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Man-made and ecological habitat fragmentation: study case of the Volcano rabbit *(Romerolagus diazi)*

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Abstract

Documented the fragmentation of the habitat of the volcano rabbit *(Romerolagus diazi).* Two different processes of fragmentation are illustrated, namely; man-made and ecological. Man-made fragmentation has occurred through splitting the original distribution range into islands by highway construction, farming, and intensive burning and grazing activities. The ecological fragmentation is due to environmental discontinuity, which is reflected in a mosaic of vegetational communities or habitats. The ecological amplitude of the habitat types has been analyzed by canonical correlation analysis. Six habitat types were distinguished. Habitat type 2, open pine woodland *(Pinus hartwegii-Festuca tolucensis)* habitat type 3 mixed alder pine forest (*Alnus firmifolia-Muhlenbergia macroura*) and habitat type 4, pine forest (*Pinus* spp. *Muhlenbergia quadridentata*) provide most of the suitable ecological conditions for the survival of the volcano rabbit. The two processes of fragmentation habitat are threatening the survival of this endangered Mexican lagomorph. These two habitat fragmentation processes are discussed in light of their role in conservation and management.

Introduction

Habitat fragmentation can be defined as the discontinuous spatial distribution of a species within its distribution range, which originally was formed as a single continuous unit (Nilsson 1978; Haila and Hanski 1984; Soule 1986). The forming process, which is named insularization (Wilcox 1980), of this segregated distribution has been mainly attributed to various types of disturbances. These disturbances can be man-made Robbins 1979; Whitcomb et al. 1981; Lynch and Whigham 1984) or ecological (disrupting of the landscape by discontinuities of the environment; Whitaker 1973; Wilcove et al. 1986). Unlike man-made habitat fragmentation, ecological habitat fragmentation has been poorly documented. The assessment of the ecological amplitude of mammalian species requires deep understanding of habitat (mainly vegetation). Documentation on habitat fragmentation is essential for management and conservation purposes, since it has been determined as one of the major causes of extinction of species (Diamond 1984; Harris 1984; Simberloff and Abele 1984). Data gathered to study the endangered Mexican volcano rabbit (*Romerolagus diazi* Ferrari-Pérez 1893) are used to document these two types of fragmentation processes. Implications of both fragmentation processes are discussed in the light of their importance to conservation and management plans.

Study area

The distribution range of the volcano rabbit *(Romerolagus diazi)* is restricted to Central Mexico, mainly to the volcanos "Pelado", "Tláloc", "Popocatépetl", and „Iztaccíhuatl" (Hoth et al. 1987). The area lies between 18° 50′–19° 25′ N, and 98° 30′–99° 16′ W. The altitude ranges from 2,600 to 5,450 m a.s.l. The topography is irregular. The dominant soil types are Andosol and Lithosol. The climate characterized by a rainy and dry season, is temperate, ranging from mild to cool, with a mean

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annual temperature of 11 °C. Further, it is sub-humid, with a mean annual rainfall of approx. 1,000 mm (García 1981). According to Rzedowski (1988) there are three main vegetation communities distributed in the area: 1. alpine grassland depicted by *Festuca livida* and *Arenaria bryoides;* 2. pine forest characterized by *Pinus hartwegii* and *Pinus montezumae;* and 3. fir forest dominaed by *Abies religiosa.* A number of mammals present in the area (e.g., the gopher *Pappogeomys merriami;* the volcano rabbit *Romerolagus diazi*) are considered to be endemic species and endangered (Ceballos and Galindo 1984). The area contains a rather peculiar plant and animal assemblage both from Nearctic as well as from Neotropical origin (see Velázquez 1992 for description of the study area).

Material and methods

Man-made habitat fragmentation is illustrated by monitoring the changes observed in the distribution area of the volcano rabbit. This monitoring has been based on publications which document the distribution of the volcano rabbit (De Poorter and Van der Loo 1979; Hall 1981; Granados 1981; López-Forment and Cervantes 1981; Bell et al. 1985; Hoth et al. 1987). Recently, Velázquez et al. (1991) mapped the present distribution of this species. All authors mentioned above, attribute habitat disruption to human activities. A map showing the oldest and the most recent distribution of the rabbit was prepared in order to show the man-made habitat fragmentation.

