Body Size and Altitude Partitioning of the Hares Lepus Europaeus and L. Corsicanus Living in Sympatry and Allopatry in Italy

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Body size and altitude partitioning of the hares *Lepus europaeus* and *L. corsicanus* living in sympatry and allopatry in Italy

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We present morphological and ecological data on hares of the genus *Lepus* living on the Italian peninsula and Sicily. During 16 years, we analysed specimens shot by hunters with respect to their habitat choice and distribution. Our morphometric data confirmed the existence of two different but closely related species, i.e. *Lepus europaeus* present in central and northern Italy and *Lepus corsicanus* endemic to central and southern Italy and Sicily. The distribution of the two hare species overlaps in a wide area of central Italy, tentatively estimated to be $>$ 200 km. In terms of altitude, *L. europaeus* and *L. corsicanus* do not differ significantly when they live in allopatry. However, when they coexist in sympatry, *L. corsicanus* occurs at altitudes significantly higher than *L. europaeus. L. europaeus* inhabits significantly higher altitudes when it lives in allopatry than when it lives in sympatry, and *L. corsicanus* inhabits significantly higher altitudes when it lives in sympatry than when it lives in allopatry.

Key words: ecological coexistence, habitat choice, Italy, Lepus corsicanus, Lepus europaeus

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In Europe, the colonisation by hares seems to have followed a combination of biogeographical (expansion and reduction of ice extension due to glacial and interglacial periods) and antropogenic factors (artificial introductions in both historical and recent times for hunting purposes; Lind 1963, Fargher 1977, Thulin 2003).

The Italian peninsula is inhabited by three species of the hare genus *Lepus*, one of which *L. timidus* is found only along the Alpine massif, whereas the other two species *L. europaeus* and *L. corsicanus* are present across the whole territory (Angelici & Spagnesi 2007).

The European hare *L. europaeus* has been considered to be present across the whole Italian peninsula and on Sicily (Toschi 1965), but Homolka & Zima (1999) stated that it is absent from Sicily. According to Toschi (1965), the subspecies *L. europaeus meridiei* is found in the northern and central regions of Italy, whereas the endemic subspecies *L. europaeus corsicanus* is found in the central and southern regions of Italy and on Sicily. This latter taxon is characterised by its smaller size and the yellow-brown-reddish dorsal colouration (Toschi 1965). De Winton (1898) described this taxon by analysing specimens from Corsica, whereto it was

introduced possibly during the 16th century (Angelici 1995), and where it was recently rediscovered after a period of supposed extinction (Scalera & Angelici 2003). Palacios et al. (1989) and Palacios (1996) highlighted relevant morphometric differences between *L. e. corsicanus* and *L. e. meridiei* by analysing cranial biometry, hair structure and dental characteristics of Museum specimens originally collected during the 19th century and during the first decades of the 20th century, when restocking with hares for hunting purposes had not yet begun. According to these authorities, *L. europaeus* and *L. corsicanus* are distinct species with no evidence of hybrid specimens (Hoffmann 1993). More recently, mitochondrial DNA analyses fully confirmed the specific status of *L. corsicanus* (Pierpaoli et al. 1999, Riga et al. 2003).

A critical threat to free-ranging hare populations in Italy is the frequent use of restocking for hunting purposes, even though these restocking procedures are usually unsuccessful (Angelici et al. 2000). The restocking programmes have been extremely intense during the last 50 years, with thousands of captive specimens released every year into the wild. The hares often come from eastern European countries, from northern Europe and even from South American countries (mainly Argentina and Uruguay) from where the species have been imported for many years. As expected, the presence of foreign specimens caused rarefaction and even disappeance of *L. e. meridiei* due to hybridisation, and rarefaction of *L. corsicanus* possibly due to occurrence of interspecific competition (Angelici 1995, Angelici & Luiselli 2001).

Another relevant problem concerning Italian hares relates to the high pressure inferred from hunting of free-ranging populations, without causing any difference between the different taxa. Indeed, *L. corsicanus* is actually considered Critically Endangered (CE), following the IUCN (1996) categories (Amori et al. 1999), or Endangered (EN; Angelici & Luiselli 2001).

