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Research paper

Red squirrel *Sciurus vulgaris* abundance in coastal cliffs in the South of Spain

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Abstract

Red squirrel Sciurus vulgaris *abundance in coastal cliffs in the South of Spain.* We studied the abundance of red squirrels, a medium-sized forest rodent widely distributed throughout the Palearctic, in the cliffs of Maro-Cerro Gordo (south of Spain, Málaga-Granada), a protected area with a great marine influence. We investigated the abundance of squirrels in this area in relation to two scales: (1) home range, as signs per square meter; and (2) landscape, as active nests per 1 x 1 km UTM grids. We tested the influence of land use and habitat features on the abundance of squirrels. On the home range scale, squirrel activity was higher in mature pines located near cliffs and in pines near freshwater channels. The cliffs hosted the best pine forest patches, and despite being very close to the sea, squirrels often used these as feeding areas but not as areas for building nests. On the landscape scale, squirrel nests were rarer in grids with more herbaceous crops and were more abundant in grids with longer freshwater streams. These results suggest that the squirrels in this area may have adapted to life at this site and to the marine influence via a differential use of habitat. The squirrels' use of the best feeding areas suggests saline stress is counteracted by establishing nests in humid areas away from cliffs.

Key words: Abundance, Coastal cliffs, Habitat use, Marine influence, Nests, Red squirrel

Resumen

Abundancia de la ardilla roja Sciurus vulgaris *en los acantilados del sur de España.* Se ha estudiado la abundancia de la ardilla roja, un roedor forestal de talla media ampliamente distribuido por todo el Paleártico, en los acantilados de Maro-Cerro Gordo (sur de España, Málaga-Granada), un espacio protegido con una gran influencia marina. La abundancia de ardillas en este espacio se estimó a dos escalas: (1) en el territorio, en forma de signos por metro cuadrado y (2) en el paisaje, en forma de nidos activos por cuadrícula UTM de 1 x 1 km. Asimismo, se estudió la influencia de los usos del suelo y las características del hábitat en la abundancia de la ardilla. A escala de territorio, hubo más indicadores de actividad de la ardilla en pinos maduros ubicados cerca de los acantilados y en pinos cercanos a cauces de agua dulce. Los acantilados albergaban las mejores zonas de pinar y, a pesar de estar muy cerca del mar, las ardillas a menudo las utilizaban como áreas de alimentación, pero no como áreas para establecer nidos. A escala de paisaje, los nidos de ardilla eran menos frecuentes en las cuadrículas con más cultivos herbáceos y más abundantes en las cuadrículas con cauces de agua dulce más largos. Estos resultados sugieren que las ardillas de esta zona pueden haberse adaptado a la vida en este espacio y a la influencia marina haciendo un uso diferencial del hábitat. El uso de las mejores zonas de alimentación implica un estrés salino para las ardillas que se compensa anidando en zonas húmedas y alejadas de los acantilados.

Palabras clave: Abundancia, Acantilados, Uso del hábitat, Influencia marina, Nidos, Ardilla roja