Ecological fragmentation has been based on the study of the vegetation communities. Data from a vegetation survey carried out within the core distribution areas of the volcano rabbit were used to define the habitat types (Velázquez et al. 1992). The vegetation was sampled according to the school of Braun-Blanquet (1951). In every relevé the following data were gathered: percentage cover per species, percentage cover per vegetation-layer, percentage of rock-outcrops, percentage of bare ground, altitude, and abundance of rabbits based upon pellet-counts. The vegetation communities (resembling habitat types) were defined by performing two-way species indicator classification analysis (TWINSPAN; Hill 1979; Hill and Gauch 1980). A total of 108 sampling units was used to quantify and to relativize the abundance of the rabbit. The relative abundance was estimated for every habitat type by pellet-counts (Osterveld 1983; Gibb 1970; Krebs et al. 1986). Since the volcano rabbit defecates in defined places forming latrines (Cervantes and Martines 1992), latrine-counts were made rather than individual pellet-counts. Canonical Correspondence Analysis (CCA) was performed in order to elucidate the environmental variables that govern the major distribution of the habitat types (Ter Braak 1986, 1987), and therefore the distribution of the rabbit. The Monte Carlo Permutation Test was used to measure the significance of the "eigenvalue" of the first axes, and the Student-T Test was used as an exploratory approach to measure the statistical contribution of the environmental variables (Ter Braak 1988). The results obtained by CCA are presented in a biplot ordination diagram. This diagram shows the variables that explain most of the variation along the first two ordination axes. Furthermore, it shows the ecological amplitude of the most important habitat for the rabbit. The discussion over the ecological fragmentation of the volcano rabbit populations is based upon this ordination diagram. A level of $P < 0.05$ was considered as significant throughout the analysis.

Results

The fragmentation of the habitat caused by man is illustraed by comparing the most outstanding changes observed in the distribution range of the volcano rabbit (Tab. 1). De Poorter and Van der Loo (1979) and Hall (1981) reported a distribution range of approx. 1,500 km^2, forming one single unit. Other sources of information (Granados 1981; López-Forment and Cervantes 1981) stated that the distribution range split into three main areas, namely, Volcano "Nevado de Toluca", "Sierra Ajusco and Chichinautzin", and "Sierra Nevada". The fragmentation into these three areas was attributed mainly to deforestation and agriculture encroachment. Bell et al. (1985) and Hoth et al. (1987) documented the shrinking process of the distribution range to 280 km^2. Bell et al. (1985) and Hoth et al. (1987) restricted the distribution of the volcano rabbit to "Sierra Nevada" and "Sierra Ajusco and Chichinautzin". Furthermore, within these two sierras the species was found only in four volcanic formations; "Iztaccíhuatl", "Popocatépetl", "Tláloc", and "Pelado". According to Hoth et al. (1987) the drastic fragmentation of the habitat was caused by deforestation, agriculture encroachment, highway construction, and bunchgrass disturbances (e.g., grazing, burning). The detailed distribution map of the species given by Velázquez et al. (1991) shows the present distribution range, which is divided in 16 units.

Table 1. **Shrinking and fragmentation processes of the habitat of the Volcano rabbit *(Romerolagus diazi)***

Distribution range (ha)	Number of fragments	References
150 000	1	De Poorter and Van der Loo (1979)
140 000[a]	1	Hall (1981)
50 000[a]	3	Granados (1981)
27 000	3	López-Forment and Cervantes (1981)
28 000	4	Bell et al. (1985)
28 000	4	Hoth et al. (1987)
38 650	16	Velázquez et al. (1991)

[a] Values estimated from the reference since they were not literally given.

The map of Velázquez et al. (1991) permits accurate illustration of the actual man-made habitat fragmentation of the rabbit (Fig. 1). The distribution units given by Velázquez et al. (1991) were considered as isolated populations, since interpopulation genetic flow seems unlikely. This was mostly attributed to intensive human activities such as farming, grazing, burning, and timbering. Furthermore, roads and human settlements serve as barriers to existing rabbit populations.

Regarding ecological fragmentation, six habitat types were identified. The characteristic preferential plant species were used to name the habitat types as follows: habitat 1, alpine bunch-grassland *(Arenaria bryoides-Festuca livida-Calamagrostis tolucensis);* habitat 2, open pine woodland *(Pinus hartwegii-Festuca tolucensis);* habitat 3, mixed alder-pine forest *(Alnus firmifolia-Muhlenbergia macroura);* habitat 4, pine forest (*Pinus* spp.-*Muhlenbergia quadridentata*); habitat 5, open fir forest *(Abies religiosa-Festuca amplissima);* and habitat 6, dense fir forest *(Abies religiosa-Senecio barba-johannis-Cupressus lindleyi).* A detailed description of these habitats and their ecology is given in separate reports Rzedowski 1988; Velázquez et al. 1992; Almeida et al. 1992).

