



HAL
open science

Space use patterns of mountain hare (*Lepus timidus*) on the Alps

Francesco Bisi, Mosé Nodari, Nuno Miguel dos Santos Oliveira, Elisa Masseroni, Damiano G. Preatoni, Lucas A. Wauters, Guido Tosi, Adriano Martinoli

► **To cite this version:**

Francesco Bisi, Mosé Nodari, Nuno Miguel dos Santos Oliveira, Elisa Masseroni, Damiano G. Preatoni, et al.. Space use patterns of mountain hare (*Lepus timidus*) on the Alps. *European Journal of Wildlife Research*, 2010, 57 (2), pp.305-312. 10.1007/s10344-010-0429-2 . hal-00625149

HAL Id: hal-00625149

<https://hal.science/hal-00625149>

Submitted on 21 Sep 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Space use patterns of mountain hare (*Lepus timidus*) on the Alps

Francesco Bisi · Mosé Nodari · Nuno Miguel Dos Santos Oliveira · Elisa Masseroni · Damiano G. Preatoni · Lucas A. Wauters · Guido Tosi · Adriano Martinoli

Received: 19 October 2009 / Revised: 29 June 2010 / Accepted: 1 September 2010 / Published online: 21 September 2010
© Springer-Verlag 2010

Abstract Populations on the limits of species' distribution can show different behavioral adaptations to strong ecological pressure than in the central part of the range. We investigated space use patterns of alpine mountain hare (*Lepus timidus*) at two areas on the southern edge of the species' range. We monitored 34 hares between 2005 and 2008, estimating home range size, overlap, and site fidelity, and compared our results with space use in Scottish and North-European populations. Home ranges of mountain hares did not differ between two study areas with different habitat types. Subadult animals used larger ranges than adults and both age groups reduced home range size in autumn, a period that might be critical for hares due to changes in diet and/or high energy expenditure during the previous breeding season. Home ranges in these alpine populations were smaller than in Scandinavian populations but within the range of populations in different habitat types in Scotland. Seasonal home ranges overlapped considerably, but differed among the sexes: male–female overlap

was higher than same sex (male–male and female–female) spatial overlap. Seasonal shifts of home ranges were small, and site fidelity remained high over the seasons, suggesting that resource distribution remained constant throughout the year and that the knowledge of an intensively frequented area is an important element of habitat quality. We concluded that habitat structure and availability of mates interact in affecting mountain hare space use in alpine habitats.

Keywords Mountain hare · Home range · Site fidelity · Overlap · Distribution edge

Introduction

Increasing rates of environmental change, exacerbated by climate warming and/or growing human pressure (Sala et al. 2000; IPCC 2001), can lead to range contractions or expansions, variation in population dynamics and cause (local) extinction in species with narrow ecological niches (Thomas et al. 2006). Populations on the limits of a species' distribution range are generally considered to be under stronger ecological and genetic pressure than more central populations (Hampe and Petit 2005; Holt and Keitt 2005; Pearson et al. 2009). Moreover, populations at the edge of a species distribution may also have lower genetic diversity, due to habitat fragmentation, lower effective population size, and spatial isolation (Eckert et al. 2008). Consequently, at range margins, the population dynamics and spatial behavior of a species are likely to differ with respect to populations from the centre of the range. This can have strong implications for species management/conservation strategies near range margins. Therefore, exploring home range size, shape, and internal structure is of general

Communicated by C. Gortázar

F. Bisi (✉) · M. Nodari · D. G. Preatoni · L. A. Wauters · G. Tosi · A. Martinoli
Department Environment-Health-Safety,
University of Insubria Varese,
Via J.H. Dunant 3,
21100 Varese, Italy
e-mail: francesco.bisi@gmail.com

E. Masseroni
Oikos Institute Via Crescenzago 1,
20134 Milan, Italy

N. M. Dos Santos Oliveira
Animal Biology Department, Faculty of Science,
University of Lisbon,
Lisbon, Portugal

interest to population and conservation ecologists since knowledge of the size, shape, structure, and location of the home ranges is essential for defining and producing effective management strategies (e.g., Conner et al. 1999; Hanski et al. 2000; Lurz et al. 2000; R uhe and Hohmann 2004; Wauters et al. 2005). Here, we explore space use of mountain hare (*Lepus timidus*, Linnaeus 1758) living in alpine communities and compare our results with spacing behavior in populations living in the central part of their range.