In this paper, we 1) present new morphological data that might be useful in discriminating the two *Lepus* species, 2) examine the distribution and the habitat choice of the two taxa living in allopatry and sympathy and 3) compare the distribution of the two taxa with those of other vertebrate species having similar distribution patterns, to provide a biogeographic interpretation. Then, based on these results, we address the conservation and management problems relative to the interaction between the two species. Data given here are particularly relevant, not only because they report detailed information on an endangered hare species, but also because they can be used as a tool for reliable management planning of hares in Italy.

Material and methods

Study area

We collected all data presented here between 1981 and 1997 at several localities of peninsular Italy and Sicily (Angelici 1995, Angelici & Luiselli 2001). Samples were collected from local hunter communities that agreed to permit examination of their catches. From every capture locality we recorded altitude.

Source and animals

We examined hare specimens shot by hunters across the study area and throughout the study period. Hunters randomly shot the two species, hence they spent equal efforts on shooting the two species in each study area. However, the relative hunting effort was uncontrolled among study areas; so, we could not exclude that the different sample sizes among study areas did not depend on relative abundance differences of hares in the various areas, but merely on different hunting efforts in the various fields. Nonetheless, within each area, the observed differences in the relative number of shot hare species most likely reflect different population abundance of each species at the various sites.

In total, we measured 56 *L. europaeus* specimens and 42 *L. corsicanus* specimens.

The hares were discriminated to species level by examination of the pelage in accordance with the indications used by De Winton (1898) and Toschi (1965). Moreover, after the first period of research we noticed that the specimens attributable to *L. corsicanus* were always characterised by a darkish pelage on the nape of the neck, which was totally absent in *L. europaeus*. This morphological characteristic was reported for the first time by Angelici (1989).

All measurements collected from every specimen were taken on adult animals only, by using the method of ossification of the epiphyseal cartilage of the ulna and the radius, calibrated for *L. europaeus,* as described in Broekhuizen & Maaskamp (1979). These hares were shot by hunters during the hunting seasons (during approximately October-January). From each examined animal we re-

