Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 25 (2): 95–100, 2014
OPEN ACCESS
Available online at:
http://www.italian-journal-of-mammalogy.it/article/view/9961/pdf
doi:10.4404/hystrix-25.2-9961

Research Article

Seasonal habitat use in Eurasian red squirrels residing in Iberian hedgerows

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Keywords:
Sciurus vulgaris
sighting rate
microhabitat
conservation

Article history:
Received: 21 March 2014
Accepted: 29 September 2014

Acknowledgements
I wish to thank José Luis Robles for reading this manuscript and for his valuable comments and suggestions. This paper is a research contribution of the Ecology and Conservation of Flora and Fauna Group at Valladolid University, Spain.

Abstract

Hedgerows are considered habitat corridors for Eurasian red squirrels (*Sciurus vulgaris*). However, in north Iberia, a red squirrel population resides in hedgerows separating meadows. This study assesses seasonal microhabitat selection in this peculiar squirrel population. The detection rate was higher in winter and autumn than in spring and summer because of the confluence of different biological and environmental factors. Red squirrels were mainly arboreal, though they used the ground to some degree throughout the year. The height at which individuals were seen in shrubs/trees was maximum in spring related to intensive use of high poplars. A seasonal variation in plant selection was found. Red squirrels selected oaks, ivy and poplars positively in winter, poplars, ashes and willows in spring, hazels, wild cherries and willows in summer, and hazels, ashes and willows in autumn, linked with shelter, nest-site and food requirements. Conservation of dense hedgerow networks with a high diversity of shrub and tree species is encouraged.

Introduction

Habitat loss and fragmentation are major threats to biodiversity (Fischer and Lindenmayer, 2007), and the evidence from well-designed studies suggests that habitat corridors are usually valuable conservation tools (Beier and Noss, 1998; Debinski and Holt, 2000). Some species use hedgerows as movement conduits in fragmented woodlands, but more investigations are required to understand their role in increasing habitat connectivity (Davies and Pullin, 2007). Eurasian red squirrels (*Sciurus vulgaris*) (hereafter red squirrels or simply squirrels) live in all types of woodlands with trees that produce fruits and seeds with high energy content (Lurz et al., 1995; Bosch and Lurz, 2012). Habitat fragmentation negatively affects red squirrels as too small wooded patches preclude their presence, though their population density can remain high in occupied patches if habitat quality does not decrease (Delin and Andrén, 1999; Rodríguez and Andrén, 1999; Verbeylen et al., 2003a; Koprowski, 2005). In general, habitat corridors such as hedgerows enhance dispersal of red squirrels, positively influencing their presence and density (van Apeldoorn et al., 1994; Wauters et al., 1994a; Wauters, 1997; Mortelliti et al., 2011). Hedgerows, however, are not considered a permanent habitat for red squirrels, according to the available literature (Bosch and Lurz, 2012).

In the Iberian Peninsula, red squirrels have a wide distribution except for the south-west, and inhabit mostly conifer forests, in particular *Pinus* pine forests, though they can also be found in broadleaved forests in the north, especially *Fagus* beech and *Quercus* oak woodlands and other stands including *Castanea* chestnut and *Juglans* walnut groves (Palomares, 1988; Castién and Mendiola, 1989; Blanco, 1998; Mathias and Gurnell, 1998; Ferreira et al., 2001; Velasco et al., 2005; Purroy, 2007; García and Mateos, 2008; Talegón, 2009; J.L. Robles personal communication 2013). In addition, in the Torío river valley, north-west Spain, a red squirrel population resides in a dense network of hedgerows between meadows, where some research has been carried out on nest-site selection and nest characteristics (Hernández, 1999, 2004). Few more studies have been conducted on the biology and ecology of the red squirrel in the Iberian Peninsula (Purroy and Rey, 1974; Piqué, 1997; Hernández, 1999; Ferreira et al., 2001), in contrast to some areas of its vast distribution range, such as Britain, Sweden, central Europe, Italy and the Far East, where it is a much better known species (e.g. Andrén and Delin, 1994; Petty et al., 2003; Verbeylen et al., 2003b; Jianzhang at al., 2006; Amori et al., 2002; Bosch and Lurz, 2012).

