Habitat use of coexisting introduced eastern cottontail and native European hare

(Article begins on next page)

20 December 2024

iris - AperTO

Habitat use of coexisting introduced eastern cottontail and native European hare

Sandro Bertolino[a], Nicola Cordero di Montezemolo[a], and Aurelio Perrone[b]

[a] Department of Agriculture, Forest and Food Sciences, Via L. da Vinci 44, 10095 Grugliasco (TO), Italy
[b] Wildlife Science, Via Cossolo 68/A, 10029 Villastellone (TO), Italy

Word count: 6182

ABSTRACT

The niche of introduced species and that of native ones may overlap, thus causing detrimental effects on the latter through competitive interactions. We used radio telemetry to investigate habitat partitioning during the active period by the introduced American eastern cottontail (*Sylvilagus floridanus*) and the native European hare (*Lepus europaeus*) in sympatric conditions. Home ranges of cottontails varied from 1.1-2.2 ha in autumn to 3.0-3.6 ha in summer. In hares, home ranges were 30.5-33.8 ha in summer and increased to 49.5-85.9 ha in winter. Both species used an overall area composed of about 27% of natural habitats (i.e., meadows, woodlands, shrubby habitats, shores, and uncultivated land) and over 70% of field crops. The coexistence of the two species appeared to be facilitated by habitat partitioning. Habitat use of cottontails was characterized by a preference for natural habitats at the study area level as well as within the home ranges, while hares showed a preference for crop fields at both spatial scales and a seasonal selection of meadows within home ranges. Habitat overlap measured with the Pianka index was 0.57-0.64 in autumn and winter, and increased in summer and spring to 0.73-0.78. Our results provide evidence of different resource selection strategies adopted by these two sympatric lagomorph species. Hare populations are often found in agricultural landscapes at low-densities, while cottontails are currently spreading throughout Northern Italy to such an extent that an eradication programme appears unfeasible. In this situation, conservation measures for hares and other species should also take into consideration the presence or possible arrival of cottontails. Habitat restoration measures that would increase the amount of fallow lands and shrublands may favour cottontails more than hares. In areas where introduced lagomorphs are present, the necessity of natural open landscapes for hares may be better faced by increasing the presence of meadows, that are seasonally used by hares and not by cottontails.

Keywords: *Lepus europaeus*; *Sylvilagus floridanus*; Lagomorpha, agro-ecosystems; species introduction.

Introduction

Interspecific competition is an important factor in structuring ecological communities. The 'Theory of limiting similarity' predicts that interspecific competition should lead to a reduction in the niche overlap of competing species. (MacArthur and Levins 1967). As a result of the selective processes that determine a segregation of an ecological niche, similar species may coexist for a long time (Rosenzweig 1981). There are numberless resource axes that could be partitioned by species; still, habitat use and diet are the most important (Schoener 1974). Yet, the introduction of non-native species may interfere with this process. The niche (e.g., how species use habitats and food resources) of the new species and that of the native species (one or even more) might overlap, thus causing detrimental effects that may lead to extinction, especially of the latter, via mechanisms of competitive exclusion. Competitive interactions between introduced and native species have been investigated by several studies that included also lagomorph species (e.g. Stott 2003; Thulin 2003; Flux 2008).

The eastern cottontail (*Sylvilagus floridanus*) is a lagomorph native to America that was introduced into some European countries for hunting purposes; apparently, though, wild populations survived only in Italy (DAISIE 2011). The first introduction into this country dates back to the 1960s; in later years the species was further introduced into several other places (Bertolino et al. 2011c). The cottontails distribution is largely restricted to north-western regions, where the European hare (*Lepus europaeus*) is the only native lagomorph present in the lowlands. In this area of intensive agriculture, hare populations often occur at low densities, as a result of habitat degradation, agricultural intensification, diseases, and over-hunting (Angelici and Spagnesi 2008). On the contrary, in the past 10 years the cottontail has dramatically expanded its range and population densities increased in many areas (Bertolino et al. 2011c). In such a context, inquiring about the possible negative impact of cottontail on hare populations is of fundamental importance for the conservation of the latter.

Competition should be mediated by a similar ecological niche and by the possibility for the introduced species to reach higher densities. Effective tests on exploitation competition are provided by removal experiments (Redfield et al. 1977) and by comparing the population performance in either sympatric or allopatric species (Gurnell et al. 2004). However, considering that in order to coexist species should differentiate their ecological niche, a high niche overlap is assumed to be a prerequisite for competition to occur, and the availability of information on resource exploitation is therefore important for understanding interspecies relationships.

