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Daytime Habitat Selection by Introduced Eastern Cottontail *Sylvilagus floridanus* and Native European Hare *Lepus europaeus* in Northern Italy

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We used radiotelemetry to investigate resting sites habitat selection by introduced eastern cottontail (*Sylvilagus floridanus*) and native European hare (*Lepus europaeus*) under sympatric conditions. We tracked 24 hares and 34 cottontails in a protected area of northwestern Italy. Hares were found in different sites every week, while cottontails used the same site for two weeks, and occasionally for longer. It is supposed that this periodic nest switching reduces the risk of predation and parasitism. Hares and cottontails forms were located in different habitats and characterized by dense vegetation cover near the ground. This cover increased from winter to summer in both species, while in autumn it continued to increase in cottontails only, and decreased in hares. Cottontails selected shrubby habitats near the river, and avoided crop fields in all seasons. Hares were more adaptive in their search, using high herbs and shrubs all year round, wheat fields in spring, maize in spring and summer, and stubbles in winter. Arguably, partial niche differentiation is necessary to allow the coexistence of similar species. In our study area, hares and cottontails differentiated in the use of resting sites habitats, presumably so as not to compete in this part of their ecological niche.

Key words: forms, habitat partitioning, introduced species, resting sites, vegetation cover

INTRODUCTION

The coexistence of potentially competing species is made possible by niche differentiation in diet, habitat selection, and activity pattern (Rosenzweig, 1981; Brown et al., 1994). Segregation in habitat use should involve the selection of different feeding and resting sites. Daytime refuges are important resources for the survival of nocturnal mammals, providing them with protection from environmental conditions and predators, and security for their offspring. Thus, the availability of such refuges may be a limiting factor affecting the distribution and status of populations (Dooley and Dueser, 1990).

The introduction of species into an ecosystem could interfere with this mechanism of resource sharing and lead to competition among species (Sidorovich et al., 1999; Gurnell et al., 2004). This happens because niche partitioning is the result of selective processes acting on species that have coexisted for long periods. Human-mediated introductions break down spatial, ecological, and biological barriers, changing community compositions and modifying previous competitive equilibria (Olden et al., 2004).

The eastern cottontail (*Sylvilagus floridanus*) is a lagomorph native to North America that was introduced into Italy

for hunting purposes in the early 1960s (Mussa et al., 1996). The main populations are found in the northwestern regions of the country, where the European hare (*Lepus europaeus*) is the only native lagomorph present in the lowlands (Silvano et al., 2000; Vidus-Rosin et al., 2008). In this area, dominated by intensive agriculture, hare populations are often at low densities, as a result of habitat degradation, diseases, and over-hunting (Spagnesi and Trocchi, 2002). Possible negative interaction between these two lagomorphs has been assumed, although early results suggest that the two species can coexist (Vidus-Rosin et al., 2009; Bertolino et al., 2011a). The cottontail is also a possible vector of diseases that can be transmitted to native lagomorphs (Tizzani et al., 2002). For instance, imported cottontails introduced to Italy have introduced several species of protozoan intestinal parasites of North American origin (Bertolino et al., 2010).

Hares are generally inactive during the day when they rest, crouched on the ground, in sites called forms that provide protection from unfavorable weather conditions and predators (Angelici et al., 1999; Jennings et al., 2006; Pépin and Angibault, 2007). The cottontail has apparently similar requirements; optimal habitats for this species have to include open foraging areas such as grasslands and pastures, and an abundance of dense shrubs or other escape cover (Allen, 1984; Althoff et al., 1997; Vidus-Rosin et al., 2010; Bertolino et al., 2011b).

The availability of suitable diurnal resting sites is thought to have an impact on hare populations (Smith et al., 2004).

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Therefore, in areas where the cottontail is expanding and reaching high densities (Silvano et al., 2000; Vidus-Rosin et al., 2008, 2009; Bertolino et al., 2011a), competition for resting places may influence the fitness of individuals and, in the long-term, the status of the native species. To describe the characteristics of the areas used by these two lagomorphs, such as their daily resting places, is thus important to investigating the possible mechanisms of coexistence and/or competition between them. Accordingly, we used radiotelemetry to investigate resting sites habitat selection by cottontail and hare under sympatric conditions. The main aim of the study was to determine the characteristics of the vegetation around their resting places by comparing the habitats used by the two species. Considering that vegetation cover around the forms is probably meant to provide protection from predators and adverse weather conditions (Althoff et al., 1997; Bond et al., 2002; Smith et al., 2004), we predicted that both species selected similar microhabitats with high vegetation cover. As a consequence, to avoid competition for resting sites, they were supposed to occupy different macrohabitats.

