

## Population Density and Habitat Use of the Introduced Eastern Cottontail (*Sylvilagus floridanus*) Compared to the Native European Hare (*Lepus europaeus*)

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**Sandro Bertolino, Aurelio Perrone, Laura Gola, and Ramona Viterbi (2011)** Population density and habitat use of the introduced eastern cottontail (*Sylvilagus floridanus*) compared to the native European hare (*Lepus europaeus*). *Zoological Studies* 50(3): 315-326. We summarized the distribution of the eastern cottontail (*Sylvilagus floridanus*) introduced into Italy and documented population densities of and habitat selection by the species compared to the native European hare (*Lepus europaeus*). The cottontail is presently in a large area in the northwestern part of the country, and there are other small populations in the northeastern and central parts. Cottontails were present in 13 surveyed areas with good populations, while hares were common in only some of them. Cottontails and hares partially differentiated the habitats they used as daily resting sites and during feeding activities. Natural herbaceous vegetation was used as resting sites by both species, but they differed in the use of shores by hares and shrubby areas by cottontails. During feeding, cottontails were found in natural herbaceous vegetation, poplar plantations, meadows, and stubble fields, usually close to shelter which may be used as refuge. Hares were mainly observed in open fields, such as meadows, winter crops, and natural herbaceous vegetation, but at  $\geq 50$  m from refuges. Our results suggest that the coexistence of the 2 species is mediated by a partial separation of spatial niches. <http://zoolstud.sinica.edu.tw/Journals/50.3/315.pdf>

**Key words:** Coexistence, Competition, Italy, Lagomorph, Resource partitioning.

Intentional release is the main vector of mammal introductions into Europe, while escaping is the 2nd (Genovesi et al. 2008, Hulme et al. 2008). Considering activities related to invasions by alien mammals, hunting accounts for 21% of the 266 known cases (Genovesi et al. 2008). Many of these introduced species were intentionally imported and released into the wild by private and hunting associations, and sometimes also by game and wildlife management agencies (Long 2003, Bertolino 2009). With recently increasing awareness about the threats entailed by biological invasions, many national laws and

international agreements either ban or discourage new introductions. Accordingly, most managers realize that the introduction of mammals is no longer regarded as appropriate (Bertolino 2009). However, many species are already established in Europe, sometimes with very large ranges and impacts (Bertolino 2008, Genovesi et al. 2008).

The eastern cottontail (*Sylvilagus floridanus*) is a lagomorph native to the American continent that was introduced into some European countries for hunting purposes, but in recent times, wild populations have only survived in Italy (DAISIE 2008). The 1st introduction into the country dates

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back to 1966 (Mussa et al. 1996); this species was then introduced many other times, but data on these releases are not available (Angelici and Spagnesi 2008).

Research conducted in captivity and in enclosures in France highlighted the risks of crop damage and possible space and food competition with other lagomorphs (Arthur and Chapuis 1983, Chapuis et al. 1985). The cottontail is also a possible vector of diseases that can be transmitted to native lagomorphs (Tizzani et al. 2002). Imported cottontails introduced to Italy also carried 7 species of *Eimeria*, a genus of protozoan intestinal parasite, of North American origin (Bertolino et al. 2010). For these reasons, the Council of Europe recommended the eradication, either actively or passively, of cottontails from Europe (Recommendation no. R 85-14, 1985). This did not happen in Italy, where the species is now widespread in the northwestern part of the country. Cottontails seem to have spread mainly along the Po Plain river network where there are relicts of natural vegetation (Silvano et al. 2000, Vidus-Rosin et al. 2008, Bertolino et al. 2011b). Here, the European hare (*Lepus europaeus*) is the only native lagomorph present (Silvano et al. 2000, Vidus-Rosin et al. 2008, Bertolino et al. 2011b). The species is still widespread in this area, although often present at low population levels. Hence, competition between these 2 lagomorphs is possible (Meriggi 2001), although first results suggest that the 2 species can coexist in the same areas (Vidus-Rosin et al. 2009, Bertolino et al. 2011a). Hare populations are limited in Italy by habitat degradation, diseases, and over-hunting (Spagnesi and Trocchi 2002). In this situation, further interference from an introduced lagomorph could have negative effects.