The aim of this study is to shed more light on the ecology of the peculiar squirrel population associated with hedgerows in northern Iberia. In particular, seasonality in habitat use and microhabitat selection was analyzed. A high seasonal variation is expected to happen because of the marked climatic seasonality in the study area and high floristic richness of the hedgerows.

Methods

Study area

The study area covers 78 ha and is located in the Torío river valley, between Palacio and Manzaneda (42°43′–42°44′N, 5°30′–5°31′E; 900 m a.s.l.; León province, Castilla y León autonomous community), in north-west Spain. Biogeographically, it forms part of the Carpetano-Leonese sector in the Mediterranean West Iberian province (Rivas-Martínez, 2007). Hot summers, cold winters and moderate rainfall with a short dry summer season characterize the area. The landscape is mainly composed of hedgerows that separate irrigated meadows grazed by livestock and cut for hay (Fig. 1), bordered by riparian woodland on the west side and slopes covered with Pyrenean oak (*Quercus pyrenaica*) woods interspersed with small Scots pine (*Pinus sylvestris*) plantations on the east side. Some hedgerows border Canadian poplar (*Populus* × *canadensis*) plantations. Estimated hedgerow density is 3.3 km per 10 ha. This area is located in a transition zone, south of the Cantabrian mountain range, in an extensive hedgerow network of great conservation value for flora and fauna (Hernández and Alegre,

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Figure 1 – Typical hedgerow-meadow landscape in the study area in November.

Figure 2 – Red squirrel on a tree in the study area in May, seen in hedgerow-meadow mixed with oak wood habitat.

1991; Hernández, 2007, 2008, 2009; Hernández and Zaldívar, 2013). About thirty species of broadleaved, chiefly deciduous shrubs, trees and climbers are found in the hedgerows. The landscape and the density and structure of hedgerows are very similar throughout the study area and have hardly changed in recent decades.

Considering three months per season in the six-year main study period (2001-2006), i.e. n=18 months for each season in this period, mean (± standard deviation) average monthly temperature was 3.5 ± 1.3 °C in winter (December-February), 10.0 ± 2.6 °C in spring (March-May), 19.4 ± 1.2 °C in summer (June-August) and 11.7 ± 4.3 °C in autumn (September-November). Considering the three months in each season as a whole during this study period, i.e. n=6 years, mean rainfall was 130.0 ± 63.1 mm in winter, 135.8 ± 28.7 mm in spring, 56.5 ± 27.6 mm in summer and 166.1 ± 86.0 mm in autumn. Meteorological data were provided by the Agencia Estatal de Meteorología (AEMET) for the La Virgen del Camino station, situated near to the study area at the same altitude.

Data collection on squirrels

During 1986-2007, the red squirrels directly observed in the study area and the details of these sightings were recorded during field trips conducted to investigate the natural history of arboreal vertebrates in the hedgerows. Most of the field trips were conducted during the 2001-2006 sub-period, in a systematic way, with 41 trips in winter, 96 in spring, 134 in summer and 84 in autumn. On each trip during the sub-period, half of the study area was explored by walking around it slowly, stopping frequently, following the edge of the hedgerows and marginally (≈10% sampling effort) the edge of the oak woods. On each trip, the area complementary to that of the previous trip was explored. More than 85% of field trips were conducted in the morning in all seasons, and the rest in the afternoon. The morning trips lasted from one hour after sunrise to 12:00 h (solar time) and the afternoon trips from 12:00 h (solar time) to one hour before sunset, as there was not enough light at dawn or dusk for sampling to be carried out. During 1986-2000 and 2007 the study area was visited without a defined sampling effort for each field trip, thus data from these years were not considered to estimate the detection rate of squirrels. Pseudo-replication rate was probably low in such a large area with visits distributed over many years. Red squirrels usually occupy overlapping home ranges varied in size but considerably smaller than the study area, and their longevity at 6 months of age is about 3 years (Lurz et al., 2005; Bosch and Lurz, 2012). The recorded circumstances were those observed without later approaching the individuals, as their position and behavior could be influenced by the presence of the observer.