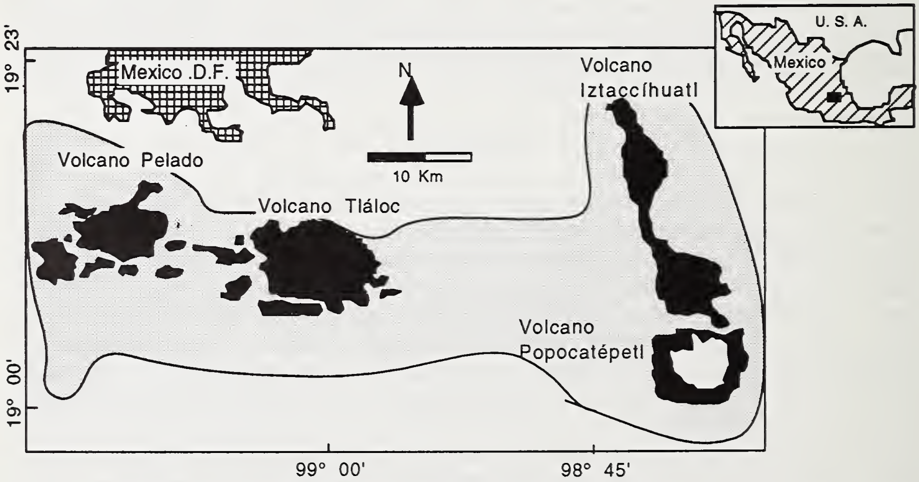

Fig. 1. Comparative distribution ranges of the volcano rabbit *(Romerolagus diazi).* The area hatched with points (□) represents the distribution range given by Hall (1981), which was based on the marginal records. The 16 patches in black (■) are the present distribution areas (Velázquez et al. 1991). All fragments are separated by man-made barriers such as: roads, inhospitable habitats, and human settlements. Therefore, inter-population genetic flow between the 16 fragments inhabited by *Romerolagus* seems unlikely

Table 2. **Matrix of canonical correlation coefficients**

The ordination of the habitat types is represented by the species axes. The variable axes are given as explanatory variables of the distribution of the habitat types. The actual ecological amplitude is shown in the ordination diagram (Fig. 2)

	Species axis I	Species axis II	Variables axis I	Variables axis II	Ground layer
Species axis I	1				
Species axis II	0.045	1			
Variables axis I	0.950[a]	0	1		
Variables axis II	0	0.834[a]	0	1	
Ground-layer	0.8	–0.154	0.855[a]	–0.185	1
Herb-layer	–0.622	0.339	–0.663	0.407[a]	–0.565
Tree-layer	0.836[a]	–0.001	0.893[a]	0	0.643
Rocks	–0.143	0.059	–0.152	0.071	–0.139
Bare ground	–0.122	0.063	–0.131	0.076	–0.123
Altitude	–0.191	–0.518[a]	–0.204	–0.622[a]	0.026
Rabbit abundance	–0.273	0.08	–0.292	0.095	–0.165

	Herb layer	Tree layer	Rocks	Bare ground	Altitude
Herb-layer	1				
Tree-layer	–0.526	1			
Rocks	0.07	–0.145	1		
Bare ground	0.11	–0.282	0.055	1	
Altitude	0.005	–0.087	–0.097	0.116	1
Rabbit abundance	0.43	0.316	0.064	0.335	0.032

[a] Significant at $P < 0.05$.

The canonical correlation coefficient between first species axis and the first variable axis (r, 0.95), allowed reliable ecological elucidation to explain the distribution of the habitat types. This result was obtained by CCA (Tab. 2). The distribution of the six habitat types is explained mostly by the altitude (axis I, $\lambda = 0.293$) and by the percentage of tree cover (axis 1, $\lambda = 0.737$). These two variables explained 71 % of the total variation (51 % percentage of tree cover and 20 % altitude). The Student-T exploratory test shows that the percentage of tree cover contributes significantly to the regression along the first axis ($T = 5.98$; d. f. 105; $P < 0.05$), as well as the ground-layer coverage ($T = 3.60$; d. f. 105; $P < 0.05$). The altitude ($T = 4.71$) and the herb-layer ($T = 3.90$) contributed significantly to the regression of the second axis. The 20 random data-set generated by "Monte Carlo Permutation Test" yielded lower "eigenvalues" than the ones obtained by the ordination analysis. This result indicates that the canonical ordination analysis could not have been obtained by chance only ($P < 0.05$).