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Introduction

The red squirrel *Sciurus vulgaris* Linnaeus 1758 is a medium-sized rodent widely distributed throughout the Palearctic. It is linked to forest and arboreal environments (Purroy 2017). This herbivorous and granivorous species inhabits deciduous and coniferous forest masses in most of its distribution area. In Europe, the red squirrel is present in cold and temperate coniferous and deciduous forests, small woodlots, and suburban and urban areas (Krauze-Gryz and Gryz 2015). The species inhabits pine and spruce forests (Turkia et al 2018) that may contain yews, and it is also found in mixed forests of beech *Fagus* spp, chestnut *Castanea* spp, walnut *Juglans* spp, hazel *Corylus* spp, maple *Acer* spp, and oak trees *Quercus* spp (Tonkin 1983, Wauters et al 1992, Cagnin et al 2000). In the northern Iberian Peninsula, the species is present in habitats similar to those in Europe: beech, hazel, oak, fir *Abies* spp and *Picea* spp, and pine forests (Purroy and Rey 1974). In the Euro-Siberian region, the red squirrel is found in copses of poplar *Populus* spp, in ash trees *Fraxinus* spp and also in in wooded hedges or willows *Salix* spp if they are located close to pine forests (Hernández 1999, 2014). However, in the Mediterranean region, red squirrels are only found in mature pine forests that include holm oaks *Quercus rotundifolia* Linnaeus 1758, and in trees that reach heights of at least 6-8 m (Purroy 2007). It is found in almost all species of mature pine forests (Arrizabalaga et al 2007), from Aleppo pine *Pinus halepensis*, stone pine *P. pinea*, and Monterey pine *P. radiata* to maritime pine *P. pinaster*, Scots pine *P. sylvestris*, and black pine *P. nigra*. They can even be found at altitudes reaching 2,500 m in the Sierra Nevada Mountain range (Palomares 1988). They have also been found in other conifers, such as cypresses *Cupressus sempervirens* (Piqué et al 2007), and in urban parks and human-transformed habitats that contain ornamental trees (Krauze-Gryz and Gryz 2015). Populations are found too in some urban parks in Spain and Portugal (Piqué 1997, Rocha et al 2017, Barroso et al 2021) and several other European countries (Lawton et al 2015). Indeed, urban areas with predictable anthropogenic food supplies are becoming important habitats for red squirrels in many cities (Jokimäki et al 2017). Occurrence of the species has recently expanded both at a national and regional level (Ferreira et al 2001, Duarte et al 2023). This expansion is related to the reforestation of conifers (Purroy 2007) because the red squirrel takes advantage of such new plantations to colonize (Petrucci-Fonseca and Mathias 1987) using hedgerows to settle into established populations and to create new settlements (Hernández 2014). In the southern areas of the Iberian Peninsula, the species has increased its area of distribution threefold in recent years (Duarte et al 2023). On a European scale, it does not pose major conservation problems, except for competition with the American gray squirrel *Sciurus carolinensis* Gmelin 1788 in areas where this latter has been introduced (Gurnell et al 2015). There are stable populations in Europe (Bertolino et al 2007) but populations in the Mediterranean are decreasing due to habitat loss and fragmentation (Amori et al 2010). Despite this, it is a species of least concern both in Europe and in the Iberian Peninsula (IUCN 2023).

Most studies on this squirrels' habitats have been carried out in mountainous areas or in inland forest areas (e.g., Purroy and Rey 1974, García and Mateos 2008, Rima et al 2010), and little is known about the its presence at sea level or in coastal forest masses. Coastal habitats are characterized by environmental conditions that usually lead to stress and require special adaptations in the fauna residing in these habitats (Asensi and Díez 1993, Larson et al 2005). The stress resulting from the salinity of coastal areas has been linked to the significant influence of insolation, aridity, wave power, wind, and limited nutrients (Hesp 1991).

Mammals' ability to move gives them an adaptive advantage over other sessile organisms, but it does not exclude them from the effects of marine habitats if they live very close to the sea. For this reason, adaptations resulting from living near extreme coastal conditions are to be expected, especially in species that have relatively small ranges.

This study analyzed populations of red squirrels inhabiting coastal cliffs in the south of Spain by examining squirrel abundance on two scales: home range level (i.e., habitat) and landscape level. We hypothesized that the squirrels in this area have adapted in a particular way, be it behavioral or through habitat selection, to the environmental stress caused by living close to the sea, thereby allowing them to live in the area.

Material and methods

Study area

The study was carried out on the cliffs of Maro-Cerro Gordo in Málaga and Granada in southern Spain. This is a protected area of 19.1 km^2, of which only 3.8 km^2 is land and the rest (80 %) is water extending for one nautical mile. The protected terrestrial strip thus extends for a maximum of 1.4 km inland. The altitude ranges from 0–300 m a.s.l. The climate in Maro is subtropical (Capel-Molina 1981), with the temperature generally varying between 8 °C and 31 °C throughout the year. The monthly rainfall ranges between 1 and 150 mm (annual total rainfall 315 to 380 mm), with May to September being the driest months (Agencia Estatal de Meteorología).