Individuals were considered to be together, i.e. pertaining to the same contact, if they were following or chasing each other, or were less than 10 m apart. For each contact, the following data were recorded: date, solar time and noteworthy weather conditions (snow, heavy rain); predominant habitat in a 50 m radius, namely, hedgerow-meadow, oak wood, poplar plantation, orchard, pine plantation, or a combination of these habitats (for contacts involving more than one individual a radius of 50 m around the equidistant point between them was considered); individuals on the ground or in a shrub/tree (including climbers); height at which each individual was located and plant species used if the individual was in a shrub/tree; number of individuals; behavior of each individual (still or in action, activity type).

Selection of shrub/tree species by squirrels

The selection of plant species by the red squirrels seen in shrub/tree was analyzed considering only data obtained in the main habitat in the study area precisely where a high variety of woody plants live, i.e. hedgerow-meadow, by comparing the use they made of each plant species with its availability. Plant species availability was estimated by conducting eight sampling days within the period 28 September-15 October 2004, when approximately 9 km of hedgerows were covered (≈35% of all the hedgerows, evenly distributed in the study area), recording the presence-absence, but not the number of individuals of each species (shrubs, trees, climbers) in 2 m long fragments (n=330 fragments) situated every 25 m (modified from Hernández and Alegre, 1991). Multispecific complexes of *Rubus* brambles, *Rosa* roses and *Salix* willows were classified as single species. Selection of each plant species was estimated by the Jacobs' index (Jacobs, 1974):

$$S = \frac{(u - a)}{(u + a - 2ua)}$$

where u (use) is the proportion of individuals seen on a given plant species in relation to the total number of individuals seen on shrub/tree, and a (availability) is the proportion of occurrences of that plant species in relation to the total occurrences of plant species. Correction of u and a values for a total of 1 is required for calculations. This index varies between -1 (maximum negative selection) and 1 (maximum positive selection), with a value 0 if selection does not occur (i.e. red squirrels used the plant species according to its availability). The maximum height of each hedgerow fragment was also recorded to compare the height at which the squirrels were seen with the maximum available height.

Data analysis

The chi-square test (χ^2) was used to compare series of frequencies, and the one-way ANOVA (F) to compare more than two means (Fowler et al., 1998). Standard deviation (SD) was estimated as a measurement of

dispersion. $p<0.05$ was considered statistically significant. Unless otherwise stated, statistical analyses refer to the 1986-2007 period. In all the analyses, winter was December to February, spring March to May, summer June to August and autumn September to November. Each analysis indicates whether contacts (a contact may involve more than one individual) or individuals are being referred to.

Results

General behavior and detection rate

A total of 142 red squirrel contacts involving 154 individuals were recorded during 1986-2007. The mean number of individuals observed per contact was 1.24 ± 0.60 in winter (n=25 contacts), 1.07 ± 0.26 in spring (n=43), 1.04 ± 0.21 in summer (n=23) and 1.04 ± 0.20 in autumn (n=51), with no significant seasonal differences (one-way ANOVA $F_{3,138} = 2.45$, $p>0.05$). They were therefore generally solitary individuals. Some intraspecific chases were observed in winter, summer and autumn, always involving less than 10% of individuals (Tab.1, which summarizes the circumstances of squirrels when they were sighted). During the 2001-2006 sub-period, 112 contacts were recorded, 17 of them in winter, 29 in spring, 19 in summer and 47 in autumn. During this sub-period, the number of contacts was high in autumn and winter in relation to the number of field trips made (41.5-55.9%), medium in spring (30.2%) and low in summer (14.2%), with significant seasonal differences (χ^2_3=22.34, $p<0.001$).