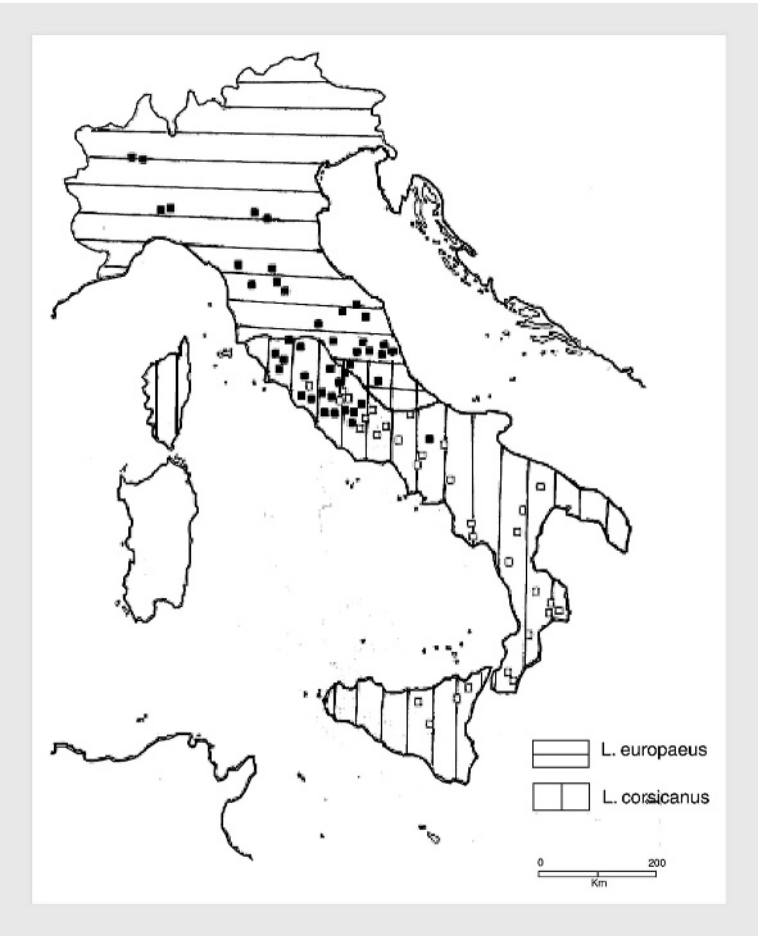

Figure 1. Hypothetical reconstruction of the original ranges of *Lepus europaeus* and *L. corsicanus*, and specific capture localities of *L. europaeus* (■) and *L. corsicanus* (□). The actual distribution of *L. europaeus* in Italy is affected by the hunting restocking, i.e. introduction also into areas from which the species was originally absent.

corded the following measures: body mass to the nearest 0.1 kg (measured by a REBÜRE, Germany, 0-25 Kg dinamometer, calculated before the entrails), body, head, tail, hindfoot and ear length (using a precision calliper; all to the nearest 0.1 cm). Body mass was measured only in males and non-pregnant females.

Statistical analysis

All statistical tests were made using the STATISTICA for Windows (version 6.4) PC package. The variable altitude for both species was log-transformed to achieve homoscedasticity, i.e. to meet the assumption for ANOVA models.

Results

Distribution

Based on data in Toschi (1965) and Palacios (1996), a hypothetical reconstruction of the supposed original ranges of the two hare species is presented in Fig. 1. In our study *L. europaeus* was found in the northern and central regions of the Italian peninsula, the southernmost individual examined coming from central Molise (in the province of Campobasso). We had no data at hand with regard to the northern and northeastern part of Italy, where, however, *L. europaeus* is surely present (Toschi 1965).

L. corsicanus samples were collected from the central Apennines and southwards, including Sicily (see Fig. 1). The northernmost specimen examined was captured in northern Latium (in the province of Viterbo at approximately 42°16'N latitude and 11°54'E longitude). Thus, the contact zone between the two species extends over 220-270 km (see Fig. 1).

Morphology

The two species differed significantly in terms of most of the examined morphological parameters, but especially body mass, body length and head length were markedly different (One-way ANOVA:

Table 1. Morphological characters of the hare species *Lepus europaeus* and *L. corsicanus*; means are given ± 1 S.D.

Morphological character	*Lepus europaeus*	*Lepus corsicanus*	P
Body mass (in kg)	3.33 ± 0.28	2.22 ± 0.19	< 0.001
Head to body length (in mm)	11.51 ± 0.61	9.93 ± 0.23	< 0.001
Tail length (in mm)	9.36 ± 0.73	8.67 ± 0.90	< 0.01
Hindfoot length (in cm)	14.14 ± 0.59	12.58 ± 0.44	< 0.001
Ear length (in cm)	12.78 ± 0.58	11.43 ± 0.58	< 0.01

in all cases at least $P < 0.0001$; Table 1). There were no significant differences in mean body size (i.e. body mass, body length and head length) between sympatric and allopatric populations, in either species (One-way ANOVAs: for both species at least $P > 0.322$), i.e. the sympatry did not produce any effect on the morphological traits of each of the two supposed competitors.

Habitat choice

When they live allopatrically, *L. europaeus* and *L. corsicanus* did not differ significantly in terms of altitude (Two-way ANOVA: $P > 0.3$; Fig. 2). However, when they coexist in sympatry, *L. corsicanus* inhabits places situated at altitudes significantly higher than *L. europaeus* (One-way ANOVA: $P < 0.01$). *L. europaeus* inhabits significantly higher altitudes when it lives allopatrically than when it lives sympatrically (One-way ANOVA: $P < 0.05$), and *L. corsicanus* inhabits significantly higher altitudes when it lives sympatrically than when it lives allopatrically (One-way ANOVA: $P < 0.05$). Two-way ANOVA revealed an effect of species ($P < 0.05$) and of the interaction species*condition (sympatric/allopatric; $P < 0.01$). However, it should be noted that the localities at which hares were shot do not necessarily tell us very much about where they live.