Mountain hare is a boreo-alpine species with a wide distribution area (Angerbj orn and Flux 1995; Thulin and Flux 2003). In Europe, isolated alpine populations occur above 1,300 m in the mountains of France, Germany, Switzerland, Austria, Slovenia, and Italy (Couturier 1964; Isakovic 1970; Mitchell-Jones et al. 1999; Thulin and Flux 2003; Nodari et al. 2005). Although the ranging and the spacing behavior of mountain hare have been studied in Scotland (Hewson 1976; Hewson and Hinge 1990; Hulbert et al. 1996) and Scandinavia (Hiltunen et al. 2004; Dahl 2005a, b; Kauhala et al. 2005; Hiltunen 2006), virtually nothing is known about the social structure and home range characteristics of Alpine mountain hare *Lepus timidus varronis*.

Here, we report findings of an investigation into the home range and space use patterns of mountain hares from two areas in the Central Alps (Lombardy, Italy), which differ in habitat structure and composition.

Materials and methods

Study area

Mountain hares were studied in central Italian Alps in two different study areas. San Giacomo di Fraele (named ‘‘SG’’), is in the Stelvio National Park at 1,950 m asl nearby the artificial Cancano lakes (46°32' N, 10°16' E). The area is dominated by a homogeneous dwarf mountain pine (*Pinus mugo*) woodland with trees of both prostrate and arboreal habit. The undergrowth is composed of heather (*Erica carnea*), juniper (*Juniperus communis*), blueberry (*Vaccinium myrtillus*), and lingonberry (*Vaccinium vitis-idaea*). The second study area is in the nearby Vezzola valley (named ‘‘VZ’’) at 2,050 m asl, approximately 6 km from SG (46°29' N, 10°16' E). The habitat is a mixed forest with similar proportions of Norway spruce (*Picea abies*), Arolla pine (*Pinus cembra*), and larch (*Larix decidua*) with a homogeneous central patch of mountain pine (*P. mugo* about 20% of the entire forest). The undergrowth is composed mainly of heather (*E. carnea*) and rhododendron (*Rhododendron ferrugineum*) with juniper (*J. communis*) and blueberry (*V. myrtillus*).

Trapping and radio-tracking

Between March 2005 and March 2008, we trapped 34 mountain hares using Tomahawk single door cat/rabbit collapsible traps (66×25×25 cm, model 205, Tomahawk Live Trap Co, Tomahawk, WI, USA). In each study area, 25 traps were placed in a grid at 70-m intervals, for a total effort of 1,383 trap nights. Traps were covered with a synthetic outer shell fabric and a smaller wire mesh 1×1 cm to prevent the trapped hares from being injured by predators. Traps were pre-baited for at least 1 week with dry ‘‘alfalfa’’ (trade name of a *Medicago sativa* based food preparation). The trapping period changed each year depending on snow cover, usually from the beginning of January to the end of March. The traps were activated at dusk and checked at dawn. We trapped and radio-tagged 21 adult hares (ten males and 11 females) and 13 subadults (six males and seven females). We radio-collared the hares with ATS adjustable necklace transmitters weighing 35 g with a 24-h set mortality sensor (M1930 transmitters, Advanced Telemetry Systems Inc., Isanti, MN, USA). Hares were sexed and aged (subadult, under 7–8 months old, or adult) by observation of external genitals and by Stroh’s tubercle palpation (Stroh 1931). Radio-tagged hares were located using Wildlife receivers TRX-2000S (150–151 MHz, Wildlife Materials Inc., Murphysboro, IL, USA) and three-element ATS and Wildlife directional Yagi antenna.