Theoretical and empirical studies show that partial niche differentiation in diet, habitat selection, or activity patterns is necessary to allow the coexistence of similar species (Rosenzweig 1981, Mitchell et al. 1990, Brown et al. 1994). Thus, an overlap of niches is a prerequisite for competition. The aims of our study were to summarize the present distribution of the cottontail in Italy and to document the densities and habitat selection of cottontail compared to the native brown hare. Spatial and temporal patterns of the densities of sympatric populations may be evidence of species' interactions. A decreasing density of 1 species linked to an increase of another could be an indication of negative interactions between 2 species (Schoener 1983). This effect

is usually studied at the population level, by observing whether the density of 1 species has changed as the result of the arrival of another one (Bonesi et al. 2004). However, since data on the population dynamics of hares and cottontails are not available, we evaluated spatial patterns using different areas as replicates. If one of the 2 lagomorph species has a detrimental effect on the other, we predicted (1) a negative correlation between the densities of the 2 species in different areas. To avoid competition, sympatric species should differentiate their ecological niches, using resources in different ways (Rosenzweig 1981). Thus, if these lagomorphs compete for habitat use, they (2) should select similar habitats.

## MATERIALS AND METHODS

### Distribution in Italy

A map of the species distribution in Italy was compiled from different sources (Fig. 1). For the Piedmont, information was collected by contacting the Osservatorio Faunistico Regionale (the regional Wildlife Service), other local wildlife services, personnel of parks and protected areas, local hunting units, wildlife managers, and scientists. For the other parts of Italy, reference papers were used (Spagnesi and Trocchi 2002, Angelici and Spagnesi 2008, Vidus-Rosin et al. 2008).

### Study areas

Surveys on cottontails and hares were carried out in 13 zones along the Po River, the Orba River, and adjacent areas in Vercelli and Alessandria Provinces (Piedmont Region, northwestern Italy, Appendix I). All areas except 2 are inside the Po and Orba River Park, one is inside the Bosco della Partecipanza di Trino Vercellese park, and another is in the Fontana Gigante nature reserve. In 4 cases, the study areas extended outside the parks in protected areas managed by the Wildlife Services of Vercelli and Alessandria Provinces. Hunting is prohibited in all areas.

In zones along the Orba River, 60%-65% of the surface area was covered by cultivated fields (Appendix I). Crops were mainly wheat and maize, and during the study period, wheat was growing, while maize fields were plowed or contained stubble. Another 20%-30% of the surface area was covered by natural habitats,

including small woodlots, shrubby areas, and herbaceous vegetation. In areas along the Po River, the surface area covered by cultivated fields was lower, except at Trino. Other cultivation in these areas consisted of rice fields and poplar plantations. The portion covered by natural vegetation considerably varied at 5%-50%.

For the overall area, the annual number of rainy days is 60-90 (minimum-maximum), mostly concentrated in spring and autumn, with 900-1000 mm rainfall per year. Average monthly values of the minimum daily temperature are generally  $< 0^{\circ}\text{C}$  from Dec. to Feb., while the average monthly values of maximum daily temperature are always  $> 0^{\circ}\text{C}$  (Biancotti et al. 1998).

### Fieldwork

We carried out night counts to evaluate population densities and habitat selection of lagomorphs during feeding activities. The same areas were also walked during the day to study habitat selection for resting sites.

At each site, a transect was drawn on a map using roads and fields accessible with a 4-wheel drive vehicle to sample the study area

in a representative manner with respect to the available habitat types. Hares and cottontails were counted at night using a spotlight census (Langhein et al. 1999). The night surveys were carried out by 3 people: 1 driver and 2 observers. The vehicle was driven at 8-10 km/h, and the driver slowed down or stopped at gaps in hedges when necessary. The observers scanned the fields with a hand-held 100-W halogen spotlight. Both observers and driver also scanned directly ahead. Visibility in different habitats was evaluated by repeatedly considering landmarks visible at the edge of the beam and measuring the effective length of the beam; this was taken as the distance at which a piece of red reflective material simulating the reflection of a hare's eye could still be distinguished. The total area surveyed along each transect was evaluated on a 1: 10,000 scale digitized map based on the total length of the transect route and the length of the beam in each habitat. Each transect was covered 3 times between Oct. 2002 and Mar. 2003, when vegetation in the cultivated fields was low. Surveys began 2 h after nightfall, and 2 areas were covered on 1 night. The order of the areas changed on different nights to ensure that individual sections were surveyed at different times. Surveying was terminated in the event of heavy rain or moderate to thick mist.

For every animal observed, we recorded details of the habitat, time, weather, and map reference; the distance of the animal from a refuge area (trees, shrubs, and natural vegetation with tall herbs) was measured on a 5-level scale (0,  $< 10$ , 11-50, 51-100, and  $> 100$  m) with the aid of a laser rangefinder (Leica LRF 800, Solms, Germany). Since foxes are a potential predator of hares and cottontails (Chapman et al. 1980, Reynolds and Tapper 1995), their presence was recorded as well.