Microhabitat selection

The percentage of red squirrel contacts recorded in hedgerow-meadow alone or mixed with other habitats (oak wood, poplar plantation, orchard) was > 80% in all seasons (Tab.2). The number of individuals observed in shrub/tree ($\approx$ 70-90%) was always higher than on the ground (remaining individuals), with no significant seasonal differences (χ^2_3 = 3.97, $p>0.05$) (Figs. 2 and 3). The mean height at which individuals were observed in shrub/tree was $\approx$ 5.5-6 m in winter, summer and autumn, and $\approx$ 9 m in spring (see sample size and SD in Fig.4), which resulted in significant differences between seasons (one-way ANOVA $F_{3,119} = 4.88$, $p<0.01$). For comparison, the mean maximum height of the hedgerows was 11.8 ± 9.0 m (n=330 fragments).

Twenty-nine species were detected in the samplings of hedgerow woody plants and a total of 1818 occurrences were recorded, *Rubus* spp. (16.2% occurrences), *Rosa* spp. (10.1%), wild privet (*Ligustrum vulgare*) (9.7%) and blackthorn (*Prunus spinosa*) (7.7%) being the most predominant. Considering only squirrels in shrub/tree in hedgerows and the three most preferred plants in each season ($S>0.50$ in all cases), they selected Pyrenean oak, common ivy (*Hedera helix*) and black poplar (*Populus nigra*) in winter, black poplar, European ash

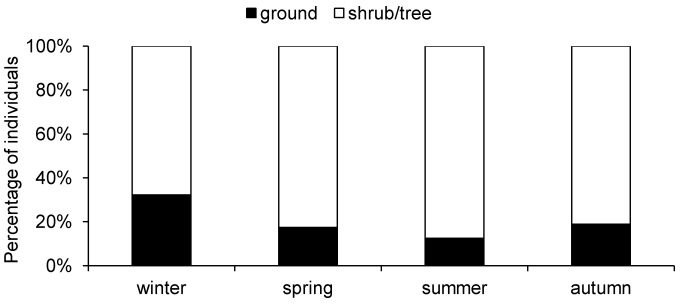

Figure 3 – Seasonality in the use of ground or shrub/tree by red squirrel individuals. Number of observed individuals: 31 in winter, 46 in spring, 24 in summer, 53 in autumn.

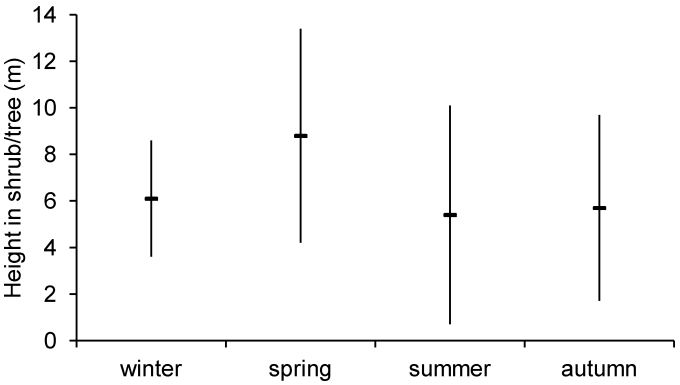

Figure 4 – Seasonality in the mean height ($\pm$ SD) at which red squirrel individuals were observed in shrubs/trees. 465 Number of observed individuals: 21 in winter, 38 in spring, 21 in summer, 43 in autumn.