The coastal strip of Maro is 12 km long and extends between Torre de Maro (Nerja: 36° 45' 06'' N 3° 49' 50'' W) and Calaiza beach (La Herradura, Almuñécar: 36° 43' 58'' N 3° 45' 44'' W). It is very sinuous, with many sea ledges and inlets (see fig. 1). The terrestrial section is characterized by the 150 m cliffs and numerous coves with stony beaches. Geologically, there are highly tectonized metamorphic formations of schist and quartzite together with marble and some conglomerate outcrops. The upper part of the cliffs is covered by *Aleppo pine* forests of varying degrees of maturity and thermophilic shrubs and scrubland, such as mastic tree *Pistacia lentiscus*, boxwood *Buxus balearica*, kermes oak *Quercus coccifera*, Mediterranean dwarf palm *Chamaerops humilis*, rosemary *Salvia rosmarinus*, various species of thorny bushes *Rhamnus oleoides* and *Rhamnus alaternus* and

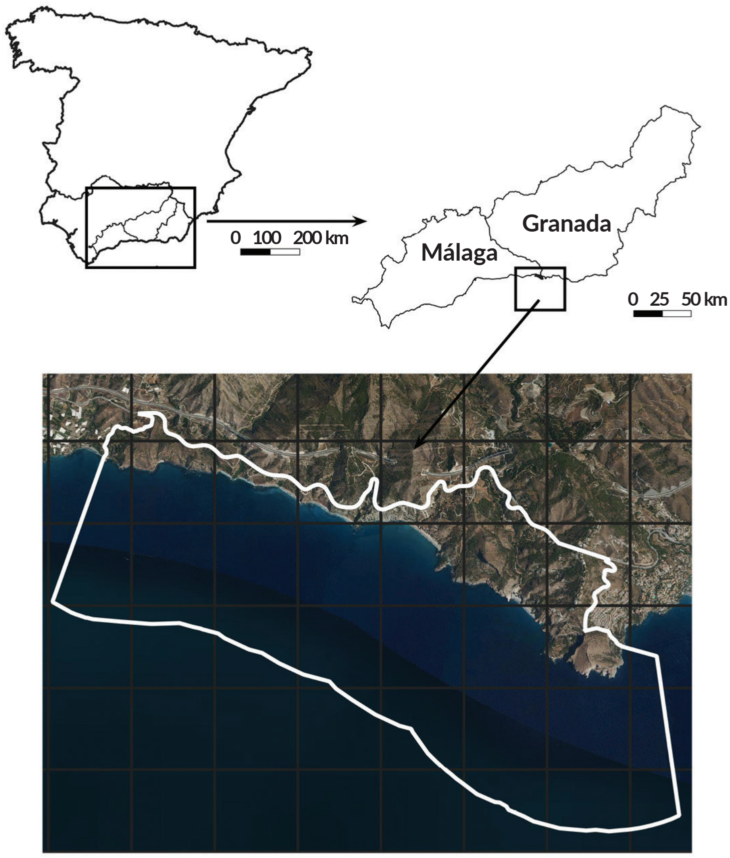

Fig. 1. The study's location in Andalucía in the south of Spain. The protected Maro-Cerro Gordo cliffs (1 x 1 UTM grids) are located between the provinces of Málaga and Granada.

Fig. 1. *Lugar del estudio en Andalucía, en el sur de España. Los acantilados protegidos de Maro-Cerro Gordo (cuadrículas UTM de 1 x 1) están situados entre las provincias de Málaga y Granada.*

rockroses *Cistus* spp, and needle grass *Stipa tenacissima*. Grasslands also cover the area, and rupicolous vegetation grows on the cliffs' vertical walls and crevices. There are also some cultivated areas that were formerly sugar cane plantations. Today these areas are vegetable gardens and almond and olive tree orchards, with some subtropical trees on the periphery.

Sampling design

The study was carried out between March and July 2019 in the terrestrial strip of the protected space. We divided the study area into 14 1 x 1 km Universal Transverse Mercator (UTM) grids, from which random points were used as the sample. At least one pine specimen had to be near each point, and the points were separated from each other by at least 300 m. This distance was to ensure an area three times the size of the red squirrel territories (0.9 to 3.0 ha during summer in Mediterranean environments, in accordance with Piqué 1997), thereby guaranteeing the independence of the points (see below). A total of 66 sampling points were generated inside the protected space and nearby land, with an average of 4.4 ± 0.2 per grid (range: 3 to 6 sampling points per UTM).