Studies on habitat use and partitioning between lagomorphs already provided evidences of possible competitive effects. In Ireland, the native Irish hare (*Lepus timidus hibernicus*) and the introduced European hare have comparable niche breadths that highly overlap, suggesting the potential for competition between the species (Reid and Montgomery 2007). In Australia, larger home ranges kept European hares distant from European rabbits (*Oryctolagus cuniculus*) for most of the night, but the area used by rabbits was not avoided by hares (Stott 2003).

Both hares and cottontails have adapted to cultivated landscapes typical of the Po Plain in Northern Italy. In fact, higher densities of cottontails in the native ranges are associated with the presence of uncultivated land, habitat diversity and development of hedges. Landscape diversity is generally important for cottontails, which need herbaceous habitats connected with hedgerows that provide permanent cover and small patches of cultivation that provide food supply (Chapman et al. 1980; Swihart and Yahner 1982). Similar habitat requirements were observed for cottontails in Italy (Vidus-Rosin et al. 2008, 2010; Bertolino et al. 2011a,

b). In farmlands, hare density increases with the abundance of winter crops and herbaceous habitats. Permanent grasslands usually sustain lower hare densities than arable farmlands, but a positive effect is reported for extensively managed meadows (Meriggi and Alieri 1989; Hutchings and Harris 1996; Zellweger-Fischer et al. 2011). Among other crops, wheat is generally favoured by hares, that prefer farms with some uncultivated fields because these provide cover and food all year round (Tapper and Barnes 1986; Hutchings and Harris 1996; Vaughan et al. 2003). In conclusion, also hares may benefit from a greater habitat heterogeneity, especially in intensively managed areas (Smith et al. 2004).

The previously observed patterns of habitat selection of these two species may drive to either coexistence or a decline of one species as a result of competition. We already reported that in our study area the two species located their daytime resting sites in different habitats, avoiding competition in this part of their ecological niche (Bertolino et al. 2011a). Cottontails selected almost only shrubby habitats and avoided crop fields in all seasons. Hares were more adaptive in their search, using natural areas and crop fields according to the season.

We, thus, examined habitat use and partitioning by sympatric cottontails and hares during nocturnal feeding activity. Habitat use was assessed at two spatial scales: we considered how species select their habitats 1) at a landscape level and 2) within home ranges. Considering the habitat preferences of the two species (e.g. Chapman et al. 1980; Vaughan et al. 2003; Bertolino et al. 2011a, c), we predicted a partial segregation in habitat use, with cottontails preferring natural habitats with dense cover, and hares rather exploiting open habitats and crop fields. We hypothesized that a coexistence of the two species was made possible by their different use of landscape or habitat structures. By exploring the comparative importance of diverse habitat and landscape features to hares and cottontails, our aim was also to determine management measures that could benefit the native species.

Material and methods

Study area

The study area was located on the right bank of the Orba river (Piedmont region, northwestern Italy, 44° 49' N, 8° 40' E), in a natural reserve, and in the adjacent game reserve where hunting was prohibited. The landscape was composed by a narrow shore, and, when moving away from the river, by a small woodland and a shrubby area that border with fallow lands, and a mosaic of meadows, field crops and a few poplar plantations (Fig. 1). The shore was partially covered with 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. The shrubby area was a thick stripe of *Rubus* spp. and *Rosa* spp. with few trees. Crop fields were mainly cultivated with wheat and maize, according to a rotation system.

During 2003 the density of the two species evaluated through night counts (mean ± SD of three repetitions) was recorded to be 19.9 ± 1.5 cottontails 100 ha^{-1}, and 16.4 ± 7.2 hares 100 ha^{-1} (Bertolino et al. 2011c).

Trapping and telemetry

Cottontails were captured every other month throughout the study period. Cage traps (double entry traps, "100x40x40 cm, Gibis", France) were set in the field, baited with carrots

and lettuce, and checked at sunset and after dawn. Since hares did not enter the traps, we used static nets to capture them: 10-30 beaters flushed the hares from cover into the nets that had been placed across the potential escape routes. Handling procedures consisted of sexing, measuring, and marking the animals with ear-tags. Each trapped lagomorph was individually marked with ear-tags (a Monel No 3, National Band and Tag Co., USA and a coloured tag with number). Adult animals were fitted with a radio collar (MI-2M, Holohil Systems Ltd., Canada with a life span of 24 months) of 25 g and equipped with a mortality motion sensor. Our aim was to continuously monitor 10-15 animals for each species for one year (2005). Animals which were predated or died for other reasons were replaced by as many other individuals during the following trapping session. At the end of the study, if possible, radio-tagged individuals were caught to retrieve transmitters and subsequently released.