MATERIALS AND METHODS

Study area

The study area was located on the right bank of the Orba river (northwestern Italy, 44°49'N, 8°40'E), inside a natural reserve and the adjacent game reserve, where hunting was prohibited. Moving away from the river, the landscape was composed of a narrow shore, a small woodland (3 ha), and a shrubby area, then a field with spontaneous vegetation and a mosaic of meadows, field crops, and a few poplar plantations (Fig. 1). The shore was partially covered by shrubs and low trees, mainly willows (*Salix* spp.) and poplars (*Populus* spp.). The woodland was mainly composed of black

locust (*Robinia pseudoacacia*) and common oak (*Quercus robur*), with a rich understory of hawthorn (*Crataegus monogyna*), black elderberry (*Sambucus nigra*), and common buckthorn (*Rhamnus cathartica*). The shrubby area was a thick stripe of *Rubus* spp. and *Rosa* spp. with few trees. Crop fields were cultivated with wheat, maize, sunflower, and beet under a rotation system.

Capturing and radiotracking

Cottontails were captured every two months from December 2004 to October 2005. Cage traps (single catch, double entry, spring door traps, 100 × 40 × 40 cm Gibis, France) were set in the field and baited with carrots and lettuce. They were checked twice a day, at sunset and after dawn. Since hares did not enter the traps, we used static nets to capture them: 10–30 beaters flushed hares from the cover into nets that had been set along the escape routes.

Handling procedures consisted of sexing, weighing, measuring hind-foot length, and marking the animals with ear-tags (a Monel No 3, National Band and Tag Co., USA and a rabbit colored tag with number). Adult animals were fitted with a radio collar (MI-2M, Holohil Systems Ltd., Canada) of 25 g, with a mortality motion sensor. Our aim was to continuously monitor 10–15 animals per species for one year. Animals lost to predation or for other reasons were replaced by other individuals in the following trapping sessions.

Re-locations of animals started two days after their release. The animals were tracked on foot using a Custom (Electronics of Urbana Inc., Model CE 12) receiver and a hand-held 4-element Yagi antenna (Biotrack). Animals were located 3–4 nights a week during their nocturnal activity by means of a triangulation method (Kenward, 2001). We used these fixes to evaluate home range areas with the 100% minimum convex polygon method, using Ranges 7 software (South et al., 2005). Once a week, we used the homing-in technique (Kenward, 2001) to locate the resting sites during the day. Every site was marked and geo-referenced by means of Garmin II Plus GPS.

Trapping and handling of cottontails and hares complied with the Italian laws on animal research, and were carried out under the permission of Regione Piemonte.

Habitat selection

Resting sites habitat selection was evaluated at two spatial scales: at the macrohabitat level, we considered the habitat types selected by the animals in relation to their availability in the study area; at the microhabitat level we considered the structure and the cover of the vegetation around the form.

Selection at the macrohabitat level was evaluated considering the proportion of the occurrence of hare and cottontail forms in each habitat type (habitat use). We calculated a resource selection function (Manly et al., 2002) using the proportional habitat composition in the study area as a measure of habitat availability. The area available for each species was computed as the minimum convex polygon containing all the home-ranges of the animals sampled for that species (Fig.