We conducted daytime surveys to study habitat selection during resting times. Transect walks were carried out in the areas censused by spotlight. A single area was systematically covered using parallel transects, with a random first start. Transects were spaced 300 m apart to avoid detecting the same animal on 2 neighboring transects. The researcher walked through the area in the middle of the day when hares and cottontails were most likely to be resting in their forms. Flushed animals were recorded together with the time and habitat in which each hare or cottontail was found. Flushed animals were observed and located when they stopped, this position was



**Fig. 1.** Distribution of the cottontail in Italy (black). Continuous lines indicate borders of different regions.

recorded to avoid double counts but was not used in the data analyses. During a pre-trial, each area was walked once; subsequently, from Nov. to Mar., only those areas ( $n = 7$ ) where more than 8 hares or cottontails had been observed were surveyed another 2 or 3 times in order to increase the sample size. Habitat selection for resting sites and during feeding activities were evaluated by pooling the data of all surveyed areas.

### Patch structure and attributes

We evaluated the effect of environmental variables on the density of lagomorphs at 2 spatial scales. The density recorded during a spotlight census depends on the presence of hares and cottontails in the scanned fields. This in turn could be influenced by the characteristics of the fields during the survey period (e.g., the presence of wheat, plowed areas, or stubble). For this reason, we recorded environmental variables in the area covered by the spotlight.

At the landscape level, population densities of hares and cottontails are influenced by the environmental characteristics of the larger area. The proportion of cultivated fields and natural vegetation or other habitat characteristics within the home range of individuals could influence their life-history parameters and have an effect at the population level. Therefore, we evaluated the environmental characteristics at this scale, considering an area related to the movement of the animals. Mean home ranges are 30-40 ha for hares (Broekhuizen and Maaskamp 1982, Tapper and Barnes 1986, Smith et al. 2004, Bertolino et al. unpubl. data) and 3-4 ha for cottontails (Chapman et al. 1980, Bertolino et al. unpubl. data). Hence, we added a buffer of 700 m, corresponding to the diameter of a circular area of about 40 ha, on both sides of each transect.

We used 1: 10,000 scale digitized maps of land cover (edited by Regione Piemonte and Istituto per le Piante da Legno e l'Ambiente, Torino, Italy) imported into ArcView 3.2 GIS software (Environmental Systems Research Institute, Redlands, CA, USA) to evaluate variables that describe the structure and composition of the landscape in relation to the ecological characteristics of the 2 lagomorphs at both spatial scales (Appendix II).

Habitat variables related to farmland and natural vegetation included the proportions of the area covered by woods, shrubs, natural vegetation with tall or low herbs, meadows, poplar plantations,

winter crops, rice fields, plowed areas, and stubble (Appendix II). During the daytime surveys, the proportions of farmland devoted to crops (winter cereals), stubble, and ploughed areas were recorded; data were used to update the land-cover maps of the areas and make them more detailed through digitization of these new categories. We used the Patch Analyst extension of ArcView 3.2 to calculate the mean patch size, edge density, and the Shannon diversity index of each area.

### Data analysis

Densities of hares and cottontails were calculated as the mean number of animals observed during the 3 night counts divided by the area surveyed, scaled to 100 ha. We used the same procedure for foxes, but we considered this to be only a crude index of their abundance since a larger area must be surveyed to obtain an effective density estimation for predators (Heydon et al. 2000).

Correlations between the lagomorph densities and fox population indexes were evaluated using Pearson's correlation coefficient. Mean values of densities and population indexes were compared using Student's *t*-test. Their distributions were skewed and thus were log-transformed [ $\log_{10}(x + 0.01)$ ] before analysis. Non-parametric procedures were run as a double-check to see if they delivered similar results.

Habitat selection during foraging (night) and for resting (day) sites were evaluated considering the proportion of hares and cottontails observed within each habitat class (habitat use). We calculated a resource selection function (Manly et al. 2002) using the habitat proportional composition within the study area as a measure of habitat availability. Selection ratios ( $w_i$ ) for each habitat type were expressed as:

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

The index ranges from 0 (maximum negative selection) to infinity (maximum positive selection), with 1 defining the value expected by chance (no selection). The statistical significance of the results was tested by comparing the statistic:

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

with the corresponding critical value of a Chi-squared distribution with 1 degree of freedom. The standard error of the index was calculated by:

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

where  $u_+$  is the total number of records sampled; the null hypothesis that hares and cottontails selected foraging and resting habitats in proportion to availability was assumed (Manly et al. 2002). We applied the Bonferroni correction for the number of statistical tests (habitat types) to correct the level of significance and avoid type I errors (Rice 1989). This index was chosen because it allows greater accuracy in statistical comparisons (Atienza 1994, Mainly et al. 2002).

