasses are less abundant, they use abandoned burrows and cracks (Cervantes et al., 1990). This atypical breeding behaviour may be one of the causes of the discrepancy in home range sizes as suggested by different authors. For example, Cervantes & Martínez (in press) record a home range of 2,500 m² (0.25 ha), whereas Velázquez et al. (in press) argue that individuals move freely within a range of c. 3.5 ha, even in suitable habitat. Volcano rabbits may use more restricted areas where little protective cover is available. The close relation between this rabbit and bunchgrass has been appreciated from the time of the Aztecs, as evidenced by its Aztec name "zacatochtle", from zacatl = zacate (bunchgrass) and tochtle = conejo (rabbit). This Aztec name, slightly modified to "zacatuche", is still widely used.

Some authors have stated that the distribution and abundance of the volcano rabbit are negatively influenced by the larger cottontail rabbits *Sylvilagus cunicularius* and *S. floridanus* (Fa et al., 1992). In contrast, our observations throughout the species' range confirm the sympatry of volcano and cottontail rabbits. Rather than competition, habitat characteristics and human disturbance seem to play a major role in determining the abundance and distribution of volcano rabbits. Grazing and burning may temporarily or permanently modify the floristic composition and structure of the subalpine bunchgrassland-pine communities (SB-PC), thereby influencing their suitability for volcano rabbits. Preliminary results from studies in an area where fire has been set to the SB-PC twice a year suggest that *Romerolagus* has moved into less favourable habitats. The spatial distribution and abundance of rabbits in the newly occupied vegetation communities, however, differs significantly from the original situation in SB-PC. In contrast, SB-PC burnt once every two years were reoccupied by *Romerolagus*, which reached similar densities as before. So the long-term effect of grazing and burning as well as the exclusion of volcano rabbits by cottontails have yet to be confirmed.

A number of gaps in our knowledge of the ecology of *Romerolagus* probably is due to our poor knowledge of the species' autecology. Notwithstanding this, it is clear that the volcano rabbit's ecology differs from that of many other lagomorphs. There are no population estimates of volcano rabbits for the entire distribution area. Recent field work in El Pelado volcano near Mexico City indicates that the abundance of volcano rabbits varies substantially among plant communities (Velázquez, 1993b). A population estimate for the entire volcano showed a considerable variation ($\bar{x} = 6488$; range 2478-12120 rabbits). Volcano rabbits as well as African rock hares *Pronolagus* spp. and the Ryukyu rabbit *Pentalagus furnessi* from islands in the south of Japan, seem to be highly selective in their habitat choice, whereas most widely distributed rabbit genera such as *Oryctolagus* and *Sylvilagus* occupy a great variety of habitats (Chapman & Flux, 1990). These authors strongly emphasize the need to carry out experimental research, to gain insight into the autecological aspects of the volcano rabbit.

5. Conservation

Why is the volcano rabbit endangered? Species extinction is not a random process. Certain biological characteristics make some species more susceptible than others, such as large body size, high trophic level, habitat and/or diet specialization, low dispersal ability, restricted geographical range and tropical distribution. In turn, some of these properties are again related to low rates of increase and low population densities (Marshall, 1988).

The volcano rabbit exhibits some of these characteristics. It has an extremely restricted range occupying only the higher elevations of a few volcanoes near Mexico City. It is a habitat specialist and may also be specialized in its diet. We know little of its dispersal abilities, but these are likely to be relatively low. These characteristics by themselves, however, do not render the volcano rabbit unique. The proportion of endemic species in Mexico is extremely high. At present, more than 20,000 vascular plants, approximately 280 amphibians, 700 reptiles, 500 mammals and 1,000 bird



Fig. 3. Cone of Pelado volcano. Dissecting roads are found at the apparently most inaccessible areas. Photograph taken in 1988 by A. Velázquez.

species have been recorded in Mexico (Galindo-Leal, 1993). More than half of the plant species, reptiles and amphibians and one third of the mammals are endemic (McNeely et al., 1990).