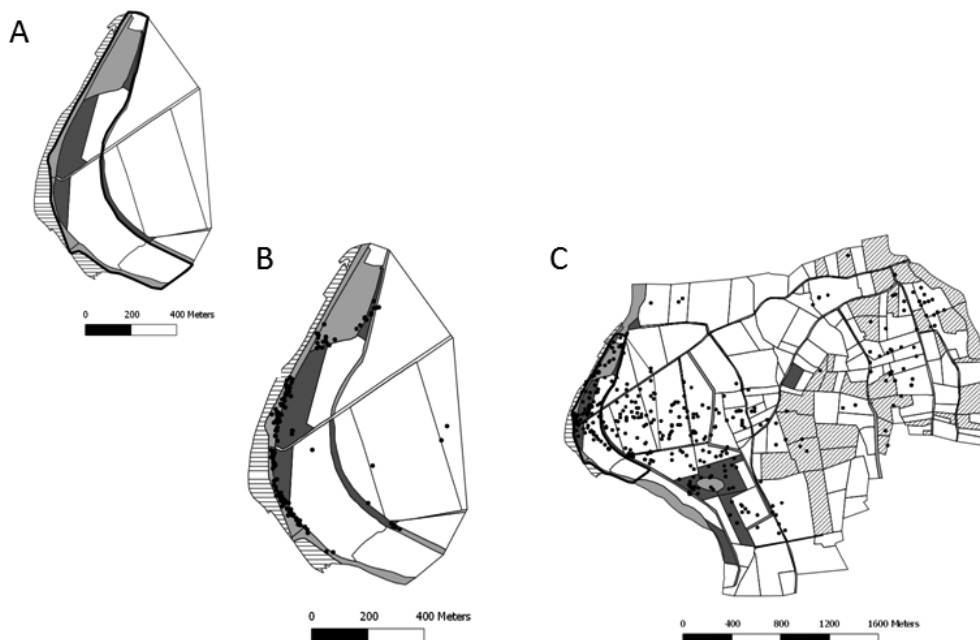


Fig. 1. Areas used by radiotracked cottontails (*Sylvilagus floridanus*), (B) and hares (*Lepus europaeus*), (C); the continuous black line in map (A) indicates the boundary of the area where cottontails and hares were captured. The black dots indicate the resting site localizations for the two species. Horizontal lines: shores; light grey: woody habitats (woodlands, shrubs and hedgerows); dark grey: spontaneous vegetation; diagonal lines: meadows; white: crop fields.

1). The selection ratio (w_i) for each habitat type was expressed as:

$$w_i = \text{proportion used}_i / \text{proportion available}_i$$

The index could range from 0 (maximum negative selection) to infinity (maximum positive selection), with 1 indicating the value expected in absence of selection. The statistical significance of the results was tested by comparing the following statistic

$$S = (w_i - 1)^2 / \text{se}(w_i)^2$$

with the corresponding critical value of a chi-square distribution with one degree of freedom. The standard error of the index was calculated as:

$$\sqrt{(1 - p_i) / (u_+ * p_i)}$$

where u_+ is the total number of forms sampled. The null hypothesis that hares and cottontails selected resting habitats in proportion to their availability was assumed (Manly et al., 2002). This index was chosen because it allows for more accurate statistical comparisons (Atienza, 1994; Manly et al., 2002). We applied the Bonferroni correction for the number of statistical tests (habitat types) to correct the level of significance (Rice, 1989).

We used a 1:10000 digital map of land cover (edited by Regione Piemonte and Istituto per le Piante da Legno e l'Ambiente) imported into ArcView 3.1 GIS software (ESRI - Environmental Systems Research Institute, California) to determine habitat variables. These were the proportion of the area available to each species and covered by woods, shrubs, spontaneous vegetation, meadows, shores, poplar plantations, wheat, maize, beets, sunflowers, ploughed areas, stubbles, and dirty tracks. During daytime surveys, the proportion of farmland devoted to different crops, stubble, and ploughed areas were recorded. The data were then used to update the seasonal land cover maps of the areas available to the species and make them more detailed through the digitization of these new categories.

At the microhabitat level, vegetation cover around the forms was measured using the procedure proposed by Althoff et al. (1997). The coverage of the vegetation was estimated using a 1.5 m high and 10 cm wide density board (Nudds, 1977). This was divided into 6 horizontal sections, each being 25 cm high and colored alternately black and white. The board was placed horizontally and vertically, always with an end within the form, and observed through the vegetation cover. The percentage of each board section overlapping the vegetation cover was assessed as: 1 = 0–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; 5 = 81–100%. To facilitate the measurement of the plant cover, each section was further divided into 10 (5 by 2) squares of 5 × 5 cm. In each form, the board was observed vertically and horizontally from 2 out of 8 possible directions (cardinal and intermediate directions), which were randomly selected. The vertical and horizontal density scores for the six sections were computed as the mean of the two measurements.

Data analyses

A form fidelity index was calculated for every animal as the ratio between the number of forms changed during the radiotracking period and the highest possible number of changes (amounting to the number of weeks of radiotracking minus 1) (Bertolino and Cordero di Montezemolo, 2007). A

form fidelity value of 1 meant that lagomorphs changed form every week, while 0 meant that only one form had been used.