We used stepwise multiple-regression analyses to determine whether landscape variables influenced the abundance of lagomorphs at the 2 spatial scales considered. The fox population index was included in the modeling as a measure of predation pressure, while the density of either of the 2 lagomorphs was included to search for possible competitive effects.

A stepwise method was used to select variables to be included in each step. Relaxed significance levels of  $p = 0.10$  and  $= 0.15$  were respectively used for entry and retention in the model so as to consider any possible variable that could have an effect on the density of the 2 species.

We chose the stepwise selection model rather than other methods related to the information criteria theory (e.g., Akaike information criterion and BIC), because our goal was to explore species-habitat relationships and thus create explanatory models. Information criteria models are more precise in estimating regression coefficients when building predictive models (Stephens et al. 2005), while stepwise selection is generally more efficient when building explanatory models (Ludden et al. 1994).

For spotlighted areas, we included variables describing the landscape composition as possible explanatory variables (variables 1-10 in Appendix II). For the 700-m buffer zone around the transects, we included variables describing the landscape composition and the pattern of mosaic structure in the multiple regressions (variables 1-8 and 11-13; variables 1 and 2 were pooled as “woody vegetation”).

Since the number of study areas was limited, we acknowledge that the low case/predictor ratio decreased the power of the analysis, and only very large effects could be detected. To ensure a homoscedastic and normal distribution, we arcsine square root- and log-transformed the data

prior to analysis (Zar 1996). Multicollinearity was tested with the Pearson correlation. All statistical analyses were performed with SPSS vers. 13.0.1 (SPSS 2001).

## RESULTS

### Distribution in Italy

The cottontail is present in a large area in the northwestern part of Italy that includes most of the Piedmont and the western part of Lombardy (Fig. 1). Other small populations are also located in Venetia, Friuli, Liguria, Emilia Romagna, Tuscany, and Umbria. Unsuccessful introductions were attempted in Marche, Latium, and on Marettimo I. (Angelici and Spagnesi 2008).

Data on the spatial spread of the cottontail are available for Alessandria Province (Piedmont). Herein, the range recorded at a municipality level increased linearly from 1995 to 2003 (Fig. 2,  $R^2 = 0.99$ ,  $F_{1,6} = 933.7$ ,  $p < 0.001$ ).

### Population sizes

The mean density of hare populations ( $7.55 \pm 10.80$  animals/100 ha, range 0-29.86 animals/100 ha, Table 1) was lower than that of cottontail populations ( $24.69 \pm 28.20$  animals/100 ha, range 4.40-110.41 animals/100 ha;  $t = -2.98$ ,  $d.f. = 26$ ,  $p < 0.01$ ). The mean densities of the 2 species were positively correlated ( $r = 0.74$ ,  $p < 0.01$ ).

Cottontail densities were higher along the Orba River ( $56.19 \pm 40.57$  animals/100 ha) than along the Po River ( $15.24 \pm 8.58$  animals/100 ha;  $t = 2.28$ ,  $d.f. = 11$ ,  $p < 0.05$ ). Hare densities along the 2 rivers (Orba River  $24.06 \pm 8.02$  animals/100 ha; Po River  $2.59 \pm 3.77$  animals/100 ha) also significantly differed ( $t = 4.52$ ,  $d.f. = 11$ ,  $p < 0.001$ ).

The fox population index ranged 0-1.78 (mean,  $0.69 \pm 0.50$ ), without a significant difference between areas along the Orba and Po Rivers ( $t = 0.94$ ,  $d.f. = 11$ ,  $p = 0.37$ ). This index increased with the densities of hares ( $r = 0.80$ ,  $p < 0.001$ ) and cottontails ( $r = 0.59$ ,  $p < 0.05$ ).