The monitoring of the released animals began immediately after capture, and the animals were followed constantly for 24 h through homing-in (White and Garrott 1990) to check that radio-collars did not disturb normal hare behavior. In the following stages, we used triangulation (White and Garrott 1990) for the localisation of animals: two or more operators simultaneously detected the bearings of the signals coming from each animal using a 1° precision compass. On average, the distance between operators and tracked animals was <1 km. We monitored hares throughout the year 1 week per month, 6 h per day, taking one location (hereinafter called ‘‘fix’’) every 15 min during daytime and nighttime (four periods of 6 h each, starting at 0600, 1200, 1800 and 2400). At each fix, a hare’s location and activity (1=active, 2=not active) were recorded.

Home range analysis

Subsequently, all data were converted to the Italian coordinate reference system (Gauss-Boaga, West zone, Rome1940) in a GIS database Arcview 3.2 (ESRI Inc. 1999), and Locate II 3.11 software (Nams 2006) calculated the animals’ locations from the triangulation bearings. For each year, we estimated home range size at a seasonal basis: winter (December–March, ground continuously covered with snow), spring–summer (April–August, also called ‘‘breeding season’’, this is

the season with vegetation growth, mating and breeding activity), and autumn (September–November, post-breeding season, with no vegetation growth and no continuous snow cover). For hares that were monitored both as subadult and as adult, all data were used, and the individual was classified as subadult from its capture until the end of the following spring–summer (maximum age of a “subadult,” 13–14 months), and as adult afterwards. Within each season, between 20 and 848 fixes were collected per individual ($n = 119$ home ranges estimates, mean \pm SD = 91 ± 110).

All home range analyses were performed using R software 2.9.0 (R Development Core Team 2007). In a first step, we explored internal home range structure for core areas of high activity, examining the utilisation distribution (UD, range size included in 5% incremental isopleths containing between 20% and 95% of fixes) of the fixed kernel density estimator (KDE; Kenward et al. 2001). A one-way ANOVA with size of range included in a given isopleth as dependent variable and isopleth from the UD with a given percent of fixes (at 5% increments from 20% to 95% of all fixes) as class was calculated to define the core area. We estimated home range size using the fixed KDE (Worton 1989) with adjusted smoothing factor (KDE with *hadj*), following the method to calculate *hadj* proposed by Wauters et al. (2007).

Home range overlap, within each season, was expressed as percentage of overlap of a hare’s range with the home range of all other hares (Wauters and Dhondt 1992), and the number of overlapping hares of each sex was determined. Since capture–mark–recapture data indicated that >85% of resident hares were radio-collared (Bisi et al., unpublished data), we felt confident that the overlap analysis revealed the true social system.

Statistical analysis

We used 95% and 85% KDE as dependent variable in general linear models, which explored effects of study area, season, sex, and age classes (subadults and adults), using number of locations as covariate. Because some individuals were monitored in different periods, individual was used as a repeated measure. Only home range estimates based on more than 20 radio locations per season were used. Data on seasonal home-range size did not deviate from a normal distribution (Shapiro–Wilk statistic, $W > 0.9$). A final model was selected using a backward procedure excluding step by step from the complete model the factor that was least significant until only significant factors were left. Interpretations of final models were based on Tukey’s honestly significant difference test (hereinafter indicated as HSDt). Distribution of residual values of each selected final model did not deviate from a normal distribution (Shapiro–Wilk statistic, all $W > 0.9$).

Data of percentage overlap with animals of the same sex or with animals of the opposite sex did not deviate from a

normal distribution (Shapiro–Wilk’s $W = 0.94$, $p = 0.10$). Therefore, we used percent home range overlap with animals of either sex, calculated from the annual 95% KDE home ranges of all hares resident in 2006 and 2008 (largest sample size), as the dependent variable in a general linear model. We tested the fixed effects of study area (SG and VZ), season, and sex by overlapping sex interaction (e.g., Wauters et al. 2005). The interaction term allowed us to explore whether overlap differed among the sexes, in other words whether there were differences in overlap for male by males, male by females, female by males, and female by other females.