Differences by sex in the mean distance between the forms that were consecutively used by the same animal were evaluated by means of the *t*-test, after transforming the data using the square root to normalize them (Zar, 1996). Vegetation density scores were typically skewed and could not be normalized with common transformations. We thus used non-parametric tests, comparing the values between the two species with the Mann-Whitney test and among seasons with the Kruskal-Wallis ANOVA. When the differences in vegetation cover among seasons were significant, the Mann-Whitney test was used to compare the value of each season with that of the previous season. The significance level was corrected with Bonferroni. All statistical analyses were performed with SPSS v 13.0.1 (SPSS, 2001).

RESULTS

A total of 24 hares and 34 cottontails were fitted with radio collars. In 2005 we followed a seasonal average of 9.8 ± 1.7 hares and 16.3 ± 2.8 cottontails.

We located 227 different cottontails' forms that were used from one to nine consecutive weeks (females mean 3.3 ± 2.4 weeks, males mean 2.6 ± 1.9 weeks). Mean site fidelity index was 0.43 ± 0.23 (males 0.46 ± 0.19 , females 0.40 ± 0.26), indicating a form switching occurring every two weeks. The mean distance between forms consecutively used by the same animal was similar in males (41.5 ± 80.3 m) and

Table 1. Resting sites habitat selection (selection ratio: w_i) by cottontails (*Sylvilagus floridanus*) and hares (*Lepus europaeus*). Habitat availability (Avail.) changed according to seasons and species. After Bonferroni corrections *P*-values were significant at 0.004 for hares and 0.005 for cottontails. ++ used at $P < 0.001$; -- avoided at $P < 0.001$; ~ avoided at $P < 0.005$.

Habitat	Winter		Spring		Summer		Autumn	
	Avail.	w_i	Avail.	w_i	Avail.	w_i	Avail.	w_i
<i>Sylvilagus floridanus</i>								
Woodlands	5.14	1.95	5.14	0.38	5.14	0.00	5.14	0.00
Shrubs	6.47	++13.70	6.47	++14.12	6.47	++12.15	6.47	++15.31
Shores	6.93	0.00	6.93	0.00	6.93	0.72	6.93	0.00
Spontaneous veg.	8.16	0.00	8.16	0.22	8.16	0.64	8.16	0.00
Wheat	43.21	--0.00	43.21	--0.13				
Maize			12.30	--0.00	56.02	--0.11		
Beets			16.67	--0.00	4.25	0.70		
Stubbles					11.91	0.00	11.91	0.00
Ploughed	28.97	--0.00					60.27	--0.00
Dirty tracks	1.12	0.00	1.12	0.00	1.12	0.00	1.12	0.00
<i>Lepus europeaus</i>								
Woodlands	0.89	1.04	0.89	0.75	0.89	0.00	0.89	++12.51
Shrubs	3.38	++7.94	3.38	++4.57	3.38	0.94	3.38	++6.62
Shores	0.82	++15.8	0.82	++10.61	0.82	++7.78	0.82	0.00
Spontaneous veg.	4.11	++2.70	4.18	++2.73	4.18	++2.80	4.18	++6.96
Meadows	18.30	--0.10	18.30	0.99	18.30	0.55	18.30	--0.00
Poplar	1.55	0.00	1.55	0.00	1.55	0.00	1.55	0.00
Wheat	17.40	1.43	17.36	++1.70			25.63	--0.00
Maize			27.96	++0.43	27.85	++1.72		
Beets			14.39	--0.14	14.39	--0.07		
Sunflowers			4.52	0.45	9.13	0.87		
Stubbles	10.34	0.36			16.04	0.73	10.76	++2.54
Ploughed	40.98	--0.43	4.42	0.00	1.24	0.00	32.26	0.32
Dirty tracks	2.23	0.00	2.23	0.00	2.23	0.00	2.23	0.00

females (27.7 ± 22.6 m; $t_{192} = -0.03$, $P = 0.10$).

Hares used a total of 384 forms and only in 10 cases the animals were found in the same form they had used during the previous week; thus, the site fidelity index was close to 1 (males 0.95 ± 0.08 , females 0.97 ± 0.04). The mean distance between forms used by the same animal did not differ between males (314 ± 474 m) and females (285 ± 247 m; $t_{352} = -1.40$, $P = 0.07$).