The characteristic preferential species of the six habitat types and the variables (arrows) included in the analysis are shown in the ordination diagram (Fig. 2). In this figure, it can be observed that habitat types 2 and 3 were positioned rather close to each other near the center of the ordination diagram. At the right end of the first axis, habitat types 5 and 6 were also positioned relatively close. Clustering of habitat types along the ordination axis suggests that these habitats are distributed along similar ecological conditions (TER BRAAK 1987, 1988). Furthermore, the herb-layer seems to play an important role in determining the ecological amplitude of habitat 2. In relation to the rabbit distribution, the canonical correlation coefficient of the tree-layer and herb-layer reached the highest scores (–0.526 and 0.430, respectively). Tree-layer and herb-layer were the variables that explained most of the distribution and relative abundance of the rabbit (Tab. 2). On the other hand, the

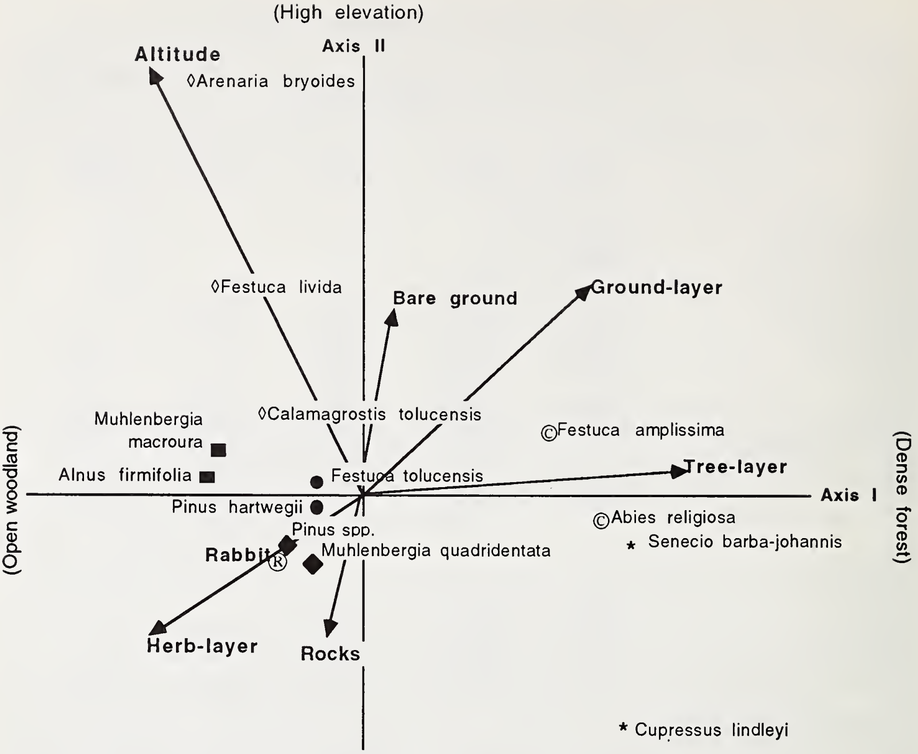

Fig. 2. Ordination diagram of the habitat types present in the distribution range of the volcano rabbit *(Romerolagus diazi)* obtained by Canonical Correspondence Analysis ($\lambda 1 = 0.737$; $\lambda 2 = 0.293$; scaling $\alpha = 1$). Habitat 1 (◇) = alpine bunch-grassland *(Arenaria bryoides-Festuca livida-Calamagrostios tolucensis);* habitat 2 (●) = open pine woodland *(Pinus hartwegii-Festuca tolucensis);* habitat 3 (◆) = mixed alder-pine forest *(Alnus firmifolia-Muhlenbergia macroura);* habitat 4 (■) = pine forest (*Pinus* spp.-*Muhlenbergia quadridentata*); habitat 5 (©) = open fir forest *(Abies religiosa-Festuca amplissima);* and habitat 6 (★) = dense fir forest *(Abies religiosa-Senecio barba-johannis-Cupressus lindleyi)*

centroid of the variable rabbit (®) is positioned within the ecological amplitude of habitats 2, 3 and 4. This suggests that habitat types 2 and 3 are indicative of the most suitable environmental conditions for the volcano rabbit. In other words, the abundance of the rabbit is restricted due to environmental conditions in habitat types 1, 5, and 6. Finally, the present mosaic of habitats and their relation to the rabbit abundance demonstrates ecological fragmentation.