Red squirrel abundance

We used a relative abundance index to estimate squirrel abundance in each sampling point. We followed Arrizabalaga et al's (2007) methodology to identify the remains of the pine kernels and pine cones eaten by squirrels in a 1 m^2 circular area that was randomly located under the pine tree canopies at each sampling point. To avoid possibly confusing these signs with those of rats *Rattus* sp. we ensured that there was an active squirrel nest in the area when consumed pine cones were found. We counted only recent remains, discarding those that were very dry and that could not be verified. We considered as fresh remains those that were still a reddish color and very frayed (Piqué et al 2007). The number of pine cones eaten in each sampling point was recorded and used as evidence of squirrel abundance (Moleón and Gil-Sánchez 2003). We also recorded the number of red squirrel nests found in each sampling point and grouped them according to their UTM grids (i.e., total number of nests found per UTM grid). We only considered active nests (i.e., those with recently consumed remains under the pine canopy, as explained below). Nests were systematically searched inside a 100-m radius buffer around each sampling point (see next section for more details concerning this buffer).

Table 1. Variables and factors used to characterize the home range (habitat) and the landscape occupied by red squirrels at the Maro-Cerro Gordo cliffs: FCC, surface of the canopy projected from the vertical towards the ground; * used only in landscape analysis; ** used only in habitat analysis.

Table 1. *Variables y factores utilizados para describir el territorio (hábitat) y el paisaje ocupados por la ardilla roja en los acantilados de Maro-Cerro Gordo: FCC, superficie del dosel proyectada verticalmente hacia el suelo; * variable utilizada únicamente en el análisis del paisaje; ** variable utilizada únicamente en el análisis del hábitat.*

Variable: code	Type
Pastureland (Past): coverage expressed as a proportion of the total	Continous (%)
Scrubland (Scrub): coverage expressed as a proportion of the total	Continous (%)
Riverside vegetation (River): coverage expressed as a proportion of the total	Continous (%)
Dense pine forest (PineD): FCC >= 50 %, coverage expressed as a proportion of the total	Continous (%)
Sparse pine forest (PineS): FCC < 50 %, coverage expressed as a proportion of the total	Continous (%)
Pine class (Pclass): estimation of the degree of maturity of the pine patch	Categorical:
	0 no pines
	1 young: height < 3 (m)
	2 young: 3 to 6 (m) high
	3 mature: high > 6 (m)
Herbaceous crops (HerbC): coverage expressed as a proportion of the total	Continous (%)
Tree crops (TreeC): almond, olive or fruit and subtropical trees;	
coverage expressed as a proportion of the total	Continous (%)
Urban (Urb): built-up areas and associated infrastructure	Continous (%)
Beach: coastal habitat, coverage expressed as a proportion of the total	Continous (%)
Habitat/land use diversity (Shannon)	Continous (bits)
Cliff: presence of cliffs less than 100m from the buffer or in the UTM grid	Binomial:
	0 absence
	1 presence
Total lengh of streams in the UTM grid (Lstream)*	Continous (m)
Distance to the coastline (Dcoast): from the centroid of the UTM grid or the centre of the buffer	Continous (m)
Distance to close stream (Dstream)**	Continous (m)

Habitat monitoring

A buffer with a radius of 100 m was defined around each sampling point as this is the typical radius of a circular summer squirrel territory in a Mediterranean environment, in accordance with the home range sizes estimated by the Piqué (1997) study conducted in Collserola park (Barcelona, Spain), an area very similar to our study area.

We digitized the land coverage inside each buffer. We considered land coverage types and the distance to some of the territory's environmental characteristics that could be relevant for the squirrels (see table 1). We conducted the digitization of land cover using QGis 3.22 (QGIS Development Team 2022) according to the most recently updated information about Andalusia from the Spanish Land Occupancy Information System (Junta de Andalucía 2022). This information system provides detailed land use information in terms of both coverage and plant associations, and we reorganized and summarized the information contained therein into the categories described in table 1. We also estimated the land coverage diversity in each buffer using the Shannon index (Magurran 2004). The land use for each of the study's 1 x 1 UTM grids was also digitalized.