The monitoring started 2 days after their release. The animals were tracked on foot and located 3-4 nights a week by triangulation of 2-3 bearings taken from designated stations; UTM coordinates were obtained using bearings plotted onto a detailed map of the study area. Telemetry location errors averaged 46 ± 19 m, as determined by field trials. We tracked the animals 1-2 times per night, with at least a 2-hour interval for consecutive fixes.

Trapping and handling procedures complied with the Italian laws on animal research. Moreover, they were carried out under the permission of the Regione Piemonte Authority and were subject to advice from the Institute for Environmental Protection and Research.

Statistical analysis

We used the Kernel method (fixed Kernel with location density and only contours, and fixed multiplier 1 as smoothing multiplier) to calculate home ranges (95% fixed Kernel estimates, K 95) and core areas (50% fixed Kernel estimates, K 50) with Ranges 7 software (South et al. 2005). We also calculated 100% minimum convex polygon (MCP) home range estimates, because they are commonly reported in literature, so as to allow comparability with other studies. Home-range size reached an asymptote at 25-30 locations. Thus, we used a minimum of 30 point locations to estimate home-range sizes (see Appendix A in supplementary data), this value being similar to those used by other studies (Bond et al. 2002; Smith et al. 2004).

Considering small sample sizes for some seasons and sex, home range and core area sizes of each species were compared with non-parametric Kruskal-Wallis ANOVA followed by Holm's sequential Bonferroni-corrected Mann-Whitney tests in order to detect which pairs of groups were different (Holm 1979). Variables were log-transformed to meet the assumptions of normality and homogeneity of variances.

To assess the possibility that cottontails and hares selectively use habitats and thereby partition overlapping areas, we developed a vegetation map of the study area. The borders of our study area were defined by plotting all the radiolocations of cottontails and hares onto a map and obtaining the MCP for each species (Fig. 1). The study area of cottontails turned out to be included in the larger study area of hares. We used a 1:10,000 digital map of land cover to assess habitat variables. During daytime surveys, the proportions of farmland devoted to different crops, stubble, and ploughed areas were recorded; the data were used to up-date the seasonal land cover maps of the areas available to the species and make them more detailed through the digitisation of these new categories.

Compositional analysis evaluated with the Add-In Tool 6.2 written by Smith (2005) was used for each species to assess whether habitat selection during nocturnal activity differed from random, and to provide a preference habitat ranking (Aebischer et al. 1993). Compositional analysis uses data from all individuals, each representing a sampling unit,

which avoids problems of autocorrelation of data points. Habitats that were not selected were given the value 0.001, as recommended by Aebischer et al. (1993).

We studied habitat selection at two hierarchical levels in order to reflect the animals' use of available habitats at different spatial scales. Firstly, the animal lives in a defined part of the study area (home range), and secondly, it will select specific sub-areas within its home range. For the purpose of analysis of the home range selection (second-order selection, Johnson 1980), habitat availability was defined as the proportion of each habitat type within the study area, while habitat use was defined as the proportion of each habitat within the K95 home range. In analysing habitat selection within home ranges (third-order selection), availability was defined as the proportion of cover within each home range, and habitat use was defined as the percentage of locations of each radio-collared lagomorph within each habitat type. Aebischer et al. (1993) recommended a sample size of 10 animals per group; however, significant differences may be detected when the number of radio-tracked individuals exceeds the number of habitat types. Poplar plantations and sunflower fields that were present in the study area but were not available to most of the animals were removed from the analysis (Aebischer et al. 1993).

The inter-specific habitat use overlap (O) was determined on a seasonal basis according to the proportion of fixes recorded in each habitat, using Pianka (1973) symmetric equation. This index values range from 0 (no habitat overlap) to 1 (total habitat overlap). To assess whether the observed habitat overlap occurred by chance, overlap values were compared with appropriate null models (Gotelli and Graves 1996). The species-habitat use matrix was randomized by shuffling the original values among the resource states using algorithms RA2 and RA3. RA2 simulation replaces the habitats used with random numbers, but retains the zero structure of the matrix, whereas RA3 retains the species niche breadth, but replaces the zero values with random numbers. We used EcoSim software ver. 7 (Gotelli and Entsminger 2009) to calculate expected niche overlap indices, generating 30,000 random Monte Carlo permutations with the two algorithms (Lehsten and Harmand 2006). A significant niche overlap would occur when the observed value is greater than 95% of the simulated values and a significant niche segregation occurs when the observed value is lower than 95% of the simulated mean values.