The area used by cottontails covered a surface of 71 ha (Fig. 1), with 26.7% of it consisting of natural habitats and 72.2% of field crops (Table 1). Animals located their forms mainly in shrubby habitats in all seasons, avoiding field crops and using woodlands, shores, and spontaneous vegetation proportionately to their availability. Likewise, the home ranges of all radio-tracked hares covered an area of 619 ha (Fig. 1), with 27.5% of it consisting of natural habitats (18.3% of meadows and 9.2% of woodlands, shrubby habitats, shores and spontaneous vegetation) and 70.3% of field crops (Table 1). Hares located their resting sites in a wide range of habitats. Natural habitats (spontaneous vegetation, shores and shrubby habitats) were selected year round, while crop fields were used on a seasonal basis (Table 1): wheat was important in spring, maize in spring as well as summer, and stubbles in autumn.

The resting places of cottontails were located in areas with dense vegetation cover that, however, was characterized by different patterns (Table 2). The height of the cover around the forms peaked in summer and autumn, covering over 80% of the first 75 cm in high and of the first 1.5 m in width. In winter cover densities around forms were reduced by 0.7–2.5 points at different vertical and horizontal sections, while spring values were similar to those of the previous season.

Hares forms were found in sites with dense vegetation cover too (Table 2). Mean values of vertical and horizontal cover increased from winter to summer and decreased in autumn, with a significant seasonal change in coverage. In spring and summer the vertical coverage of the vegetation was over 80% in the first 50 and 75 cm, respectively, while horizontally the density board was completely covered in these seasons. In autumn and winter the first 50 cm around the forms were covered only for 40–80%.

Overall, forms of hares and cottontails were associated with a similarly high cover in summer (Table 3). However, cottontails selected sites with higher coverage in autumn and winter, while hares selected more protected sites in spring.

Table 2. Seasonal variation in vertical and horizontal cover (mean \pm SD) on forms used by cottontails and hares. Comparisons between seasons were conducted with the Kruskal-Wallis ANOVA test. The symbol ^a indicates a significantly different cover for the same board section compared to the previous season (Mann-Whitney test with Bonferroni correction, P -values significant at 0.013). $P < 0.01^*$, $P < 0.005^{**}$, $P < 0.001^{***}$.

Distance interval (m)	Winter	Spring	Summer	Autumn	Kruskal-Wallis ANOVA (H)
<i>Sylvilagus floridanus</i>					
Vertical cover					
0.00–0.25	3.99 ± 1.30^a	4.03 ± 1.19	4.71 ± 0.84^a	4.99 ± 0.07^a	48.46***
0.25–0.50	3.30 ± 1.37^a	3.55 ± 1.39	4.66 ± 0.85^a	4.85 ± 0.72	73.19***
0.50–0.75	2.24 ± 1.37^a	3.01 ± 1.83	4.34 ± 1.32^a	4.50 ± 1.15	79.56***
0.75–1.00	1.35 ± 1.23^a	2.29 ± 1.73^a	2.58 ± 1.60	2.92 ± 1.89	27.23***
1.00–1.25	0.96 ± 0.98^a	1.11 ± 1.06	1.42 ± 0.95	1.88 ± 1.74	11.24*
1.25–1.50	0.56 ± 0.79^a	0.91 ± 1.02	1.37 ± 0.94^a	1.33 ± 1.46	26.80***
Horizontal cover					
0.00–0.25	2.49 ± 1.86^a	2.80 ± 1.96	4.61 ± 1.13^a	4.98 ± 0.13^a	86.14***
0.25–0.50	2.53 ± 1.68^a	3.07 ± 1.69	4.58 ± 1.15^a	4.95 ± 0.22	92.27***
0.50–0.75	2.92 ± 1.41^a	3.30 ± 1.46	4.55 ± 1.16^a	4.91 ± 0.39	91.21***
0.75–1.00	3.19 ± 1.27^a	3.61 ± 1.33	4.45 ± 1.29^a	4.59 ± 1.11	59.10***
1.00–1.25	3.46 ± 1.31^a	3.96 ± 1.20	4.39 ± 1.39	4.45 ± 1.33	38.41***
1.25–1.50	3.59 ± 1.47^a	4.16 ± 1.09	4.34 ± 1.38	4.25 ± 1.43	19.42***
<i>Lepus europaeus</i>					
Vertical cover					
0.00–0.25	3.65 ± 1.39	4.56 ± 0.88^a	4.77 ± 0.60	3.85 ± 1.22^a	64.31***
0.25–0.50	2.23 ± 2.22^a	4.08 ± 1.43^a	4.56 ± 1.01^a	3.41 ± 1.28^a	82.64***
0.50–0.75	1.64 ± 1.99^a	2.97 ± 1.91^a	4.01 ± 1.59^a	2.35 ± 1.78^a	71.36***
0.75–1.00	1.21 ± 1.80	1.94 ± 1.97^a	3.53 ± 2.01^a	1.56 ± 1.97^a	63.39***
1.00–1.25	0.95 ± 1.68	1.19 ± 1.84	3.05 ± 2.22^a	1.11 ± 1.91^a	60.65***
1.25–1.50	0.76 ± 1.55	0.91 ± 1.66	2.81 ± 2.38^a	1.00 ± 1.86^a	56.08***
Horizontal cover					
0.00–0.25	2.36 ± 2.38	4.02 ± 1.55^a	4.54 ± 0.96^a	3.03 ± 1.62^a	62.96***
0.25–0.50	2.21 ± 2.34	4.28 ± 1.32^a	4.62 ± 0.80	2.96 ± 1.76^a	79.00***
0.50–0.75	2.03 ± 2.28^a	4.21 ± 1.34^a	4.55 ± 0.99	2.95 ± 1.77^a	93.34***
0.75–1.00	1.91 ± 2.20^a	4.11 ± 1.49^a	4.57 ± 0.99	2.81 ± 1.84^a	101.59***
1.00–1.25	1.82 ± 2.22^a	4.01 ± 1.58^a	4.56 ± 0.97^a	2.76 ± 1.85^a	98.82***
1.25–1.50	1.76 ± 2.17^a	3.96 ± 1.67^a	4.49 ± 1.15	2.60 ± 1.93^a	101.10***