### Factors explaining abundances

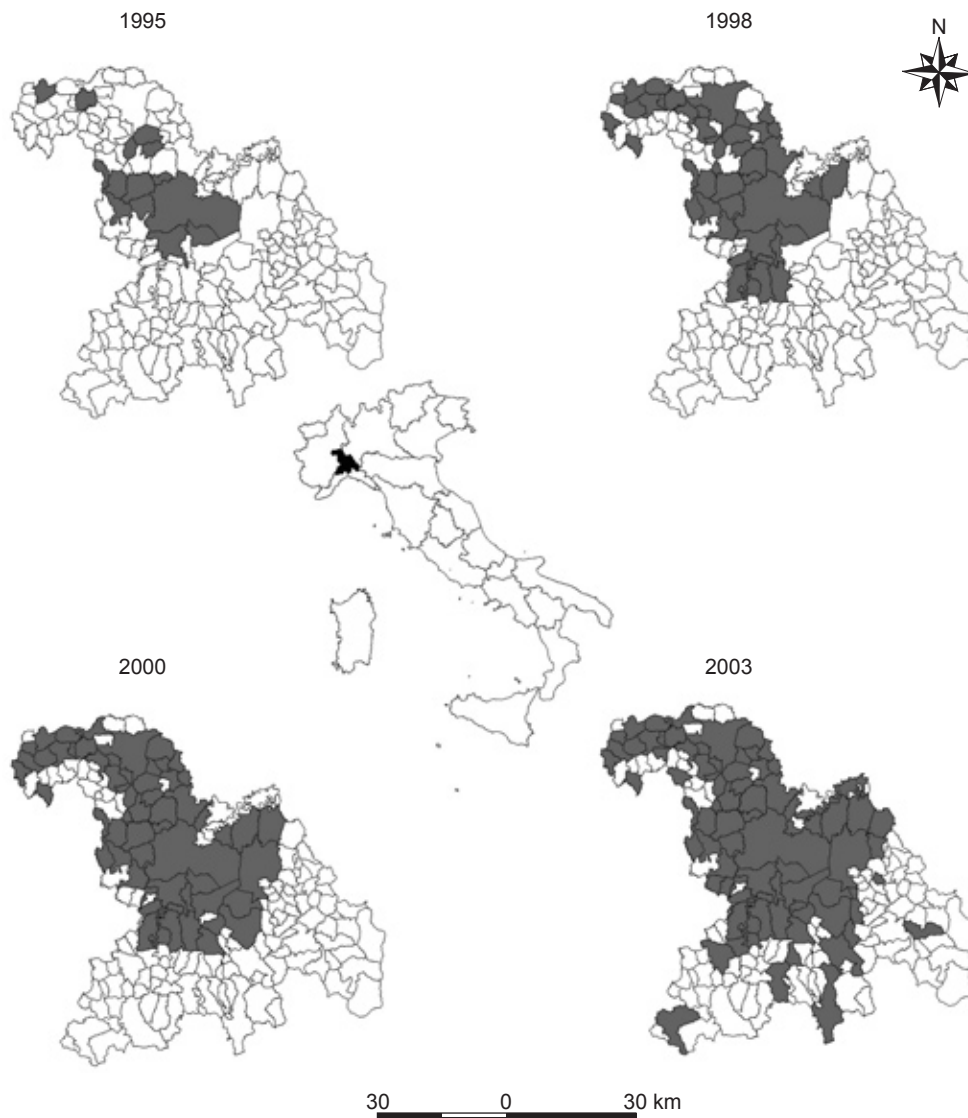
The results of multiple regressions are reported in table 2. Cottontail densities in spotlighted areas increased with the surface covered by low herbaceous vegetation and with the diversity of the landscape (Table 2). In larger

areas, the only predictor of cottontail density was the amount of edge; a variable that, however, was selected with a very low coefficient. Densities of hares in spotlighted areas increased as did the surface covered by winter crops and tall herbaceous vegetation. The variable meadow, selected only with a  $p = 0.081$ , had a confidence interval that included 0, so we could not reject the null hypothesis, i.e., that it had no relation to hare density. In the 700-m buffer zones, hares were again associated with crops and natural herbaceous vegetation, but in these larger areas, the density also increased with the mean patch size, edge density, and cottontail density.

### Habitat selection

In total, 299 hares and 999 cottontails were observed foraging at night, while 45 hares and 188 cottontails were flushed from their resting sites.

At night, cottontails were mainly observed (64.1%) in refuges or within 10 m of them, while most of the hares (59.6%) were sighted in open habitats over 50 m from refuges (Fig. 3). Both species selected low herbaceous vegetation and meadows, but they differed in the use of winter crops by hares and tall herbaceous vegetation, poplars, and stubble by cottontails (Table 3). Tall herbaceous vegetation was used as resting sites



**Fig. 2.** Spread of the cottontail in Alessandria Province from 1995 to 2003. Continuous lines indicate borders of different municipalities.