Results

Home range size

A total of 24 hares and 34 cottontails were equipped with radio collars throughout the year. Home ranges (K95) in cottontails amounted to 1.1-2.2 ha in autumn and increased to 3.0-3.6 ha in summer (Fig. 2). Core areas (K50) were 0.3 ha in winter and increased to 1.1-1.3 in summer (Appendix A and B in supplementary data). Differences between sexes were not significant (K95: $U = 410.5$, $P = 0.17$; K50: $U = 417.5$, $P = 0.20$). Home ranges and core areas differed among seasons in females (K95 $\chi^2_{(3)} = 16.13$, $P < 0.001$; K50 $\chi^2_{(3)} = 13.70$, $P = 0.005$), but not in males (K95 $\chi^2_{(3)} = 5.92$, $P = 0.11$; K50 $\chi^2_{(3)} = 7.19$, $P = 0.07$). Follow-up pairs' tests revealed that differences in females were due to larger home ranges and core areas in spring and summer than in autumn and winter (Mann-Whitney tests with $P < 0.005$) (see Appendix C in supplementary data for complete results).

In hares, home ranges (K95) were 30.5-33.8 ha in summer and increased to 49.5-85.9 ha in winter (Fig. 2). Core areas amounted to 10.9-11.4 ha in summer and 15.6-24.0 ha in winter (Appendix A and B in supplementary data). Differences between sexes were not significant

(K95 $U = 126.0$, $P = 0.71$; K50 $U = 109.0$, $P = 0.34$). Seasonal variations were evaluated statistically only for females because of the inadequate sample of male hares; however, they were not significant (K95 $\chi^2_{(3)} = 5.37$, $P = 0.15$; K50 $\chi^2_{(3)} = 3.53$, $P = 0.32$).

Habitat selection

The overall area used by hares covered 619 ha (Fig. 1) and was composed by 27.5% of natural habitats (18.3% of meadows and 9.2% of woodlands, shrubby habitats, shores, and uncultivated land) and 70.3% of field crops. The area used by cottontails covered 71 ha (Fig. 1) and was similar to that used by hares, with 26.7% of natural habitats and 72.2% of field crops. The area used by cottontails was wholly included in the area used by hares.

Compositional analysis revealed a significant difference between the composition of habitats available within the K95 of either species and the availability in the respective study areas in all seasons (Wilks lambda, all $P < 0.05$ for hare, and all $P < 0.01$ for cottontail). According to the ranking developed by compositional analysis, for cottontail this difference was due to their greater use of such natural habitats as fallow lands, shrubby areas, shores, and woodlands in all seasons (Table 2). In contrast, hares showed a preference for crop fields, using wheat fields from autumn to early spring, maize fields in spring and summer, and stubbles and plough fields from summer to winter.

Cottontails and hares did not use available habitats inside their nocturnal home ranges randomly (Table 1). Cottontails selected natural habitats and also wheat fields in winter and maize fields in summer. Hares showed a preference for crop fields in all seasons and for meadows in winter and spring.

Habitat overlap

Habitat use overlap measured with the Pianka index was 0.57-0.64 in autumn and winter, and increased in summer and spring to 0.73-0.78 (see Appendix D in supplementary data for complete results). RA3 simulations always generated lower expected overlap values than RA2. In spring and summer, niche overlap was significantly higher than expected according to the analysis with unrestricted use of habitats (RA3). However, when the zero structure of the matrix was retained (RA2), the evidence was for a random habitat resource partitioning (i.e. the habitat overlap occurred by chance) between the two species as for autumn and winter.

Discussion

Introduced species may cause detrimental effects to native species competing for the same resources. We provided evidence of habitat partitioning between the introduced eastern cottontail and the native European hare. In our study area, where the two species coexist with good populations, the competition for habitat use during nocturnal feeding activity was rather low.

The two lagomorph species used the landscape to different degrees, with the home ranges of the hares being 10-20 times larger than those of cottontails. Our results are consistent with the theory that predicts larger home ranges for larger species (Basset 1995) and also with the previous studies on the two species which reported hare home ranges to be 25-40 ha (Broekhuizen and Maaskamp 1982; Tapper and Barnes 1986; Smith et al. 2004), and native

cottontail home ranges to be 2-4 ha (Chapman et al. 1980). The hare home range sizes can vary between 26-138 ha (reviewed by Smith et al. 2004) with larger home ranges in areas with intensive agriculture and limited habitat diversity, and small ranges in areas with higher landscape diversity and a greater presence of natural habitats. Our values were similar to those reported for agricultural land in other European countries (Smith et al. 2004). Hare home range size may be similar between sexes or may be larger in males (Kunst et al. 2001; Rühe and Hohmann 2004). We did not detect any difference between sexes, but considering the small number of males due to capture sex bias this result must be taken with caution.