Discussion

In Mexico split habitats of mammalian species distributed along large areas is commonly observed (Leopold 1965; Hall 1981). The actual causes of the scattered distribution of such species is rarely documented. Human activities, environmental discontinuities, or by both factors can work simultaneously in promoting insularization (Wilcox 1980; Wilcove 1986). It is necessary to distinguish the actual cause of fragmentation for conservation and management actions (Diamond 1984; Simberloff and Abele 1984). Man-made fragmentation is certainly easy to detect, unlike ecologial fragmentation which requires detailed knowledge of the habitat and the abundance of the species. Reliable density estimates are unknown for most mammalian species, which limits proper habitat assessment studies (Van Horne 1983). In this research relative abundance estimates provided sufficient data to document the actual ecological amplitude of the volcano rabbit. Taking into account volcano rabbit presence only all habitat types are occupied except number 6 (dense fir forest characterized by *Abies religiosa-Cupressus lindleyi).* This suggests that actual ecological amplitude cannot be found through presence-absence data only (Velázquez et al. 1992). Therefore, abundance estimates are recommended to find ecologically sound relations between habitat and mammalian species. Furthermore, conservation plans ought to be base upon the actual ecological amplitude of the species.

A large number of studies have documented the impact of habitat fragmentation in bird populations (Nilsson 1978; Haila and Hanski 1984; Robbins 1979; Whitcomb et al. 1981; Lynch and Whigham 1984). This contrasts with the number of studies on habitat fragmentation in populations of mammals (Smith 1974; Velázquez et al. 1991). Interannual variability of the density in mammalian populations (Krebs et al. 1973) influences its distribution. Seasonal periods (winter-summer or rainy-dry) promote movement of mammalian populations between habitats (Kikkawa 1964; Churchfield 1980). Hence, heterogeneous landscapes are needed to fulfill all requirements for survival (Hansson 1979; Alcantara and Telleira 1991). Lagomorphs inhabit a broad range of ecologically diverse environments including disturbed, successional, and transitional habitats (Chapman and Flux 1990). Nevertheless, the urgent protection of five genera (among them *Romerolagus*) is demanded. This is mainly due to the small distribution area and specific habitat requirements of the genera (Chapman and Flux 1990). To illustrate this further, pikas *(Ochotona)* store food in caches (haypiles) which serve as a source of energy for the winter, together with other cushion plants (Smith et al. 1991). This, therefore, suggests that pika population movement between habitats is not necessary during periods of food-shortage. Personal observations of the volcano rabbit seem to suggest a rather stable microclimatic environment (beneath of the bunch-grass). This might be due to the coverage provided by the bunch-grass, which in summer is cooling and in winter warming. Therefore, it seems unlikely that the populations of volcano rabbits move between different habitats in different seasons. This, however, remains to be ascertained.

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Zusammenfassung

Anthropogene und ökologische Lebensraumverinselung am Beispiel des Vulkankaninchens (Romerolagus diazi)

Die Verinselung des Lebensraumes für das mexikanische Vulkankaninchen *(Romerolagus diazi)* wird dokumentiert. Dabei werden zwei unterschiedliche Prozesse beleuchtet: anthropogene und ökologische Fragmenation. Der Mensch zerteilt den Lebensraum in Inseln durch den Bau von Autobahnen, durch Ackerbau, intensives Abflämmen und Weidenutzung. Ökologische Verinselung ist auf Diskontinuitäten der Umgebung, die in einem Mosaik von Pflanzen und Habitaten resultieren, zurückzuführen. 6 Habitat-Typen werden unterschieden. Davon bieten zwei, der offene Tannenwald *(Pinus hartwegii – Festuca tolucensis)* und der Tannenwald (*Pinus* spp. – Muhlenbergia macroura), die günstigsten ökologischen Bedingungen für das Überleben des Vulkankaninchens. Die zwei genannten Prozesse der Habitatverinselung bedrohen sein Überleben. Diese Prozesse werden im Hinblick auf ihre Rolle bei der Erhaltung und dem Management der Art besprochen.

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