Density and habitat use of sympatric Brown hares and European rabbits in a Mediterranean farmland area of Tuscany (Central Italy)

F. Santilli 1,3, M. Bagliacca 2 and G. Paci 2

1 Game & Wildlife Management Consulting, Via F. Dini 3, 57021 Campiglia Marittima (Livorno), Italy
2 Department of Veterinary Science, Pisa University, Via delle Piagge 2, 56124 Pisa, Italy

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Use of habitat by sympatric Brown hare (Lepus europaeus) and wild European rabbit (Oryctolagus cuniculus) was investigated in a farmland area of western Tuscany from 1999 to 2011. We used spotlight counts in winter and indirect surveys on faecal pellet counts in spring–summer. The density of Brown hare increased during the study period, whereas the European rabbit population crashed in 2010 after a European Rabbit Haemorrhagic Disease (RHD) outbreak. The results of the use of habitat type differed between the observations obtained during the spotlight census and the observations obtained from the indirect surveys carried out using faecal pellet counts. The two lagomorph populations showed a great habitat overlap; however, European rabbits seem to live at a shorter distance from permanent cover such as hedgerows and woods and seem to prefer uncultivated fields and permanent crops such as olive tree groves that offer more protection from avian predators. Brown hares seem to prefer more open habitat such as arable crops and this resulted in them being less selective than European rabbits. The differences found in habitat use have probably enabled the two species to coexist for many decades and can be used to manage these lagomorphs.

KEY WORDS: Brown hare, Lepus europaeus, European rabbit, Oryctolagus cuniculus, habitat selection, competition.

INTRODUCTION

Before human intervention, Brown hare (Lepus europaeus) was present in central Europe and Mediterranean countries. In Italy, the species was historically present in the northern and central regions (VIDUS-ROSN et al. 2011), and wild European rabbit

3 Corresponding author: Francesco Santilli, Studio di Gestione Faunistica, Via F. Dini 3, 57021 Campiglia Marittima (Livorno), Italy (E-mail: pcrdis@telctu.it).

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(_Oryctolagus cuniculus_) was restricted to the Iberian Peninsula (FLUX 1993). Since both species are important game animals, both species were spread by humans in many European countries, South America, Australia and New Zealand (SMITH & JOHNSTON 2008; VIDUS-ROFNO et al. 2011). Scattered wild European rabbit populations are present in central and western Tuscany (TROCCHI & RIGA 2005; SANTILLI & BAGLIACCA 2010).

Competition between these two lagomorphs has often been speculated about, but the level of interaction and the mechanism involved in maintaining sympatry or allopatry remain unclear: Brown hare and European rabbit became sympatric relatively recently, and they occupy agricultural or pastural habitats which are also of recent origin. Hence, the two species may be in a phase of redifinition of their ecological niche which may explain the antagonistic behaviour (FLUX 2008). BARNES & TAPPER (1986) reported no evidence that Brown hares avoid European rabbits, but registered a reduction in Brown hare number where European rabbit density was very high.

The removal of European rabbits by myxomatosis in Britain and most of Europe in the 1950s was followed by an increase in the Brown hare number (MOORE 1956; ROTHCHILD 1961). However, more detailed analysis of a French shooting estate (BIRKAN & PEPR 1983) showed this increase was short lived, and the Brown hare and European rabbit population were responding to different climatic factors. European rabbit abundance tend to be negatively affected by high precipitation during spring and low temperature during winter, whereas Brown hares seem to be negatively affected by rainy weather during late summer/autumn (RODEL & DEKKER 2012). HOMOLKA (1987) noted a high degree of dietary overlap between European rabbits and Brown hares, but BARNES & TAPPER (1986) suggest that the decline in Brown hare numbers since the 1960s appears to be quite unrelated to the recovery of the European rabbit population since European rabbits and Brown hares do not overlap (also, when they fed in the same field, European rabbits fed along the edges while Brown hares fed in the center). More recently, KATONA et al. (2004) also did not observe a significant increase in the local Brown hare abundance after the extinction of European rabbits in Hungary.