Habitat overlap measured with the Pianka index was low in autumn and winter, and increased in summer and spring. However, comparing with appropriate null models that retained in the structure of the matrix the habitats not used by the two species (RA2 algorithm) the evidence was for a random habitat resource partitioning indicating that the habitat overlap between the two species occurred by chance and not for a similar ecological constrain of the two species.

As we predicted, when establishing their home ranges, the two species used areas with a different proportion of natural habitats and crop fields. Hares showed a marked preference for crop fields, using wheat and maize fields during the growing seasons, but also stubbles, plough fields, and fallow lands in autumn, before wheat started growing. A similar preference for crop fields was observed in the habitat selection within home ranges, together with the selection of meadows in winter and spring. This pattern of habitat use is in accordance with those reported by studies conducted in areas where introduced species do not occur (Tapper and Barnes 1986; Meriggi and Alieri 1989). Hares usually feed in open ground areas with short growing crops or in meadows. For this reason, on arable landscapes hares are often associated with small to medium crop fields - especially wheat and beet - and high habitat diversity that provides them with better feeding conditions (Marboutin and Aebischer 1996; Vaughan et al. 2003; Reichlin et al. 2006). In our study area, wheat is sown in October and harvested in June-July, so it could provide an important food resource during winter (Meriggi and Alieri 1989), in addition to the use of meadows (Meriggi and Alieri 1989; Zellweger-Fischer et al. 2011). In contrast, cottontails made a large use of natural herbaceous and shrubby habitats, including in their ranges high proportions of fallow lands, shrubs, and shores. Natural habitats were selected also within home ranges, together with wheat and maize fields, in winter and summer, respectively. Cottontails prefer to feed near covers, probably in order to avoid predators, because they are relatively slow and vulnerable in open habitats. Among leporids, maximal running speed and the development of hind limbs relative to body size are correlated with dependence on cover (Cowan and Bell 1986). For this reason hares could use long-distance running for evasion and thus use open fields at night.

A niche differentiation between the two lagomorph species was also found in the same area in the use of daytime refuges (Bertolino et al. 2011a). Cottontails restricted their choice to shrubby habitats, while 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 stubble in winter. This confirms the importance of natural habitats for cottontails and the possibility for hares to exploit crop fields as well as natural patches for feeding and resting.

The results of these and other studies (Vidus-Rosin et al. 2009, 2011; Bertolino et al. 2011c) suggest that the two species can coexist in the same areas with good population densities. A possible alternative hypothesis to coexistence is that one species may have forced the other into suboptimal habitats where it persists with declining populations. Habitat use by hares in our study area was similar to what observed in other areas without introduced species and do not suggest segregation into suboptimal habitats. Furthermore, we recorded a good population density of hares in the area (Bertolino et al. 2011c) that does not indicate a decline of the species. The dominance of hares on cottontails with introduced animals forced into

suboptimal habitats would be positive for the conservation of the native species, but the spread of the eastern cottontail and its presence with good populations seems not to support this hypothesis (Bertolino et al. 2011c). Long-term demographic parameters are, however, required to better evaluate the population interactions between these two species.

Another aspect that should be better considered in the interactions between the American and native species is that cottontail is a possible vector of pathologies that may be detrimental to native lagomorphs. In particular, it can be a carrier of pseudo-tuberculosis, to which hares are prone, and of myxomatosis, that is lethal to the European rabbit (*Oryctolagus cuniculus*). Cottontails have also carried to Italy several *Eimeria* parasites from America (Bertolino et al. 2010).

Predation risk could influence population densities and habitat use patterns for both lagomorph species (Chapman et al. 1980; Reynolds and Tapper 1995; Lindström et al. 1994). In a study conducted in 13 areas in the same region and including our study area, we found a positive correlation of hare and cottontail densities with fox abundance, thus supporting a possible effect of lagomorph availability on fox density but refuting a limiting effect of the predator on its prey (Bertolino et al. 2011c). In our study area we recorded one of the highest fox population indexes; therefore, we observed the habitat partitioning between the two lagomorph species in a situation with a high fox population.

Studies on habitat selection with telemetry may be influenced by triangulation error, especially in areas characterized by a fragmented landscape with small patches. Triangulation error reduces the statistical power to detect habitat selection. When habitat patches are small relative to telemetry precision, the animals may appear to use available habitat types randomly (Samuel and Kenow 1992). Despite the heterogeneity of our study area, we found a certain level of habitat selection to indicate a low influence of the triangulation error; however we caution readers in the interpretation of our results, especially those concerning the eastern cottontail that use areas with small patches.