Statistical approach

We examined the relationship between habitat and squirrel abundance on two scales. The first was home range, the smaller scale. We analyzed this using a generalized lineal mixed model (GLMM) with Poisson error distribution and a log link function model (Crawley 1993) to determine if the number of squirrel signs (i.e., the index of abundance) was related to the habitat of each sampling point. The UTM of each sampling point was considered a random effect in this model. The second scale consisted of a more extensive analysis of the landscape. A generalized lineal model (GLM) with Poisson error distribution and a log link function model was used to identify if the total number of detected active squirrel nests in each 1 x 1 UTM grid was related to the grid's environmental factors. For both scales we fitted various models, ranked these, and selected those most parsimonious on the basis of the Akaike index (AICc) for small sample sizes (Burnham and Anderson 2002).

Since cliffs were the main variable in our working hypothesis, we compared the habitat characteristics of the sampling points in the cliffs against those not in cliffs. A sampling point in a cliff was included when it was located less than 100 m from the cliff (i.e., using

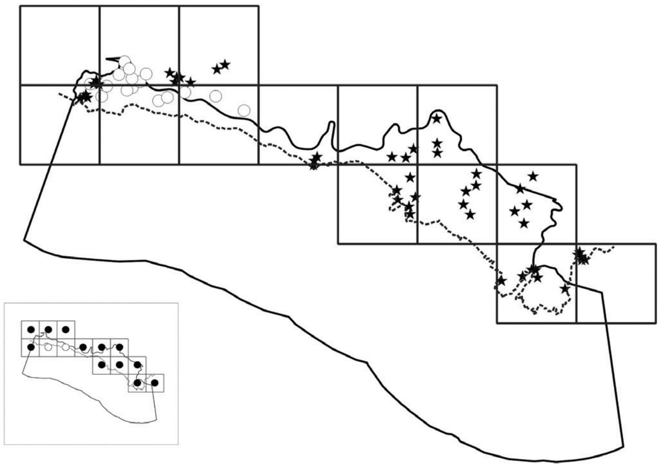

Fig. 2. Sampling points and presence of red squirrel in the land strip at the Maro-Cerro Gordo cliffs. The dashed line represents the coastline, the stars denote the positive red squirrel sampling points, and the white dots indicate the negative sampling points. The black dots in the small box indicate the presence of red squirrels, and the white dots represent the 1 x 1 UTM grids in which red squirrels were absent.

Fig. 2. *Puntos de muestreo y presencia de la ardilla roja en la franja de tierra en los acantilados de Maro-Cerro Gordo. La línea discontinua representa la costa, las estrellas indican los puntos de muestreo positivos para la ardilla roja y los puntos blancos indican los puntos de muestreo negativos. Los puntos negros del recuadro pequeño indican las cuadrículas UTM de 1 x 1 en las que la ardilla roja está presente y los puntos blancos representan las cuadrículas UTM de 1 x 1 en las que la ardilla está ausente.*

the same criteria as that for the squirrels home range). We used a non-parametric Kruskal-Wallis test (Fowler and Cohen 1992) to test for differences. All of the analyses were carried out using R (R Core Team 2021) and JASP software (JASP Team 2023), and all means are given with their standard errors.

Results

We found signs of recent red squirrel activity in 50 sampling points (75.7 %; n = 66), and no signs in 16 sampling points (24.3 %) (fig. 2), with there being an average of 8.2 ± 0.9 signs per m^2 (range: 0 to 35 signs/m^2).

The best model for home range level (table 2) showed that red squirrel abundance was significantly affected by the degree of maturity of the pine patches(pine classes; Poisson GLMM: Wald $\chi^2 = 24.745$; $p < 0.001$), nearby cliffs (Wald $\chi^2 = 5.554$; $p = 0.022$) and the distance to the nearest water stream (Wald $\chi^2 = 5.883$; $p = 0.019$) as the signs of squirrel activity increased in mature pine patches, near water streams, and close to cliffs (fig. 3).