However, knowledge of the habitat preference of the two species is necessary for the correct management of these lagomorphs in sympatric areas since the best management which maintains the contemporaneous presence of European rabbits and Brown hares can be obtained through the management of land uses.

For this reason, we studied the habitat selection between these two species which live in sympathy in a farmland area near the western coast of Tuscany. We do not know when European rabbits were introduced in this area characterized by the historical presence of the Brown hare, but local hunters report their presence for not less than 50 years.

MATERIAL AND METHODS

Study area

The study on density was carried out for 11 years (from 1999 to 2011). The 3.84 km² study area (Fig. 1) is located in the province of Livorno (western Tuscany) at a distance of about 4 km from the coastline (43°15′49″ 10°35′0″; altitude 40 m). It is part of a wider protected area (7.56 km²) established to protect small game species characterized by sandy and sandy-clay soil texture. The climate can be defined as Mediterranean temperate-warm, with a mild winter. The annual mean
Fig. 1. — Map of the study area with Kernel contours 95% of European rabbit (*Oryctolagus cuniculus*) and Brown hare (*Lepus europaeus*) populations.

Temperature is 15 °C with a maximum of 28 °C in July and a minimum of 5 °C in January. Rainfall is quite scarce; less than 700 mm per year. Land use classes (detected by aerial photographs at a scale of 1:10,000 and direct surveys) include Holm-oak woods *Quercus ilex* (1.1%), arable crops (45.5%) (winter cereals 67.2%, alfalfa 20.2% and sunflowers 12.5%), fallow fields (3.5%), olive tree groves (31.3%), vineyards (12.5%) and human settlement (2.0%). Hedgerows covered 4.7% of the study area.

**Methods**

We mapped vegetative cover types using aerial photographs integrated by direct surveys and digitized them using ArcView 3.2. We analyzed habitat use by European rabbits and Brown hares using two different methods.

First we used spotlight counts carried out from a moving car (maximum speed: 5 km/hr) along a 9-km long transect, lighting up both sides of the transect with a handle lamp (100 w). The transect route was selected from the existing road network so as to survey each habitat type in
proportion to its relative extension; in this way the distribution of Brown hares and European rabbits within the sampled area did not differ from that of the whole study area (Meriggi 1989; Langbein et al. 1999; Barrio et al. 2010). At least two counts were carried out in December of each year when vegetation in the cultivated fields was quite low. Therefore, this is the most limiting season for both species. Each count started at least 2 hr after sunset. A laser range-finder was used to measure the perpendicular distance of the animal from the transect. In this way, the lighted area, calculated on a digitized map for each different habitat, was corrected with the effective probability of detection measured in each habitat (Thomas et al. 2010). All information was digitalized by ArcView 3.2. In 2009–2011, for every animal observed, we recorded also details of the habitat, and the position on the transect using a hand-held global positioning system (GPS) receiver. The observed frequencies and proportion of Brown hare and European rabbit in each habitat type (observed usage proportion) were then calculated (Ferretti et al. 2012) and compared with those expected (expected usage proportion) by chi square and Bonferroni confidence intervals. Selection level by the two species was measured by Jacob’s index of preference; significantly different usage from the value 0 (use as availability) was tested by calculating the confidence intervals of the index (replicates = years) (Manly et al. 1993).

The second method included indirect surveys carried out using faecal pellet counts during the same period (spring–summer 2009–2011). This method allowed us to consider the habitats where the kind of cover prevented spotlight observations and seasons not suitable for direct counts because of the height of vegetation. Pellet detections, obtained by line transect sampling (Palomares 2001), were geo-referred and recorded in a spatial database. We considered a buffer area of 100-m radius around each detection and habitat variables were described inside these plots. In the same transect we identified also plots where both species were not recorded (Ferretti et al. 2012). Plots were then identified as ‘used’ by the presence of pellets and ‘unused’ by their absence.