Our study took place in a natural reserve and a game reserve where hunting was prohibited. Considering that hunting has a great influence on the native hare (Marboutin et al. 2003; Angelici and Spagnesi 2008), we caution not to extrapolate our results to the overall agricultural landscape of northern Italy.

Hare populations in agricultural landscapes are often to be found at low-density levels and managers should consider alternatives to improve habitat quality and increase population size. The cottontail is widespread in northern Italy and any eradication programme should be presently considered unfeasible. In this context, conservation measures for hares should also take into account the presence or the possible arrival of cottontails. Optimal conservation measures have to improve native populations while avoiding to facilitate introduced species. Habitat selection of hares and cottontail recorded during this study point out that increasing heterogeneity with more natural herbaceous and shrubby areas will favour the hare but also the introduced species. On the contrary, a greater presence of crop fields may help preferentially the native lagomorph. This apparent paradox depends on the fact that the European hare is a species native to areas characterized by the steppe habitat, one that only subsequently adapted to cultivated landscapes, where food is abundant. Therefore, crop fields are a second choice to which natural grassland is preferred. The necessity of open landscapes may be better faced by increasing the presence of extensively managed meadows, that are used by hares on a seasonal basis and generally avoided by cottontails. The outcome of this habitat manipulation for both species might depend on landscape composition, predator presence, climate, and other factors. Therefore, we suggest that such a management option should be tested in future studies before its implementation over large areas.

Acknowledgements

References

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74, 1313−1325.

Angelici, F.M., Spagnesi, M., 2008 *Sylvilagus floridanus* (J.A. Allen, 1890). In: Amori, G., Contoli, L., Nappi, A. (Eds.), Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. Fauna d'Italia Vol. XLIV. Edizioni Calderini e Il Sole 24 Ore, Milano, pp. 305−313.

Basset, A., 1995. Body size-related coexistence: an approach through allometric constraints on home range use. Ecology 76, 1027−1035.

Bertolino, S., Cordero di Montezemolo, N., Perrone, A., 2011a. Daytime habitat selection by introduced eastern cottontail (*Sylvilagus floridanus*) and native European hare (*Lepus europaeus*) in northern Italy. Zool. Sci. 28, 414−419.

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.

Bertolino, S., Hofmannová, 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., 2011c. 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.

Bond, B.T., Burger, Jr., L.W., Leopold, B.D., Jones, J.C., Godwin, K.D., 2002. Habitat use by cottontail rabbits across multiple spatial scales in Mississippi. J. Wildl. Manage. 66, 1171−1178.

Broekhuizen, S., Maaskamp, F., 1982. Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in the Netherlands. Z. Säugetierkd. 47, 22−32.

Chapman, J.A., Hockman, J.G., Magaly, M., Ojeda, C., 1980. *Sylvilagus floridanus*. The American Society of Mammalogists, Mammals species 136, 1−8.

Cowan, D.P., Bell, D.J., 1986. Leporid social behaviour and social organisation. Mamm. Rev. 16, 169−179.

DAISIE, 2011. DAISIE portal: www.europe-aliens.org.

Flux, J.E.C., 2008. A review of competition between rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*). In: Alves, P.C., Ferrand, N., Hackländer H. (Eds.), Lagomorph Biology. Evolution, Ecology and Conservation. Springer-Verlag, Berlin, Heidelberg, Germany, pp. 241–249.

Gotelli, N.J., Entsminger, G.L., 2009. EcoSim: null model software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear, Jericho, VT 05465.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Press, Washington DC.

Gurnell, J., Wauters, L.A., Lurz, P.W.W., 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.

Holm, S., 1979. A simple sequential rejective multiple test procedure. Scand. J. Stat. 6, 65−70.

Hutchings, M.R., Harris, S., 1996. The current status of the brown hare (*Lepus europaeus*) in Britain. Joint Nature Conservation Committee, England.

Kunst, P.J., van der Wal, R., van Wieren, S., 2001. Home ranges of brown hares in a natural salt marsh: comparisons with agricultural systems. Acta Theriol. 46, 287−294.

Jennings, N.V., Smith, R.K., Hackländer, K., Harris, S., White, P.C.L., 2006. Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high-density and low-density populations. Wildl. Biol. 12, 179−189.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65−71.

Lehsten, V., Harmand, P., 2006. Null models for species co-occurrence patterns: assessing bias and minimum iteration number for the sequential swap. Ecography 29, 786−792.

Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P-A., Martinsson, B., Skold, K., Swenson, J.E., 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75, 1042−1049.

MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101, 377−385.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals. Kluwer Academic Publishers, The Netherlands.

Marboutin, E., Aebischer, N.J., 1996. Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*? Wildl. Biol. 2, 83−91.