The volcano rabbit is one of this large number of endemic species, many of which are also habitat specialists. The main distinctive character of the volcano rabbit is a fatal coincidence. The whole distribution area of this peculiar species is situated near the most populated urban centre of the planet: Mexico City. Such ill-fated fortune has resulted in a very high rate of habitat deterioration. There is an urgent need to slow down and carefully plan the rapid expansion of urban development and agricultural activities in this area. In recent times, most vertebrate extinctions have been the direct result of human activities. In order to prevent extinctions, it is imperative to have a thorough understanding of their main causes. At present, the most common factors are overhunting, habitat destruction, introduction of exotic predators, competitors, diseases, disruption of trophic chains and chemical pollution (Marshall, 1988). Most of these factors have contributed to the present precarious status of the volcano rabbit. Urban development, agriculture, fire and grazing all have destroyed and diminished suitable habitat. Subsistence hunting and domestic dogs are a growing concern. Exotic diseases have not played a role and little is known of the effects of pollution on volcano rabbits.

As mentioned above, the distribution of the volcano rabbit is now fragmented, not only because of the species' historical retreat to high altitude as temperatures

increased, but also because of recent habitat loss and the construction of highways dissecting its habitat (fig. 3). Small and fragmented populations are faced with genetic isolation and a higher extinction risk from random processes (Gilpin & Soulé, 1986).

A large portion of the volcano rabbit's range is now situated within national parks. Unfortunately, this has not ensured the protection of its habitat. A conservation strategy for volcano rabbits should include actions both inside and outside national parks. Inside the parks, the restoration of appropriate habitat should have priority. It will be necessary to eliminate cattle grazing inside the parks and to maintain exclusive zones for volcano rabbit conservation (Galindo-Leal, 1993). Furthermore, monitoring the species' spatial distribution and abundance on an annual basis is required to timely detect any negative population trends. Outside the parks, planning of activities such as agriculture and cattle grazing have to take into account the maintenance of habitat continuity as a priority, to ensure the long-term survival of *Romerolagus* populations.

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ABSTRACT

The volcano rabbit or zacatuche *Romerolagus diazi* (Ferrari Pérez, 1893), an endemic and endangered Mexican lagomorph, has awakened the interest of many scientists for more than a century. This is largely the result of the species' unique combination of morphological, ecological and historical characters. The first morphological description of this rabbit expressed uncertainty as to whether it was a rodent, a hare or a true rabbit. Recent research on reproduction, behaviour, habits and habitat restriction underscores the peculiar position of this species as well as its highly threatened status. The main purpose of this paper is to summarize all atypical characters and to present new evidence underlining the volcano rabbit's uniqueness.

RESUMEN

El conejo de los volcanes *Romerolagus diazi*, un lagomorfo peculiar

El zacatuche o conejo de los volcanes *Romerolagus diazi* (Ferrari Pérez, 1893) especie mexicana endémica y en peligro de extinción, ha despertado el interés de muchos científicos por más de un siglo. Esto ha sido influenciado, en la mayoría de los casos, por las características únicas de *Romerolagus* en cuanto su morfología, ecología e historia. Las primeras descripciones morfológicas de este conejo denotaron incertidumbre sobre su identidad como ratón, liebre o un verdadero conejo. Investigaciones recientes sobre su reproducción, comportamiento, hábitos y restricciones ecológicas de su hábitat enfatizan la particularidad de esta especie así como el alto riesgo a la extinción en que se encuentra. El objetivo principal de este artículo es integrar todas las características atípicas así como nuevas evidencias que exalten la distintividad del conejo de los volcanes.

SAMENVATTING

Het vulkaankonijn *Romerolagus diazi*: een bijzondere vertegenwoordiger van de Lagomorpha

Het vulkaankonijn of zacatuche *Romerolagus diazi* (Ferrari Pérez, 1893) is endemisch voor de vulkanen ten zuiden en zuidoosten van Mexico-Stad. Ruim een eeuw lang heeft dit konijn zich mogen verheugen in een grote wetenschappelijke belangstelling, dank zij een unieke combinatie van morfologische, oecologische en zoögeografische eigenschappen. Uit de eerste morfologische beschrijving van de soort spreekt twijfel of het hier gaat om een knaagdier, een haas of een echt konijn. Recent onderzoek aan voortplanting, gedrag, levenswijze en habitat heeft eens te meer duidelijk gemaakt dat het vulkaankonijn een bijzondere plaats inneemt onder de Lagomorpha. Bovendien is het thans ernstig bedreigd. Dit artikel vat de bijzondere eigenschappen van deze soort nog eens samen; ook geeft het enkele nieuwe argumenten waarom het vulkaankonijn als het ware enig is in zijn soort.

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