On the landscape scale, red squirrels occupied 12 (85.7 %; n = 14) UTM grids in the protected space, while the species was absent in just two grids (14.3 %; fig. 2). There were 63 active red squirrel nests, and the abundance of the nests was estimated at an average of 4.5 ± 1.3 per UTM (range: 0 to 18 nests).

The best model for the landscape level showed that red squirrel nest abundance (table 2) was significantly negatively affected by herbaceous crops (Poisson GLM: Wald $\chi^2 = 7.422$; $p < 0.01$) and was positively impacted by the length of the streams in each occupied grid (Wald $\chi^2 = 7.432$; $p < 0.01$). The number of squirrel nests increased in areas with fewer herbaceous crops and longer streams.

The comparison between cliff and no-cliff habitats (Kruskal-Wallis test; table 3) showed more signs of red squirrel abundance in the cliffs than in the areas with no cliffs. The cliff samples had more coastal habitats (beaches), were further away from streams, and were closer to coastlines than the sampling points with no cliffs. The urban development rates and amounts of scrubland were lower in the areas with cliffs than in those without cliffs. Lastly, the pines in the areas with cliffs were larger (i.e., they were more mature) than those in the areas with no cliffs (fig. 4).

Discussion

The number of animals that can live in any area is limited by factors often related to resource levels (Newton 1998). Competitive behavioral mechanisms such as territoriality influence density through feeding rates, survival, and reproductive fitness in the same way as predation (Dhondt 1991). Spatial heterogeneity in the habitat's complexity or quality determines the occupation and success of a species in a given area. Good habitats are occupied first. However, as numbers rise, poorer habitats may be occupied. Density can force individuals from good patches to other patches, likely reducing their survival or breeding success and thus lowering or completely decimating abundance (Wauters and Dhondt 1990). Increased habitat composition and complexity therefore often result in an increase in species abundance (Smith et al 2014).

The effects of habitat on small-mammal abundance are well known (Ecke et al 2001, Osbourne et al 2005). The role of the structural complexity or vegetation cover translates into abundance of species due to the potential food and shelter that is provided or the predators therein (Torre et al 2022). This habitat abundance

Table 2. The variation in red squirrel abundance in relation to home range and landscape in the study area. All of the different combinations between the set of variables and factors are presented: k, number of parameters; AICc, Akaike information criterion corrected for small sample sizes.

Table 2. Variación de la abundancia de la ardilla roja en relación con el territorio y el paisaje en la zona de estudio. Se presentan todas las combinaciones entre el conjunto de variables y los factores: k, número de parámetros; AICc, criterio de información de Akaike corregido para tamaños de muestra pequeños.

Model (GLM-Poisson)	*k*	AICc
Home range level (abundance as squirrel signs/m^2 in each buffer 100-m radius)		
Pclass+Cliff-Dstream	4	62.154
Pclass+Cliff-Dstream-HerbC	5	64.944
Pclass+Cliff-Dstream-TreeC	5	67.953
Pclass+Cliff-Dstream-River	5	68.003
Pclass+Cliff-Dstream+PineD	5	86.403
Pclass+Cliff	3	87.932
Null	1	93.425
Landscape level (abundance as number of squirrel active nests in each 1x1 UTM grid)		
Lstream-HerbC	3	101.345
Scrub-Past-HerbC+PineD+Lstream	6	107.514
Pclass+Cliff-Lstream	4	112.157
Past+Lstrems	3	124.836
Past+Lstrems-HerbC	4	137.365
Null	1	148.527

relationship changes according to space and time, and can be influenced by events such as fires (Torre and Diaz 2004), forest or habitat management (Cagnin et al 1998, Marfil et al 2009, Bogdziewicz and Zwolak 2014), changes in agricultural use (Michel et al 2006), and even human activity such as hunting or presence of domestic animals (Tobajas et al 2020). Different land uses therefore affect species abundance at both landscape and habitat levels.