Brown hare pellets could be discriminated from European rabbit pellets since pellets of adult Brown hares are generally isolated, large, yellow/green, very fibrous and usually have a very small upturned point at one end, whereas pellets of adult European rabbits are usually grouped, small, wrinkled, less fibrous and are often blackish or smeared black. European rabbit pellets, deposited in large accumulations (dunghills or latrines) in the same area, helped us to recognize the European rabbit pellets deposited at random throughout the area. Small yellow/green, fibrous pellets were attributed to growing hares, since juvenile rabbits remain inside the burrows until the third week and within 31.5 m of the burrows till the 10th (Kunkele & Von Holst 1996). Therefore, most pellets could be reliably identified for the purposes of this study.

All geo-referenced observations were used to determine the range of the two populations using the extension Animal Movement for Arcview. Nominal logistic multiple regression analyses were performed: the first between plots with Brown hare pellets and random control ones, the second between plots with European rabbits pellets and random control ones, and the third between plots with Brown hare and European rabbit pellets and random control ones. In this way, the problems of false absence and of the low number of cases per group with respect to the variable number are avoided (Boyce et al. 2002; Mackenzie & Royle 2005). The most important parameters were then chosen in the final model by stepwise regression (forward, probability to enter = 0.25; backward, probability to leave = 0.10). In addition, we compare the distances of each observation by the nearest permanent cover (hedgerows or woods) (SAS 2009).

RESULTS

From the results of counts carried out by the Wildlife Service of the Livorno province, European rabbit density increased by 183.8% from 1999 to 2008 and then it decreased by 85.3%; on the contrary, Brown hare density increased in the last two years, doubling initial population levels (Fig. 2).

The home range of the Brown hare population was wider than the home range of the European rabbit population: Kernel 95%, 318.0 ha vs 224.6 ha; Kernel 50%, 44.7 ha
Density and habitat use of Brown hares and European rabbits

![Bar chart showing density of hares and rabbits from 1999 to 2011.](chart)

Fig. 2. — Density of Brown hare (*Lepus europaerus*) and European rabbit (*Oryctolagus cuniculus*) in the study area from 1999 to 2011. Data of 1999 and 2003 were provided by the local Wildlife Service.

vs 37.2 ha (Fig. 1). The two species shared 58.5% and 13.4% of their home range (Kernel 95% and 50% respectively).

In the spotlighted area, Bonferroni simultaneous confidence interval and Jacob’s index (Table 1 and Fig. 3) showed that European rabbits used arable crops less than availability and olive tree groves more than availability. Brown hares tend to use all habitats considered in proportion to availability.

The indirect surveys carried out using faecal pellet counts (Table 2) showed that the olive tree groves, hedgerows and uncultivated fields were the subset of terms selected by the stepwise procedure which best discriminated the absence/presence of the two lagomorphs. In particular, uncultivated fields were associated with greater likelihood of ‘absence’ of Brown hare (not statistically significant); olive tree groves, hedgerows and uncultivated fields were associated with greater likelihood of ‘presence’ of European rabbit (*P* < 0.05); olive tree groves and hedgerows were associated with greater likelihood of ‘presence’ of both Brown hare and European rabbit (*P* < 0.05).

We registered also a significant difference in distance from hedgerows and/or woodlands between the two species (Mann-Whitney U-statistic = 1817.0; *P* < 0.001): means ± SE = 64.9 ± 7.56 and 110.4 ± 7.29 for European rabbits and Brown hares, respectively.

**DISCUSSION**

The fall of European rabbit abundance registered in 2010 was probably due to an outbreak of European Rabbit Haemorrhagic Disease (RHD); diagnosis obtained by
Table 1.
Results of Bonferroni simultaneous confidence interval analysis for the use of habitat type by European rabbits (*Oryctolagus cuniculus*) and Brown hares (*Lepus europaeus*) (EUP: expected usage proportion; OUP: observed usage proportion; pooled years).