Table 3. Results of statistical tests (Mann-Whitney) comparing vertical and horizontal covers on forms used by cottontails and hares. Cover values are reported in Table 2. $P < 0.01^*$, $P < 0.005^{**}$, $P < 0.001^{***}$, NS = not significant.

Distance interval (m)	Winter	Spring	Summer	Autumn
Vertical cover				
0.00–0.25	NS	**	NS	***
0.25–0.50	***	NS	NS	***
0.50–0.75	**	NS	NS	***
0.75–1.00	*	NS	*	***
1.00–1.25	*	NS	**	***
1.25–1.50	NS	**	NS	*
Horizontal cover				
0.00–0.25	NS	***	NS	***
0.25–0.50	NS	***	NS	***
0.50–0.75	**	***	NS	***
0.75–1.00	***	**	NS	***
1.00–1.25	***	NS	NS	***
1.25–1.50	***	NS	NS	***

DISCUSSION

Forms of cottontails and hares were characterized by dense vegetation near the ground. The two species, however, used different habitats and chose sites with different vegetation cover for most of the year. Cottontails selected shrubby habitats near the river, and avoided crop fields in all seasons. This strip of land was adjacent to spontaneous vegetation, and close to maize and wheat fields. A preference for shrublands is consistent with the results of studies conducted in North America (Morgan and Gates, 1983; Althoff et al., 1997; Bond et al., 2002). Cottontails usually search for areas with dense shrubs or other escape cover, near open foraging areas such as grasslands and pastures (Allen, 1984). It has been noted that a mixture of these habitats can also ensure a variety of microclimates throughout the year and provide shelters and food (Swihart and Yahner, 1982; Althoff et al., 1997). In their native range, however, cottontails seems to be more adaptive, and select grasslands and old fields (Trent and Rongstad, 1974; Althoff et al., 1997; Bond et al., 2002), shrubby areas (Althoff et al., 1997) and croplands (Mankin and Warner, 1999), in the light also of landscape composition and local climate.

Hares were more adaptive in their search for resting sites. Natural habitats with high herbs and shrubs were used all year round, but animals also used crop fields on a seasonal basis, when plants had grown. Wheat fields were selected in spring, maize in spring and summer, while in winter hares were also found in stubble fields. A change in day-time habitat selection through the year was already reported in hares (Pépin, 1985; Pépin and Angibault, 2007), which may help to explain the increase of hare density in areas with a mixed abundance of winter crops, spontaneous vegetation, and other habitats that provide cover all year round (Hutchings and Harris, 1996; Vaughan et al., 2003).