We also tested whether overlap was affected by the local density of hares using a linear regression of percentage overlap per individual on number of hares that overlap the individual.

We explored site fidelity of hares by calculating the percentage overlap of each individual’s home range in one season with its home range the next season. We estimated four “season with season combinations” (hereinafter called “between seasons effect”) of site fidelity, using the formula: $O_{1,2}/(A_1 + A_2 - O_{1,2})$, where $O_{1,2}$ = the common area between the two home ranges, A_1 = the total area of the first home range, and A_2 = the total area of the second home range (Dahl 2005a).

The four combinations were as follows: (1) overlap winter with breeding season ranges, (2) overlap breeding season with autumn ranges, (3) overlap winter with autumn ranges, and (4) overlap of a seasonal home range between two consecutive years (e.g., winter yr_t –winter yr_{t+1}). We used a general linear model to investigate whether degree of site fidelity (percentage between season overlap of an individual as dependent variable) was affected by sex, study area, and season.

Results

Core area analysis showed a significant increase in the pairwise comparison between 85% and 90% isopleths ($p < 0.001$); thus, the 85% KDE was used as core-area estimator. Both 95% (home range) and 85% KDE (core area) estimates of range size were used as dependent variables in general linear models (see “Materials and methods”). Since the significant explanatory factors in both models were the same, we only present results for KDE95 home range estimates as response variable in this and successive analysis.

Home range size varied between 1.24 and 156.17 ha ($n = 119$, mean \pm SD = 54.06 ± 32.78 ha, Table 1). Number of locations did not affect estimates of home range size, and there was no effect of study area and sex. None of the two-factor interactions were significant (Table 2). In the selected model only season and age affected variation in home range size. Hares used smaller ranges in autumn than

Table 1 Home range size in hectares (mean±SD), sample size, and range

	Males	Females	Both sexes
Seasons			
Autumn	48.39±32.67 (15) 15.08–127.20	35.48±30.51 (19) 1.21–135.80	41.17±31.67 (34) 1.24–127.20
Breeding	56.48±24.50 (23) 10.00–102.00	65.73±30.45 (22) 16.00–119.52	61.19±27.68 (45) 10.00–119.52
Winter	66.03±39.82 (19) 10.64–157.16	48.82±31.80 (21) 11.04–145.40	56.99±36.41 (40) 10.64–145.40
All seasons	57.68±32.55 (57) 10.00–157.16	50.73±32.90 (62) 1.24–145.40	54.06±32.76 (119) 1.24–157.16
Age classes			
Adults	52.56±29.37 (45) 10.00–127.20	45.37±31.89 (43) 1.24–145.40	49.05±30.67 (88) 1.24–145.40
Subadults	76.86±37.86 (12) 40.00–157.16	62.86±32.72 (19) 19.68–121.52	68.28±34.87 (31) 19.68–157.16

in the breeding season (season effect $F_{2,115}=4.19$, $p=0.02$; mean difference, 20 ha, HSDt $p=0.02$), and subadults used larger ranges than adults (age effect $F_{1,115}=4.89$, $p=0.03$; difference, 13.9 ha; Fig. 1).

Overall home range overlap among hares was $38\% \pm 24$ ($n=418$; range, 0–100%). In the general linear model, factors sex, season, area, and their two-way interactions were significant (sex $F_{3,121}=8.91$; season $F_{2,121}=33.0$; area $F_{1,121}=41.1$; all $p<0.001$). Males were overlapped more strongly by females than any of the other combination among the sexes (MF>MM, HSDt $p<0.01$; MF>FM, HSDt $p=0.01$; MF>FF, HSDt $p=0.01$) (Table 3). There was no difference in the degree of intra-sexual overlap between the