**Table 1.** Population densities of cottontails and hares in different areas along the Orba and Po Rivers evaluated through night counts

Area	<i>Sylvilagus floridanus</i>	<i>Lepus europaeus</i>
	Animals/100 ha ± 1 S.D.	Animals/100 ha ± 1 S.D.
Po River		
Santa Maria	16.51 ± 3.02	1.32 ± 2.29
Fontanetto	4.40 ± 2.91	0
Morano	5.30 ± 2.03	0.12 ± 0.11
Frassinetto	4.80 ± 3.56	0.63 ± 0.63
Breme	32.08 ± 5.67	1.70 ± 0.85
Fontana Gigante	14.60 ± 7.88	0.39 ± 0.39
Trino	19.17 ± 7.22	13.33 ± 2.89
Boscone	22.24 ± 5.62	2.20 ± 2.12
Isola	11.29 ± 2.35	4.12 ± 2.75
Sartirana	22.01 ± 4.91	2.08 ± 0.51
Orba River		
Mulino	12.82 ± 4.97	12.72 ± 6.31
Merlanotta	45.34 ± 17.24	29.86 ± 10.55
Retorto	110.41 ± 22.56	29.61 ± 21.88

both by hares and cottontails (Table 4). Hares also positively selected shores and low herbaceous vegetation, while cottontails preferred shrubs.

## DISCUSSION

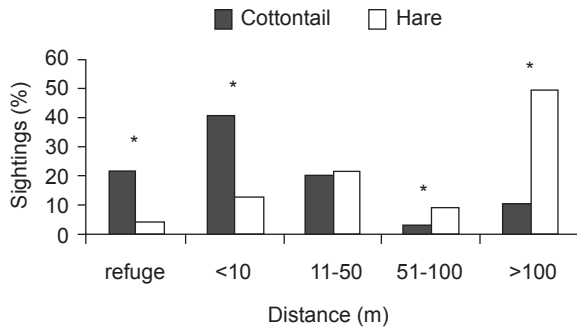
The eastern cottontail was successfully introduced into Italy, with a large and increasing range in the northwestern part of the country and other localized populations. The species is well adapted to human-disturbed habitats of northern Italy, spreading in an agriculture-dominated landscape where small patches of natural vegetation are still present. According to the spread rate recorded in Alessandria Province, it is probable that in the future, the cottontail will continue the colonization of the Po Plain eastwards and of other suitable areas in the central part of Italy.

The cottontail had become established

**Table 2.** Results of the multiple-regression models on the densities of European hare and eastern cottontail. Variables were evaluated in the area investigated with spotlights and in a buffer zone of 700 m around the transect

Model	B	S.E.	Beta	t	p	95% Confidence interval for B	
						Lower	Upper
<i>Sylvilagus floridanus</i>							
Spotlighted areas							
Low herbaceous vegetation %	2.514	0.684	0.536	3.674	0.004	1.008	4.020
Shannon diversity	1.082	0.336	0.469	3.218	0.008	0.342	1.822
$R^2 = 0.93$ . Adjusted $R^2 = 0.92$							
700-m buffer areas							
ED	0.004	0.000	0.958	11.513	0.000	0.004	0.005
$R^2 = 0.97$ . Adjusted $R^2 = 0.95$							
<i>Lepus europaeus</i>							
Spotlighted areas							
Winter crops %	2.790	0.488	0.875	5.713	0.000	1.685	3.895
Tall herbaceous vegetation %	1.773	0.744	0.361	2.384	0.041	0.090	3.455
Meadows %	2.658	1.350	0.297	1.969	0.081	-0.396	5.713
Constant	-1.438	0.336		-4.277	0.002	-2.198	-0.677
$R^2 = 0.80$ . Adjusted $R^2 = 0.73$							
700-m buffer areas							
Winter crops %	1.612	0.218	0.621	7.407	0.000	1.097	2.126
Tall herbaceous vegetation %	9.256	1.731	0.355	5.346	0.001	5.162	13.350
MPS	2.530	0.388	0.603	6.513	0.000	1.611	3.448
ED	0.004	0.002	0.197	2.195	0.064	0.000	0.009
Cottontail density	1.443	0.177	0.583	8.163	0.000	1.025	1.861
Constant	-6.220	0.734		-8.478	0.000	-7.955	-4.485
$R^2 = 0.97$ . Adjusted $R^2 = 0.95$							

B = coefficient, MPS, mean size of cultivated fields (ha); ED, edge density (m/ha).