Marboutin, E., Bray, Y., Peroux, R., Mauvy, B., Lartiges, A., 2003 Population dynamics in European hare: breeding parameters and sustainable harvest rates. J. Appl. Ecol. 40, 580−591.

Meriggi, A., Alieri, R., 1989. Factors affecting brown hare density in northern Italy. Ethol. Ecol. Evol. 1, 255−264.

Morgan, K.A., Gates J.E., 1983. Use of forest edge and strip vegetation by eastern cottontails. J. Wildl. Manage. 47, 259−264.

Pépin, D., 1985. Spring density and daytime distribution of the European hare in relation to habitat in an open field agrosystem. Z. Säugetierkd. 51, 79−86.

Pépin, D., Angibault, J.M., 2007. Selection of resting sites by the European hare as related to habitat characteristics during agricultural changes. Eur. J. Wildl. Res. 53, 183−189.

Pianka, E.R., 1973. The structure of lizard communities. Annu. Rev. Ecol. System. 4, 53−74.

Redfield, J.A., Krebs, C.J., Taitt M.J., 1977. Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal British Columbia. J. Anim. Ecol. 46, 607−616.

Reichlin, T., Klansek, E., Hacklander, K., 2006. Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. Eur. J. Wildl. Res. 52, 109–118.

Reid, N., Montgomery, W.I., 2007. Is naturalisation of the brown hare in Ireland a threat to the endemic Irish hare? Biol. Environ. 107, 129–138.

Reynolds, J.C., Tapper, S.C., 1995. Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on annual population growth. Wild. Biol. 1, 145−158.

Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology 62, 327−335.

Rühe, F., Hoffmman, U., 2004. Seasonal locomotion and home range characteristics of European hares (*Lepus europaeus*) in an arable region in central Germany. Eur. J. Wildl Res. 50, 101−111.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185, 27−39.

Smith, P.G., 2005. Compos Analysis, version 6.2 standard. Smith Ecology Ltd., Abergavenny, UK. Benton

Smith, R.K., Jennings, N.V., 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, A.B., Kenward, R.E., Walls, S.S., 2005. Ranges 7 v 1.0 for the analysis of tracking and location data. Anatrack, Wareham, England.

Stott, P., 2003. Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. Mamm. Biol. 68, 317−327.

Swihart, R.K., Yahner, R.H., 1982. Habitat feature influencing use of farmstead shelterbelts by the eastern cottontail *Sylvilagus floridanus*. Am. Midl. Nat. 107, 411−414.

Tapper, S.C., Barnes, R.F.W., 1986. Influence of farming practice on the ecology of the brown hare *Lepus europaeus*. J. Appl. Ecol. 23, 39−52.

Thulin, C-G., 2003. The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? Mammal Rev. 33, 29–42.

Trent, T.T., Rongstat, O.S., 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38, 459−472.

Vaughan, N., Lucas, E.A., Harris S., White P.C.L., 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: Alves, P.C., Ferrand, N., Hackländer H. (Eds.), Lagomorph Biology. Evolution, Ecology and Conservation. Springer-Verlag, Berlin, Heidelberg, Germany, pp. 153−165.

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.

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. (n.s.) 20, 101−110.

Zellweger-Fischer, J., Kéry, M. & Pasinelli, G., 2011. Population trends of brown hares in Switzerland: the role of land-use and ecological compensation areas. Biol. Conserv. 144, 1364–1373.

Table 1
Compositional preference order for habitat selected by hares and cottontails within the study areas and the home ranges. WOD: woodland, SHR: shrub, SHO: shore, FL: fallow land, MEA: meadow, WHE: wheat, MAZ: maize, PLO: plough, STU: stubble. Variables are separated with > symbols, with those to the left being of higher rank (preference) than those to the right. A >>> symbol indicates a significant ($P < 0.05$) difference between two consecutively ranked variables, = the absence of differences.

Season	Compositional preference order	
	European hare	Eastern cottontail
95% kernel ranges vs. total study area		
Winter	WHE>PLO> FL>STU>>>SHR>WOD>MEA	FL>SHR>SHO>WOD>WHE>PLO>STU
Spring	WHE>MAZ>FL> SHR>WOD>MEA>PLO	FL>SHR>WOD>SHO> MAZ>WHE
Summer	STU>MAZ>SHR>FL> MEA	FL>>>SHR>>>SHO>MAZ>STU>WOD
Autumn	FL>PLO>WHE>WOD> MEA>STU	FL>SHR>SHO>WOD>WHE>PLO
Radio fixes vs. 95% kernel ranges		
Winter	WHE>PLO>MEA>SHR>STU>FL	WHE>SHR>SHO>FL>WOD
Spring	WHE>MAZ=MEA=FL> SHR	SHO>WOD>FL>SHR>WOD
Summer	STU>MAZ>SHR>FL	MAZ>FL>SHR>SHO=STU>WOD
Autumn	PLO>FL>WOD>WHE>MEA	FL>SHR>PLO>WHE

Fig. 1. Study area and its location in Piedmont - Italy. Horizontal lines: shores; black: woody habitats (woodlands, shrubs and hedgerows); grey: spontaneous vegetation; diagonal lines: meadows; white: crops fields.