(*Fraxinus excelsior*) and willows in spring, common hazel (*Corylus avellana*), wild cherry (*Prunus avium*) and willows in summer, and common hazel, European ash and willows in autumn (Tab.3). Considering individuals in shrub/tree in all habitats, the use of Canadian poplars was noticeable during certain times of the year, Pyrenean oak, black poplar and common ivy being predominant (19.0-23.8% individuals in each) in winter, black poplar (36.8%) and Canadian poplar (15.8%) in spring, and common hazel (39.5-57.1%) and Canadian poplar (19.0-23.2%) in summer and autumn.

A total of 39 records (4 in winter, 15 in spring, 8 in summer, 12 in autumn) were made of different squirrel individuals eating leaves, flowers and fruits, or hoarding fruits, of at least 11 plant species, regardless of the number of units consumed. In winter, individuals fed on rose hips. In spring, most of them ate oval-shaped poplar fruit capsules and the rest willow aments, walnuts (*Juglans regia*) and unidentified food.

Table 1 – Seasonality in the general behavior of red squirrels.

Behavior	Winter % / n	Spring % / n	Summer % / n	Autumn % / n
Non-moving (including grooming)	25.8	28.3	33.3	22.6
Moving (going to another place)	35.5	21.7	25.0	41.5
Chasing conspecifics	9.7	0.0	8.3	3.8
Next (< 5 m) to its own nest (including entering and leaving the nest)	3.2	13.0	0.0	3.8
Being mobbed by birds	0.0	2.2	0.0	1.9
Inspecting bird nests	0.0	2.2	0.0	0.0
Eating in shrub/tree	12.9	28.3	33.3	11.3
Eating on the ground	0.0	4.3	0.0	1.9
Foraging in shrub/tree (excluding bird nest inspection)	0.0	0.0	0.0	3.8
Foraging on the ground	12.9	0.0	0.0	0.0
Eating food hoarded in tree trunk	0.0	0.0	0.0	1.9
Hoarding food in tree trunk	0.0	0.0	0.0	1.9
Hoarding food in the soil	0.0	0.0	0.0	5.7
Number of individuals (n)	**31**	**46**	**24**	**53**

Table 2 – Seasonality in habitat type use by red squirrels.

Predominant habitat within a 50 m radius	Winter % / n	Spring % / n	Summer % / n	Autumn % / n
Hedgerow-meadow-oak woodland-poplar plantation	4.0	7.0	0.0	2.0
Hedgerow-meadow-oak woodland	8.0	4.6	8.7	3.9
Hedgerow-meadow-poplar plantation	8.0	11.6	47.8	33.3
Hedgerow-meadow	64.0	60.5	39.1	52.9
Oak woodland	16.0	13.9	0.0	3.9
Hedgerow-meadow-orchard	0.0	2.3	0.0	3.9
Pine plantation-oak woodland	0.0	0.0	4.3	0.0
Number of contacts (n)	**25**	**43**	**23**	**51**

A contact may involve more than one individual. Individuals were considered to be together if they followed or chased each other, or were less than 10 m apart.

Squirrels consumed poplar fruits by pulling over a raceme (fructified ament) with a paw, gnawing the base whilst still holding it, eating the capsules one by one and then discarding the remains of the raceme. Perhaps the walnut record in spring was a fruit recovered from an autumn cache. In summer, hazelnuts were the most popular source of food, and a small number of cherries. In autumn, half of the individuals ate or hoarded hazelnuts and the rest consumed or hoarded haws (*Crataegus monogyna*), or ate other types of fruits (walnuts, acorns, apples (*Malus domestica*)) and dandelion (*Taraxacum* gr. *officinalis*) leaves. Squirrels consumed dandelion on the ground by biting off a leaf near its base and, holding it in its paws, nibbling and then eating it completely, doing the same with several leaves. Squirrels hoarded haws and hazelnuts in superficial cracks in tree trunks, at a height of approximately 7-10 m, and hazelnuts in the soil.