Some studies have shown that squirrels are not an exception to the principles presented above. The abundance of gray squirrel *Sciurus carolinensis* not only varies between habitats (Fischer et al 1991) but also between urban and forest areas (Williamson 1983, Jarboe et al 2021). Tree squirrel *Tamiasciurus hudsonicus* abundance also responds to a range of forest conditions (Sullivan et al 2017), and Humboldt's flying squirrel *Glaucomys oregonensis* and Townsend's chipmunk *Neotamias townsendii* abundance are associated with canopy openness and berry-producing shrubs (Weldy et al 2019). Red squirrel density varies between urban environments (Kopij 2014), urban and wild habitats (Piqué 1997), the height and maturity of pine forests, and forest species composition (Purroy and Rey 1974, García and Mateos 2008). Population dynamics of the species also differ between habitats (Wauters and Dhondt 1990).

Our results show that red squirrel abundance is associated with an area's land use and habitat features. For example, avoidance of herbaceous crops is logical for a species linked to trees and forest environments. In Maro, there were no squirrels in the two UTM grids dominated by herbaceous crops and pasturelands, and the number of squirrel nests was low in those grids in which they were a minority in proportion to the total landscape, despite the existence of favorable forest patches. This avoidance therefore represents a resource limitation as there are not enough pine trees to provide food (Piqué 1997, Arrizabalaga et al 2007), allow for nests (Hernández 1999), or support an abundant squirrel population. The existence of streams and their length are associated with a greater abundance of squirrels, expressed as more active nests. Hernández (1999, 2014) demonstrated that red squirrels may place nests in river groves because these habitats support more food resources than pure pine forests because the understories and hedges not only provide a greater variety of fruits and seeds but also cooler places during the hotter months.

At the home range level, the most important factor for the red squirrel is the existence of pine forest patches, specifically their degree of maturity, as abundance is higher the larger the pines, as reported by other authors (e.g., Purroy and Rey 1974). This preference for larger trees is related to greater safety for the species because it allows nest building and feeding at greater heights (Hernández 2014), thereby decreasing the risk of predation due to too much time spent on the ground (Tobajas et al in press).

Our results also show that cliffs play a key role in squirrel abundance as the species was more abundant in the sampling points located on cliffs. The comparison of cliff habitats and non-cliff habitats reveals that cliffs have the best pine forest patches, which is probably the

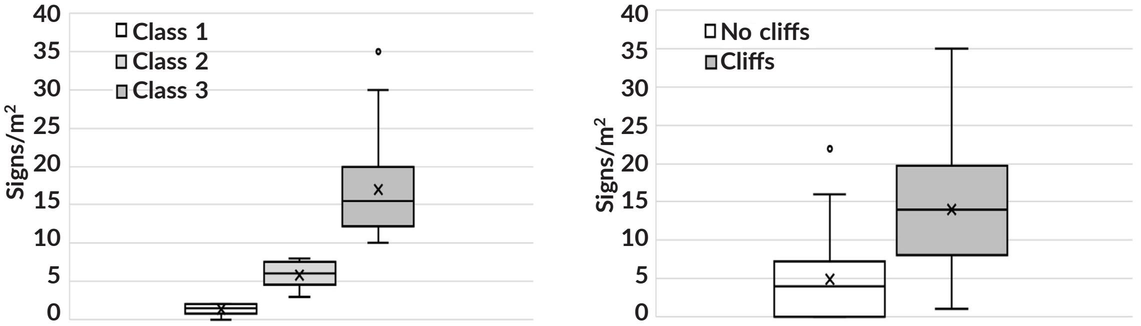

Fig. 3. Red squirrel abundance (signs/m^2) between pine classes and the cliff and no-cliff sampling points. Pine classes: 1, young, with a height of < 3 m; 2, young, with a height of 3–6 m; and 3, mature, with a height of > 6 m.

Fig. 3. *Abundancia de la ardilla roja (signos/m^2) entre las clases de pinos y entre los puntos de muestreo en los acantilados y los puntos de muestreo alejados de los acantilados. Clases de pinos: 1, jóvenes, con una altura de < 3 m; 2, jóvenes, con una altura de 3-6 m; 3, maduros, con una altura de > 6 m.*

Table 3. Differences between the cliff and no-cliff sampling points' habitats. Only the significant factors are shown.