The form cover increased from winter to summer in both species, while in autumn it continued to increase in cottontails only, and decreased in hares. Dense vegetation around the form may provide protection from avian predators and adverse weather conditions (Althoff et al., 1997; Bond et al., 2002). These habitats are particularly critical for the survival of both adults and litters in late winter and early spring (Althoff et al., 1997; Jennings et al., 2006). Smith et al. (2004) found that hares selected habitats with taller vegetation in spring and summer. To search for microhabitats with denser cover in summer may be explained by the insulating effect of the vegetation that reduces the heat load and by associated detrimental effects (Althoff et al., 1997). Cottontails searched for more protected sites than did hares in autumn and winter, probably so as to reduce heat loss in unfavorable seasons (Bond et al., 2002).

Hares were found in different sites every week, while cottontails generally changed site every two weeks and occasionally used the same form for up to two months. Radiotracked hares followed by Angelici et al. (1999) showed a similar degree of mobility, using each form for 3–4 days only. Periodic nest switching is thought to reduce the risk of predation and parasitism. This behaviour may be an adaptive strategy to avoid scent accumulation that could attract predators (Banks et al., 2002) and to reduce the risk of ectoparasite accumulation (Roper et al., 2002).

A partial niche differentiation is necessary to make the coexistence of similar species possible. Here, we compared the selected habitats and the vegetation cover of the sites used as daytime refuges by native hares and introduced cottontails. The two species searched for sites with high vegetation cover, but differed in their habitat selection. Cottontails restricted to shrubby habitats while hares used natural areas and crop fields according to the season. Ultimately, in our study area, the two species differentiated in the use of resting sites habitats, probably so as not to compete in this part of their ecological niche.

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REFERENCES

- Allen AW (1984) Habitat suitability index models: eastern cottontail. FWS/OBS 0197-6087. U.S. Department of the Interior, Fish and Wildlife Service, Division of Biological Sciences, Western Energy Land Use Team, Washington
- Althoff DP, Storm GL, Dewalle DR (1997) Daytime habitat selection by cottontails in central Pennsylvania. *J Wildl Manage* 61: 450–459
- Angelici FM, Spagnesi M (2008) *Sylvilagus floridanus* (JA Allen, 1890). In "Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. Fauna d'Italia Vol. XLIV" Ed by G Amori, L Contoli, A Nappi, Edizioni Calderini e Il Sole 24 Ore, Milano, pp 305–313
- Atienza JC (1994) La utilización de índices en el estudio de la selección de recursos. *Ardeola* 41: 173–175
- Banks PB, Norrdhal K, Korpimäki E (2002) Mobility decisions and the predation risks of reintroduction. *Biol Cons* 103: 133–138
- Bertolino S, Cordero di Montezemolo N (2007) Garden dormouse (*Eliomys quercinus*) nest site selection in an alpine habitat. *Ethol Ecol Evol* 19: 51–60
- Bertolino S, Hofmannova L, Girardello M, Modry D (2010) Richness, origin and structure of an *Eimeria* community in a population of Eastern cottontail (*Sylvilagus floridanus*) introduced into Italy. *Parasitology* 137: 1179–1186
- Bertolino S, Perrone A, Gola L, Viterbi R (2011a) Population density and habitat use of introduced eastern cottontail (*Sylvilagus floridanus*) in comparison with the native European hare (*Lepus europaeus*). *Zool Stud* 50: 315–326
- Bertolino S, Ingegno B, Girardello M (2011b) Modelling the habitat requirements of invasive Eastern cottontail (*Sylvilagus floridanus*) introduced to Italy. *Eur J Wildl Res* 57: 267–274
- Bond BT, Burger Jr LW, Leopold BD, Jones JC, Godwin KD (2002) Habitat use by cottontail rabbits across multiple spatial scales in Mississippi. *J Wildl Manag* 66: 1171–1178
- Brown JS, Kotler BP, Mitchell WA (1994) Foraging theory, patch use and the structure of a Negev desert granivore community. *Ecology* 75: 2286–2300
- Dooley JL, Dueser RD (1990) An experimental examination of nest-site segregation by two *Peromyscus* species. *Ecology* 71: 788–796
- Gurnell J, Wauters LA, Lurz PWW, Tosi G (2004) Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *J Anim Ecol* 73: 26–35