Discussion

Detection rate

The relationship between the number of contacts and field trips reflects that there was more visible activity and/or abundance of red squirrels in the study area in winter and autumn than spring and summer. On the one hand, this is probably because in winter males actively search for and chase females in oestrus and in autumn all individuals persistently look for and hoard food, and juveniles disperse from the natal site (Purroy and Rey, 1974; Wauters et al., 1990, 1994b, 2011; Lee, 2005; Lurz et al., 2005); on the other, population usually peaks in autumn and early winter because it includes the juveniles born during the year, and declines in late spring and early summer due to winter mortality and decreased food availability (Wauters et al., 2004; Purroy, 2007; Bosch and Lurz, 2012). In agreement with this, the highest percentages of moving individuals, apparently going to a distant place, were obtained in autumn and winter in the present study. Most of the individuals moving in autumn did so horizontally along shrubs/trees, which probably improved the efficiency of their trips. Also, a chase involving three individuals was observed in winter.

The low detection rate in summer, with most sightings occurring at the end of August, was also presumably due to high temperatures. Other authors have also reported diminished activity in this species associated to excessive heat, and no activity at all at temperatures > 25 °C (Purroy and Rey, 1974; Tonkin, 1983; Holm, 1987). In the study area, the mean number of summer days with temperatures $\geq$ 25 °C per month was almost 23. Also, dense foliage in shrubs and trees in spring and summer could have made it more difficult to see the squirrels. Active individuals were detected in winter when there was intense frost and/or most of the ground was covered in snow, and in spring in moderate or even heavy rain.

Microhabitat selection

The predominance of hedgerow-meadow observed in the general habitat of this squirrels population is an expected result as most of the study area is covered by this traditional landscape. A considerable importance of poplar plantations surrounded by hedgerows in the summer habitat was probably related to a preference for cooler places during this hot season. Red squirrels were mainly arboreal in all seasons, as usual in the species (Holm, 1987; Piqué, 1997; Bosch and Lurz, 2012).

Table 3 – Seasonality in use and selection of hedgerow plant species by red squirrels.

Plant species	Availability	Winter		Spring		Summer		Autumn	
		Use	*S*	Use	*S*	Use	*S*	Use	*S*
Salix spp.	3.2	0.0	-1	10.0	**0.54**	11.8	**0.60**	10.0	**0.54**
Populus nigra	4.9	28.6	**0.77**	46.7	**0.89**	5.9	0.10	10.0	0.37
Corylus avellana	5.9	14.3	0.45	16.7	0.52	70.6	**0.95**	56.7	**0.91**
Quercus pyrenaica	0.8	7.1	**0.81**	0.0	-1	0.0	-1	0.0	-1
Ulmus minor	5.3	7.1	0.15	6.7	0.12	0.0	-1	3.3	-0.24
Crataegus monogyna	6.9	0.0	-1	6.7	-0.01	0.0	-1	6.7	-0.01
Prunus avium	0.8	0.0	-1	0.0	-1	5.9	**0.77**	0.0	-1
Prunus spinosa	7.7	0.0	-1	0.0	-1	0.0	-1	3.3	-0.42
Rosa spp.	10.1	14.3	0.19	0.0	-1	5.9	-0.28	0.0	-1
Cornus sanguinea	6.9	0.0	-1	0.0	-1	0.0	-1	3.3	-0.37
Hedera helix	4.6	28.6	**0.78**	6.7	0.20	0.0	-1	0.0	-1
Fraxinus excelsior	1.0	0.0	-1	6.7	**0.75**	0.0	-1	3.3	**0.54**
Ligustrum vulgare	9.7	0.0	-1	0.0	-1	0.0	-1	3.3	-0.52

Availability: percentages (%) in relation to the total number of plant species occurrences (n = 1818) obtained in the samplings of woody vegetation. Use: percentages (%) in relation to the number of squirrels observed on woody vegetation (n = 14 individuals in winter, 30 in spring, 17 in summer, 30 in autumn). *S*: selection estimated using the Jacobs' index (Jacobs, 1974), varying between -1 (maximum negative selection) and 1 (maximum positive selection), with the value 0 if selection does not occur (the plant species was used according to its availability). For each season, the three highest values of positive selection are in bold. Only plant species used by squirrels in at least one season are considered, so unused plant species are not included (16 species with a selection value of -1 in all seasons). Crack willow (*Salix fragilis*) was the most frequently used willow species. Dog rose (*Rosa canina*) was the most frequently used rose species.