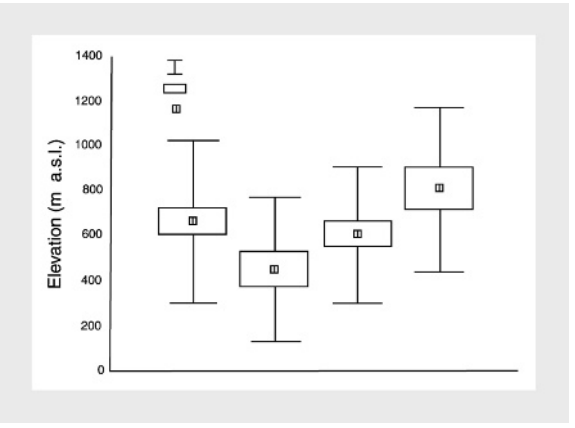

Figure 2. Box-and-whisker plot indicating means and dispersion measures of the mean altitude at which *Lepus europaeus* and *L. corsicanus* were found. For more details, see text.

Discussion

Distribution

We show that the 'sympatry zone' between the two taxa is wider than previously suspected (see data in Spagnesi & Trocchi 1992). Their distribution overlap has tentatively been estimated at > 200 km. This overlap is probably influenced by the continued restocking of *L. europaeus* for hunting purposes (Angelici 1995, but see also Benmergui et al. 1990 for a different opinion). Considering that restocking efforts are still continuing, the distribution overlap between the two hare species is possibly going to overextend also in regions where *L. europaeus* was not originally present, i.e. in southern Italy (*cf.* Toschi 1965). As mortality rates of restocked *L. europaeus* are very high (approximately 70-75%), especially in the first 10 days after introduction (Marboutin et al. 1990, Angelici et al. 1993, 2000, Angelici 1995), it seems very unlikely that restocked hares can be acclimatised, thus suggesting that the *L. europaeus* populations of central Italy are in fact autochtonous, at least in some areas. One of the southernmost areas where *L. europaeus* seems to be autochtonous (and where *L. corsicanus* is also present) is the Molise region. In fact, the presence of *L. europaeus* in this region was ascertained before the beginning of the restocking procedures for hunting purposes (Toschi 1965; F. Riga, pers. comm.), and it can hence be concluded that it is a natural presence.

Despite the restocking procedures, it is likely that the two species are experiencing a dynamic mechanism of niche separation to reduce interspecific competition (Ricklefs 1980). In fact, in the areas where the two species coexist in apparent sympatry, *L. corsicanus* tends to inhabit areas at higher altitudes, whereas *L. europaeus* inhabits areas at lower altitudes.

Biogeographical implications

The actual distribution range of *L. corsicanus*, as it emerges from our data, could be interpreted as a remnant distribution of a previously widespread

Mediterranean species which was drastically reduced by the invasion of *L. europaeus*. This latter species invaded Italy during the late Pleistocene, and there are abundant fossil materials that confirm it (Spagnesi & Trocchi 2002). An alternative hypothesis could be that *L. corsicanus* could be a post-glacial relict species (for the fossil evidence see Vigne 1988, 1990, 1992), with some genetic differentiation during glaciation. *L. corsicanus* has recently been assigned to the *L. timidus* species group (Pierpaoli et al. 1999, Waltari et al. 2004).

Moreover, *L. castroviejoi*, an endemic relict hare species of the Cantabrian Mountains on the Iberian Peninsula, is very similar to *L. corsicanus* in terms of several morphometric and morphological characteristics (Palacios 1996), and thus could also hypothetically be conspecific with *L. corsicanus*. If the conspecific status of *L. corsicanus* and *L. castroviejoi* could be confirmed by adequate genetic analyses, our evolutionary scenario would appear very plausible, with two subspecies of the same species having disjunct ranges corresponding to relictual portions of the original range. *Lepus castroviejoi* is restricted to its current limited range, possibly because of the northern invasion of *L. europaeus* and the presence of *L. granatensis* in the south Spanish districts (but see Perez-Suarez et al. 1994). In this regard, it is interesting to note that the chamois *Rupicapra pyrenaica* has a nearly identical distribution pattern, with scattered populations found in the Cantabrian Mountains (*R. pyrenaica parva*), in the Pyrenees (*R. p. pyrenaica*) and in the central Apennines (*R. p. ornata*). These scattered populations are relictual preglacial groups confined in the actual range by the 'invasion' of the closely related and widespread *R. rupicapra* (Nascetti et al. 1985, Lovari 1987, Masini & Lovari 1988).