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Brown hare</th>
<th>European Rabbit</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EUP</td>
<td>OUP</td>
</tr>
<tr>
<td>Arable crops</td>
<td>0.463</td>
<td>0.488</td>
</tr>
<tr>
<td>Fallow fields</td>
<td>0.183</td>
<td>0.159</td>
</tr>
<tr>
<td>Olive tree groves</td>
<td>0.171</td>
<td>0.207</td>
</tr>
<tr>
<td>Vineyards</td>
<td>0.195</td>
<td>0.146</td>
</tr>
<tr>
<td>Chi-square (P)</td>
<td>2.01  (NS)</td>
<td>77.40 (&lt; 0.0001)</td>
</tr>
</tbody>
</table>

** Significant differences at P < 0.01.

![Graph showing habitat selection](image)

Fig. 3. — Jacobs index of selection for the use of habitat type of European rabbit (*Oryctolagus cuniculus*) and Brown hare (*Lepus europaeus*) in the spotlighted area. *Uses significantly different from expected.

macroscopic examination of three dead European rabbits found in the area. The contemporaneous increase in Brown hare density may be not related to the European rabbit’s fall. In fact, the RHD outbreak happened in October, less than 2 months before the spotlight counts. It is unlikely that Brown hare population increased in the same
Table 2.
Nominal Logistic multivariate Fit of the habitat variables in relationship to the absence/presence of the lagomorphs; estimates (maximum likelihood) of full and final models.

<table>
<thead>
<tr>
<th>Habitat variables</th>
<th>Brown hare presence $n = (33+13)/122$</th>
<th>European rabbit presence $n = (30+13)/122$</th>
<th>Brown hare and European rabbit presence $n = 13/122$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate b (SE)</td>
<td>Chi square</td>
<td>Estimate b (SE)</td>
</tr>
<tr>
<td>Full models</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arable crops</td>
<td>+ 14 (19.9)</td>
<td>0.52</td>
<td>- 4.8 (6.16)</td>
</tr>
<tr>
<td>Fallow fields</td>
<td>+ 15 (19.9)</td>
<td>0.55</td>
<td>- 4.2 (6.24)</td>
</tr>
<tr>
<td>Olive tree groves</td>
<td>+ 14 (19.9)</td>
<td>0.52</td>
<td>- 3.7 (6.17)</td>
</tr>
<tr>
<td>Vineyards</td>
<td>+ 14 (19.9)</td>
<td>0.48</td>
<td>- 5.0 (6.16)</td>
</tr>
<tr>
<td>Hedgerows</td>
<td><strong>No Spotlightable areas</strong></td>
<td>0.47</td>
<td>+ 0.5 (6.49)</td>
</tr>
<tr>
<td>Woods</td>
<td>0 (0.00)</td>
<td>&gt; 20*</td>
<td>0.0 (0.00)</td>
</tr>
<tr>
<td>Uncultivated fields</td>
<td>- 97 (&gt; 20)</td>
<td>0.02</td>
<td>- 1.5 (6.33)</td>
</tr>
<tr>
<td>Final models</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olive tree groves</td>
<td></td>
<td></td>
<td>+ 1.30 (0.530)</td>
</tr>
<tr>
<td>Hedgerows</td>
<td></td>
<td></td>
<td>+ 5.1 (2.52)</td>
</tr>
<tr>
<td>Uncultivated fields</td>
<td>&lt; - 20 (&gt; 20)</td>
<td>0.02</td>
<td>+ 3.4 (1.74)</td>
</tr>
</tbody>
</table>

* Chi square values statistically significant; ^ unstable estimates.
year. Really, European rabbit density decreased also from 2008 to 2009 by 39.4%; the increase of Brown hare density recorded in 2010 (3 times the density of the previous year) could be due to other factors (environmental, climatic, cyclic) or a delayed response of the Brown hare population to the falling trend of European rabbit density.