With regard to the height at which they were found in shrub/tree, the high mean value estimated in spring was associated with intensive use of poplars.

A seasonal variation in plant selection by squirrels was found, though this should be considered with caution due to the relatively small sample sizes. In winter, when the majority of shrubs and trees lose their leaves, marcescent oak trees and evergreen ivy probably provided shelter, as well as tall poplars. Also, in hedgerows, squirrels prefer poplars for building their nests, even in winter (Hernández, 1999; A. Hernández personal observation). In spring, the use and positive selection of poplars increased even more as their fruit capsules were an important food source in this season. Poplar fruits are abundant in this area during April and May. In summer and autumn, the predominant use and positive selection of hazel was linked to the consumption and hoarding of hazelnuts, coinciding with their maximum availability. Red squirrels track food-rich patches and therefore their use of space is related to food availability in time (Lurz et al., 2000). Other preferences were probably the result of food (willow catkins in spring, cherries in summer) or refuge (ashes and willows, tall leafy trees, in different seasons) requirements. On the other hand, the most available plant species, i.e. shrubs that produce fleshy fruits, were generally avoided or not frequently used, perhaps because of its low height and hard to access foliage (often overly thorny and/or bushy), though some appeared to be a remarkable food source in winter (rose hips) and autumn (haws) and had neutral selection values ($S \approx 0$) in these seasons. In broadleaved forests, the importance of mature trees that provide enough shelter and a sufficiently thick canopy for the red squirrels to move around the tree tops, and hazelnuts as an excellent source of high quality food, has been indicated by several authors (Valverde, 1967; Holm, 1987; Kenward and Holm, 1993).

The squirrels in the study area had a varied diet throughout the year linked to a high woody plant diversity, which is indicative of the high plasticity of this species to adapt to a wide range of habitats. Apart from this hedgerow network, red squirrels also frequently consume fleshy fruits in autumn and winter and tree flowers in spring in other heterogeneous habitats elsewhere (Purroy and Rey, 1974; Moller, 1983; Holm, 1987; Piqué, 1997; Lurz et al., 2005). Perhaps some individuals searching for food on the ground in winter were looking for hazelnuts that had been hoarded in autumn. Some food items were stored on the exterior of trees, which is not considered common behavior in red squirrels, except for mushrooms placed on branches or in cracks on tree trunks found to be available only for a few weeks (Moller, 1986; Vander Wall, 1990; Lurz and South, 1998). Presumably, it was a short-term hoarding to prevent spoilage of fleshy fruit and food robbery, and in fact an individual was seen in early autumn eating hazelnuts that had been hidden in cracks in a tree trunk.

Conservation

The conservation, restoration and creation of hedgerows is widely considered to be beneficial for red squirrels as they act as corridors between woodland fragments (Wauters, 1997; Bosch and Lurz, 2012; though red squirrels can readily cross open fields, e.g. Mortelliti et al., 2011, and even more so in this valley in north-west Spain where the squirrel population is well-established as it has the necessary resources for them to survive. One advisable measure for improving the habitat of squirrels would be to increase the number of hazelnuts and other nut-bearing trees, such as walnuts, which are a source of nourishment when the hazelnut harvest is poor. Recent visits to the study area in 2014 revealed that the hedgerows remain apparently in good condition, and the squirrels are still present.

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Associate Editor: L.A. Wauters