- Hutchings MR, Harris S (1996) The current status of the brown hare (*Lepus europaeus*) in Britain. Joint Nature Conservation Committee, England
- Jennings NV, Smith RK, Hackländer K, Harris S, White PCL (2006) Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high-density and low-density populations. *Wildl Biol* 12: 179–189
- Kenward RE (2001) A manual for wildlife radio tagging. Academic Press, London
- Mankin PC, Warner RE (1999) Responses of eastern cottontails to intensive row-crop farming. *J Mammal* 80: 940–949
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource Selection by Animals. Kluwer Academic Publishers, The Netherlands
- Morgan KA, Gates JE (1983) Use of forests edge and strip vegetation by eastern cottontails. *J Wildl Manag* 47: 259–264
- Mussa PP, Meineri G, Bassano B (1996) Il Silvilago in Provincia di Torino. *Habitat* 61: 5–11
- Nudds TD (1977) Quantifying the vegetative structure of wildlife cover. *Wildl Soc Bull* 5: 113–117
- Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol Evol* 19: 18–24
- Pépin D (1985) Spring density and daytime distribution of the European hare in relation to habitat in an open field agrosystem. *Z Säugetierkunde* 51: 79–86
- Pépin D, Angibault JM (2007) Selection of resting sites by the European hare as related to habitat characteristics during agricultural changes. *Eur J Wildl Res* 53: 183–189
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43: 223–225
- Roper TJ, Jackson TP, Conradt L, Bennett NC (2002) Burrow use and the influence of ectoparasites in Brants' whistling rat *Parotomys brantsii*. *Ethology* 108: 557–564
- Rosenzweig ML (1981) A theory of habitat selection. *Ecology* 62: 327–335
- Sidorovich V, Kruuk H, Macdonald DW (1999) Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. *J Zool* 248: 521–527
- Silvano F, Acquarone C, Cucco M (2000) Distribution of the Eastern Cottontail (*Sylvilagus floridanus*) in the province of Alessandria. *Hystrix It J Mamm* 12: 75–78
- Smith RK, Jennings NV, Robinson A, Harris S (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *J Appl Ecol* 41: 1092–1102
- South AB, Kenward RE, Walls SS (2005) Ranges 7 v 1.0 for the analysis of tracking and location data. Anatrack, Wareham, England
- Spagnesi M, Trocchi V (2002) Lepre comune o europea *Lepus europaeus* Pallas, 1778. In "Mammiferi d'Italia" Ed by M Spagnesi, AM De Marinis, Quaderni Conservazione Natura 14, Ministero Ambiente, Istituto Nazionale per la Fauna Selvatica, Roma, pp 146–148
- SPSS (2001) SPSS for Windows, Release 13.0.1. SPSS Inc., Chicago, Illinois
- Swihart RK, Yahner RH (1982) Habitat feature influencing use of farmstead shelterbelts by the eastern cottontail *Sylvilagus floridanus*. *Am Midl Nat* 107: 411–414
- Tizzani P, Lavazza A, Capucci L, Meneguz PG (2002) Presence of infectious agents and parasites in wild populations of cottontail (*Sylvilagus floridanus*) and consideration on its role in the diffusion of pathogens infecting hares. European Association of Zoo- and Wildlife Veterinarians (EAZWV) 4th scientific meeting, joint with the annual meeting of the European Wildlife Disease Association (EWDA), Heidelberg, Germany
- Trent TT, Rongstad OS (1974) Home range and survival of cottontail rabbits in southwestern Wisconsin. *J Wildl Manage* 38: 459–472
- Vaughan N, Lucas, EA, Harris S, White PCL (2003) Habitat associations of European hares *Lepus europaeus* in England and Wales: implications for farmland management. *J Appl Ecol* 40: 163–175
- Vidus-Rosin A, Gilio N, Meriggi A (2008) Introduced Lagomorphs as a threat to "native" Lagomorphs: The case of the Eastern cottontail (*Sylvilagus floridanus*) in northern Italy. In "Lagomorph Biology. Evolution, Ecology and Conservation" Ed by PC Alves, N Ferrand, H Hackländer, Springer-Verlag, Berlin, Heidelberg, pp 153–165
- Vidus-Rosin A, Montagna A, Meriggi A, Serrano Perez S (2009) Density and habitat requirements of sympatric hares and cottontails in northern Italy. *Hystrix It J Mamm* 20: 101–110
- Vidus-Rosin A, Meriggi A, Serrano Perez S (2010) Density and habitat requirements of introduced Eastern cottontail *Sylvilagus floridanus* in northern Italy. *Acta Theriol* 55: 139–151
- Zar JH (1996) Biostatistical analysis. Prentice Hall, New Jersey

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