Eastern cottontail

European hare
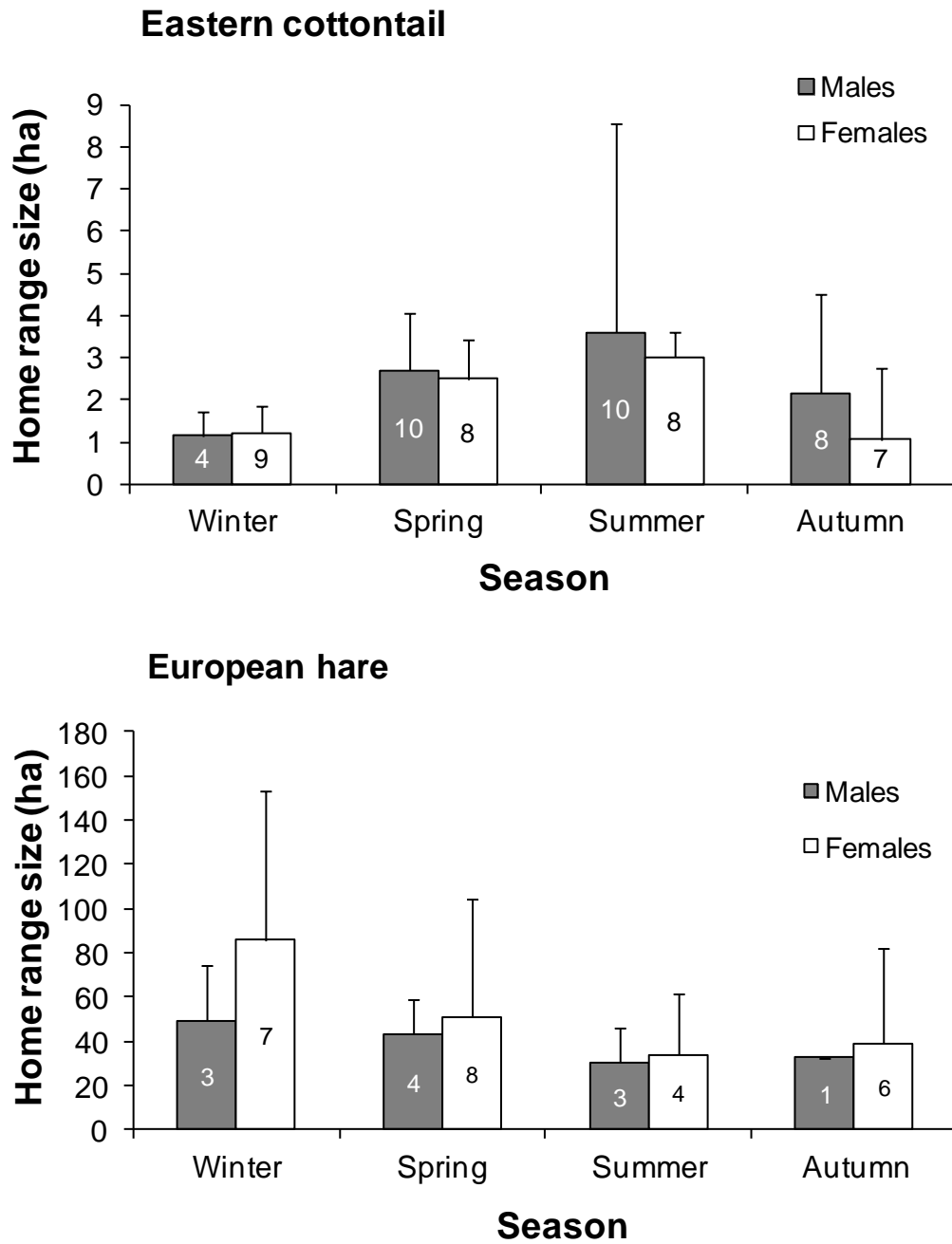
Fig. 2. Size (ha) of 95% fixed Kernel home ranges of cottontails and hares determined by radio-tracking. Bars are 1SD. Sample sizes are reported inside the bars.