**Fig. 3.** Distances from refuges of European hare and eastern cottontail observed at night. Bars with an asterisk significant differ between the 2 species ( $p \leq 0.01$ ).

in all surveyed areas, with densities of 10-30 animals/100 ha and a peak of 110 animals/100 ha. A survey conducted in 1996-1997 in Alessandria Province, including some of our study areas, reported a mean density of 4.3 cottontails/100 ha, with peaks of 25-27 animals/100 ha (Silvano et al. 2000). Thus, the cottontail populations have expanded in the meantime and will probably further increase considering that in its native range the species can reach 10-20 animals/ha, even though mean densities are usually lower (Trent and Rongstad 1974, Bittner and Chapman 1979, Chapman et al. 1980).

Viable populations of the European hare

**Table 3.** Values of the selectivity index ( $w_i$ ) and standard error (S.E.) for each habitat used by hares and cottontails as feeding areas. Significance was accepted at  $p < 0.004$  after applying the Bonferroni correction for the number of statistical tests. "Select" indicate habitats that were statistically used more (+), less (-), or equal (=) to their availability

Habitat	<i>Sylvilagus floridanus</i>			<i>Lepus europaeus</i>		
	$w_i$	S.E.	Select	$w_i$	S.E.	Select
Woodlands	0.84	0.01	-	0.13	0.04	-
Shrubs	0.82	0.01	-	0.10	0.05	-
Tall herbaceous vegetation	1.44	0.02	+	0.57	0.08	-
Low herbaceous vegetation	4.90	0.01	+	1.59	0.04	+
Meadows	1.63	0.03	+	6.32	0.10	+
Poplars	1.68	0.01	+	0.56	0.03	-
Winter crops	0.39	0.00	-	1.54	0.01	+
Rice	0.08	0.01	-	0.08	0.02	-
Plowed fields	0.16	0.01	-	0.80	0.02	-
Stubble	2.61	0.10	+	1.01	0.33	=
Shores	1.04	0.17	=	0.58	0.57	=

**Table 4.** Values of the selectivity index ( $w_i$ ) and standard error (S.E.) for each habitat used by hares and cottontails as resting sites. Significance was accepted at  $p < 0.004$  after applying the Bonferroni correction for the number of statistical tests. "Select" indicate habitats that were statistically used more (+), less (-), or equal (=) to availability

Habitat	<i>Sylvilagus floridanus</i>			<i>Lepus europaeus</i>		
	$w_i$	S.E.	Select	$w_i$	S.E.	Select
Woodlands	0.86	0.03	-	0.47	0.15	-
Shrubs	4.95	0.04	+	1.38	0.16	=
Tall herbaceous vegetation	2.36	0.07	+	6.04	0.31	+
Low herbaceous vegetation	0.49	0.07	-	1.48	0.28	+
Meadows	0.00	0.17	-	0.74	0.73	=
Poplar	0.00	0.05	-	0.00	0.19	-
Winter crops	0.03	0.03	-	0.00	0.12	-
Rice	0.07	0.06	-	0.00	0.26	-
Plowed fields	0.06	0.03	=	0.66	0.12	=
Stubble	0.00	0.48	=	0.00	2.00	=
Shores	1.70	0.56	=	9.47	2.36	+



were present in areas along the Orba River (13-30 animals/100 ha), while populations along the Po River generally had lower densities (< 4 animals/100 ha), and in 3 areas, hares were only occasionally observed. Nevertheless, the positive correlation between hare and cottontail abundances does not support competition or our 1st hypothesis.

High densities of cottontails were associated with low natural herbaceous vegetation (i.e., < 15 cm tall), habitat diversity, and development of edges. Landscape diversity is important for cottontails, which require herbaceous habitats connected to hedgerows as permanent cover (Swihart and Yahner 1982, Allen 1984, Vidus-Rosin et al. 2008 2009, Bertolino et al. 2011b). The hare density increased with the abundance of winter crops and other herbaceous habitats. An association between hares and meadows or improved grass was found by Hutchings and Harris (1996). Among crops, wheat is generally favored by hares, probably because it provides cover and food during winter (Tapper and Barnes 1996, Vaughan et al. 2003). Higher densities along the Orba River and at Trino corresponded to an increase in the proportion of winter crops and tall natural herbaceous vegetation (i.e., > 15 cm tall), while areas with very low densities were characterized by an abundance of rice fields, poplar plantations, and woods. Thus, low hare populations seemed to be connected to the presence of suboptimal habitats and not to a high density of cottontails.

Cottontails and hares differed, at least partially, in the habitats used as daily resting sites and during feeding activities. For example, winter crops were selected by hares and avoided by cottontails. During feeding, cottontails were found in a variety of habitats, including natural herbaceous vegetation, poplar plantations, meadows, and stubble fields, usually close to refuges. A preference of the cottontail for feeding in grassy areas close to woody escape cover was also reported in its native range (Bresinski and Chlewski 1976, Korschgen 1980). Hares were observed mainly in meadows, winter crops, and natural open fields, but at  $\geq 50$  m from refuges. Among leporids, the maximal running speed and the development of hind limbs relative to body size are correlated with a dependence on cover (Cowan and Bell 1986). Cottontails are relatively slow and vulnerable in open habitats, and they require access to cover to avoid predators, while hares use flight for evasion.