Morphology

Our study presents the largest data set available on *L. corsicanus*. Morphological data given in our study confirm that *L. corsicanus* is a species distinct from *L. europaeus*, with little or no overlap in body length and body mass. However, it is obvious that body size is strongly correlated with the other examined morphological variables (in all cases: $r > 0.56$, $P < 0.05$). In this regard, our data fully agree with those of Palacios et al. (1989) and Palacios (1996), who demonstrated the specific rank differences between the two taxa on the basis of craniological and morphological data, which could not be explained by a clinal decrease of body size from the northern to the southern latitudes.

Habitat choice

In summary, we found a shift in altitude in the occurrence of the two species when they were living in sympatry. Hence, partitioning of the respective ecological niches between the two species (possibly to reduce interspecific competition, *sensu* Ricklefs 1980) seems to be based on a mechanism of altitudinal partitioning. This is clearly shown by the fact that the two species were found on average at similar altitudes when they occurred allopatrically, but at different altitudes when they occurred in sympatry. The fact that *L. corsicanus* is found at higher altitudes than *L. europaeus* when living in sympatry can be tentatively explained by the fact that *L. europaeus* is bigger, probably more aggressive, more adaptable and has a higher reproductive rate than *L. corsicanus* (Angelici 1995) and thus confines *L. corsicanus* to refuge sites relatively inhospitable, e.g. the mountain sites. This pattern of altitudinal separation between sympatric hare species is not exclusive to our study system. Indeed in Europe, *Lepus timidus* is usually linked to the higher altitudes in areas where *L. europaeus* also occurs (Flux 1981, Thulin 2003), and the separation of the species into different habitats seems to be a general characteristic of hares (Flux 1981). In our study case, it is very likely that the density of the hare species at the various local sites is an important (but still unstudied) factor in regulating their coexistence. In our supposed model, *L. corsicanus* responds to density variations in *L. europaeus* where the increased number of restocked specimens may force the endemic species to shift its altitudinal distribution.

However, other factors could have affected the observed pattern, e.g. habitat changes caused by humans over thousands of years that are known to be the main factor for adaptation of hares to certain environments. Unfortunately, we did not determine the home ranges of the hares, so we cannot establish whether there is a different habitat choice depending on the yearly phase.

There are other vertebrates in the central Apennine regions which seem to experience the same mechanism of niche partitioning. Among reptiles, for instance, *Vipera ursinii* is currently confined to the higher altitudes by the concurrent presence of *Vipera aspis*, a larger and much more adaptable species (Bruno & Maugeri 1990). Among mam-

mals, a similar mechanism could probably occur between *Talpa romana* and *T. caeca*, with the latter being confined to the higher altitudes in the Apennines caused by a strong interspecific competition with the first mentioned species (Angelici 1989).

Implications for conservation

The problem of interspecific competition between the two hare species should be avoided, or at least diminished, by impeding coexistence of the two species. This aim would be achieved by outlawing, via a specific law on wildlife management, the restocking of the European hare into the areas potentially inhabited by the Apennine hare (Angelici & Luiselli 2001). We suggest prohibition of restocking of *L. europaeus* from Latium-Abruzzo (Central Italy) into the south, and into Sicily. Despite the enormous number of restocked hares (at least 10,000 specimens until 1995; Lo Valvo et al. 1997), the European hare is apparently not yet established in Sicily.

It is also urgent to study in more detail the genetic characteristics of the various populations, because available data are still scarce and conflicting (e.g. see Pierpaoli et al. 1999).

A reliable conservation practice might also consist of the maintenance of breeding pools of the two hare species in appropriate 'farms' that may be used to re-establish groups of free-ranging *Lepus corsicanus* into the areas from which it has dissappeared.

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