Table 3. *Diferencias entre los hábitats de los puntos de muestreo en los acantilados y los de los puntos de muestreo alejados de los acantilados. Solo se muestran los factores significativos.*

Factor	Kruskal-Wallis test (gl = 1)	In cliffs
Red squirrel abundance (signs/m^2)	H = 19.900; p < 0.001	Higher
Scrubland (%)	H = 12.064; p = 0.001	Lower
Urban (%)	H = 5.072; p = 0.024	Lower
Distance to streams (m)	H = 20.904; p < 0.001	Higher
Beach (%)	H = 5.413; p = 0.020	Higher
Distance to coastline (m)	H = 43.889; p < 0.001	Lower
Pine class (maturity)	H = 15.738; p < 0.001	Higher

main reason for squirrels preferring to include them in their home ranges despite their being heavily exposed to the effects of marine and coastal influence. Cliffs also have less urbanization and less scrubland, further increasing their suitability for this species.

The third important habitat factor for squirrels in Maro is the streams. The home range model coincided with the landscape model as there were more nests in grids with longer streambeds and more signs of squirrel activity near streams. However, the cliff sampling points in this study were further from the streams than the sampling points with no cliffs. This apparent contradiction may indicate that the most important factor for red squirrels is the type of pine forest, even if these forests are highly exposed to extreme environments or if there is a lack of high-quality resources such as water or humidity (Wauters et al 1992). As with other mammal species linked to freshwater habitats but that also inhabit marine environments, the salinity of marine environments can be counteracted by moving to patches where freshwater is available (Kruuk 2006).

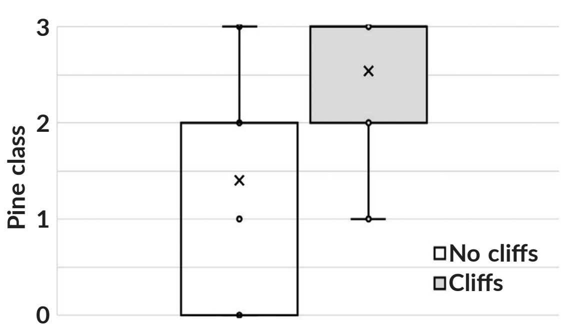

Fig. 4. Pine classes in the cliff and no-cliff sampling points: 0, no pines; 1, young, with a height of < 3 m; 2, young, with a height of 3–6 m; and 3, mature, with a height of > 6 m.

Fig. 4. *Clases de pinos en los puntos de muestreo en los acantilados y en los puntos de muestreo alejados de los acantilados: 0, sin pinos; 1, jóvenes, con una altura de < 3 m; 2, jóvenes, con una altura de 3-6 m; 3, maduros, con una altura de > 6 m.*

Although we found nests in the pine trees on the cliffs and even a few meters from the beach, cliffs were not a significant factor in the landscape model. This suggests that they are not as important for the squirrels as the existence and greater length of water streams when building nests. The cliffs were only significant in the home range model as the squirrels fed from the pines on cliffs and then returned to their nests situated in more humid areas, near streams. In addition, nests on cliffs may be more exposed to adverse meteoritical conditions (wind, rain, salinity and even swell). In other words, squirrels include the pine trees on the cliffs in their home range as feeding patches, but they prefer more humid and safer environments to build their nests and even for feeding if the surrounding pine trees are suitable.

In terms of conservation, the Maro-Cerro Gordo cliffs are not only a habitat of special interest for marine species and rupicolous vegetation, but they are important for small terrestrial mammal species such as the red squirrel since the geographical elements of these cliffs allow access to the best patches of pine forest, which red squirrels migrate to feed on.

Therefore, our results suggest that red squirrels select cliffs because they provide the pines they feed on. This leads to squirrels also needing to inhabit the most humid areas of the natural space not only because of the potential greater availability of resources or comfort during the warmer months but also because it allows them to compensate for the excess salinity surrounding the coastal cliffs.

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J. Duarte designed the study, carried out the sampling, developed the statistical analyzes and wrote the paper. M.A. Farfán reviewed and supervised the results and discussion and contributed with valuable suggestions to the final text.

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No conflicts declared

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