Foxes are considered a main predator of hares, and a possible negative effect of predation on hare populations was suggested (Reynolds and Tapper 1995, Lindström et al. 1994). We found a positive correlation of hare and cottontail densities with fox abundances, thus supporting a possible effect of lagomorph availability on fox density but refuting a limiting effect of the predator on its prey.

The recorded preferences for natural herbaceous vegetation and shores as resting sites by hares and of tall herbaceous vegetation and shrubs by cottontails are consistent with the results of other studies (Swihart and Yahner 1982, Althoff et al. 1997, Bertolino et al. 2011a). Optimal habitats for cottontails usually include an abundance of well-distributed dense shrubs or other escape cover, interspersed with more-open foraging areas such as grasslands and pastures (Allen 1984). These habitats can provide shelter and food, offering a variety of microclimates throughout the year (Swihart and Yahner 1983, Althoff et al. 1997, Bertolino et al. 2011a). Woodlands were avoided as resting places by both species. Although hares may occasionally use woods as shelter during the day (Marboutin and Aebischer 1996), low densities were found in areas with an abundance of forests (Panek and Kamieniarz 1999). In abandoned fields, cottontail numbers decreased as trees and canopy cover increased, reducing shrubby ground cover (Beckwith 1954). The selection of shores by hares is probably associated with the presence of willows and other shrubs. Early leaf-out of shrub and cover, associated with tall herbs, may provide protection from avian predators and adverse weather conditions (Althoff et al. 1997).

During this study, hares were common only in some areas, while cottontails were present everywhere with good populations and with increased densities in areas where hares were more abundant. This suggests an absence of interference competition between the 2 species, which partially differentiate their niches during feeding and resting. However, since cottontail population densities may be further increasing, the mechanisms of habitat selection by the 2 species must be investigated in areas where both lagomorphs are present with good populations.

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**Appendix I.** Habitat characteristics of the surveyed areas (values in percentage)

Area	Woodlands	Shrubs	Herbaceous vegetation	Meadows	Poplars	Rice	Crops	Shore
Po River								
Santa Maria	2.7	5.6	45.1	0.0	46.6	0.0	0.0	0.0
Fontanetto	3.2	0.5	3.8	0.1	13.9	78.6	0.0	0.0
Morano	26.7	16.2	4.0	0.0	6.3	39.4	7.2	0.3
Frassinetto	1.5	3.9	0.2	0.0	42.9	0.0	51.2	0.3
Breme	13.9	12.3	16.2	0.0	31.0	0.0	26.0	0.6
Boscone	7.0	6.6	23.5	3.2	30.6	0.0	25.8	3.3
Isola	3.5	3.8	11.6	1.3	15.1	0.0	64.7	0.0
Sartirana	7.2	14.2	21.8	1.9	40.0	0.0	13.3	1.6
Trino	9.9	3.2	1.3	0.0	0.8	18.3	66.6	0.0
Fontana	1.6	0.0	4.9	2.5	0.5	90.6	0.0	0.0
Orba River								
Mulino	3.6	3.6	13.1	12.2	0.0	0.0	66.4	1.1
Merlanotta	2.4	9.3	26.6	0.0	0.0	0.0	61.7	0.0
Monferrino	3.7	8.9	21.4	0.0	0.0	0.0	65.0	0.9

**Appendix II.** Summary of landscape variables (and their abbreviations)

No.	Variable	Description
1	Woodlands %	% of the surface covered by woodlands
2	Shrubs %	% of the surface covered by shrubs
3	Tall herbaceous vegetation %	% of the surface covered by natural herbaceous vegetation with plants > 15 cm tall
4	Low herbaceous vegetation %	% of the surface covered by natural herbaceous vegetation with plants < 15 cm tall
5	Meadows %	% of the surface covered by meadows
6	Poplars %	% of the surface covered by poplar plantations
7	Winter crops %	% of the surface covered by fields in winter crops
8	Rice %	% of the surface covered by rice fields
9	Plowed %	% of the surface with plowed fields
10	Stubble %	% of the surface with fields containing stubble
11	MPS	Mean size of cultivated fields (ha)
12	ED	Edge density (m/ha)
13	Shannon diversity	Mean size of urban patches (ha)