The results of the use of habitat type differed between the observations obtained during the spotlight census and the observations obtained by the indirect surveys carried out using faecal pellet counts. The differences might be explained either by the different seasonal period (late winter for spotlight observation and late spring/early summer for faecal pellet counts) or by the different landscapes (only open areas for spotlight observation and all over the area – open areas and shrubby cover or areas with high vegetation which do not allow spotlight observation – for faecal pellet counts). In addition, since feeding activity stimulates drop production, the faecal pellet count used to determine the use of the habitat type endorses the feeding habitats while spotlight census used to determine the use of the habitat type endorses the open areas used during early night. However, the two lagomorph populations showed a great habitat overlap, as observed also in a telemetric study carried out in a Mediterranean climatic zone of Australia (Stott 2003).

Regarding spotlight observation, the lower use of vineyards than availability by Brown hares during the winter spotlight counts may be strictly related to the seasonal crops’ vegetative stage. In winter, the arable crops present in the study area mainly consist of sprouting cereals or overwintering stubbles which offer food of high nutritive value (Reichlin et al. 2006; Zaccaroni et al. 2008). Brown hares seem to prefer more open habitat as arable crops or they are simply less selective than European rabbits. On the contrary, European rabbits avoid arable crops and prefer permanent crops such as olive tree groves that offer more protection from avian predators.

Regarding the indirect surveys carried out using faecal pellet counts, hares seem to avoid uncultivated fields. Uncultivated fields may be good resting sites for Brown hares when they are formed by small patches among crop fields (Zaccaroni et al. 2008; Neumann et al. 2011). But in this case they are represented by a large block formed by a mix of shrubby and herbaceous cover that reduces habitat heterogeneity. On the contrary, this habitat with olive tree groves and hedgerows meets the needs of the European rabbits, which have no need for large open areas, and provides a favourable combination of food availability and refuge from predators (Beltran 1991; Moreno et al. 1996; Deliafiore et al. 2008; Serrano Pérez et al. 2008; Santilli & Bagliacca 2010). Brown hares and European rabbits, in our study area, tended to live in sympathy in olive tree groves and hedgerows.

However, European rabbits seem to live at a shorter distance from permanent cover such as hedgerows and woods where they have burrows. European rabbits are relatively slow and vulnerable in open habitat and they require easy access to cover where the burrows are located, whereas Brown hares use long zigzagging flights to escape predators and are less vulnerable in open areas.

The differences found in habitat use have probably enabled the two species to coexist, as observed also for Brown hare and Cottontail (Sylvilagus floridanus) in north Italy (Vidus-Rosin et al. 2009; Bertolino et al. 2011). The diets of European rabbits and Brown hares, when studied in the same locations, are remarkably similar (Homolka 1987; Chapuis 1990; Katona et al. 2004), suggesting that the species can coexist by avoiding competition in spatial use or because their home range size differs.

Local hunters report that in the past (30–40 years ago) Brown hares and European rabbits were equally abundant in the area. This observation suggests that
habitat transformation that happened in the last few decades has hampered Brown hare populations more than European rabbit populations. Brown hares have declined throughout Europe and Italy since the 1960s (Smith et al. 2005; Santilli & Galardi 2006). However, we cannot exclude the possibility that Brown hare abundance was influenced by European rabbits through a non-investigated mechanism. Flux (1993) stated that competition between Brown hares and European rabbits includes a combination of factors, such as food competition, European rabbit parasites or simple aggressive behaviour. Graphidium strigosum is an original parasite of European rabbits that could harm Brown hares where European rabbits are abundant (Broekhuizen 1975). During our study, we observed European rabbits and Brown hares grazing within a few meters of each other and no aggressive behaviour between the two species was recorded. This observation suggests that behavioural antagonism is absent or negligible at these population densities. An increase in the incidence of the habitats which were demonstrated to be used more by only one of the two species, or an increase in the incidence of the habitats which were demonstrated to be used by both species, could be used to manage these lagomorphs. A longer monitoring of the two populations will help to clarify the interactions of the two species at different density levels.

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