sexes (MM not different from FF, HSDt $p=0.09$). Percentage overlap at study area SG was higher than at VZ, while in autumn, hares overlapped less than in the other seasons (WIN>AU and BREEDING>AU, HSDt $p<0.01$). A sex-by-area interaction ($F_{3,121}=7.45$, $p<0.001$) was explained by different patterns of inter-sexual overlap being significant only in SG but not in VZ (VZ, HSDt all $p>0.4$). The area by season interaction ($F_{2,121}=7.93$, $p<0.001$) indicated that the higher overlap at SG than VZ was significant only in winter (HSDt SG-VZ in winter $p<0.01$; other seasons, $p>0.05$). A sex-by-season interaction ($F_{6,121}=2.40$, $p=0.032$) was caused by the absence of a season effect on male–male overlap (MM, HSDt all between season combinations, $p>0.3$) and different seasonal patterns for the other combinations of overlapping sexes. Males were more strongly

Table 2 General linear model testing effects of number of locations (Num), study area, season, sex and age, and their two-way interactions on the mean home range size (estimated by 95% KDE) of mountain hare in two areas of the Italian Alps

Model parameters	Statistics
Num	$F_{1,100}=0.01$, $p=0.92$
Study area	$F_{1,100}=0.12$, $p=0.73$
Sex	$F_{1,100}=1.38$, $p=0.24$
Season	$F_{2,100}=4.14$, $p=0.019$
Age	$F_{1,100}=5.80$, $p=0.018$
Num×area	$F_{1,100}=0.54$, $p=0.46$
Num×sex	$F_{1,100}=1.32$, $p=0.25$
Num×season	$F_{2,100}=0.14$, $p=0.87$
Num×age	$F_{1,100}=0.01$, $p=0.91$
Study area×sex	$F_{1,100}=3.16$, $p=0.08$
Study area×season	$F_{2,100}=2.02$, $p=0.14$
Study area×age	$F_{1,100}=0.02$, $p=0.88$
Sex×season	$F_{2,100}=1.70$, $p=0.19$
Sex×age	$F_{1,100}=0.89$, $p=0.35$

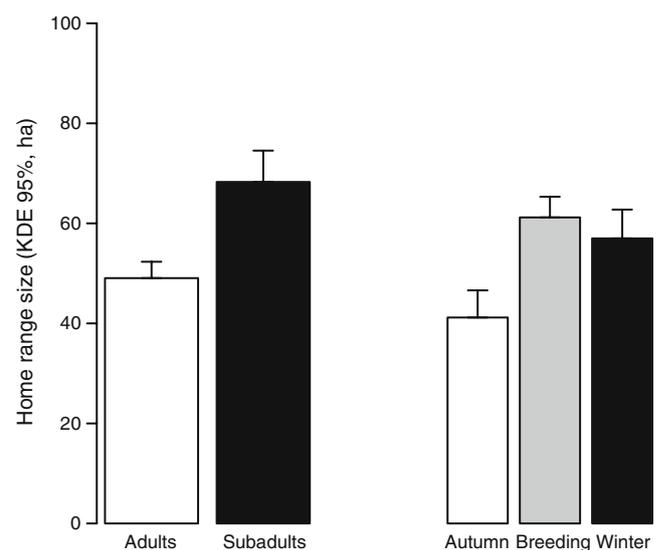
**Fig. 1** Differences in home ranges size (mean±SE) considering age classes and seasons

Table 3 Total percentage home range overlap by season (mean±SD) for each combination of sex overlapped by sex overlapper

Season	Male by males	Male by females	Female by males	Female by females
Winter	97±68	213±148	114±55	153±99
Breeding season	91±44	143±60	161±35	126±59
Autumn	19±22	71±66	37±42	49±43

overlapped by females in winter than in autumn (WIN>AU, HSDt $p<0.001$), while females were more strongly overlapped by males in the breeding season than in autumn (BREEDING>AU, HSDt $p<0.001$). Finally, intra-sexual overlap among females was most reduced in autumn (WIN>AU and BREEDING>AU, HSDt $p<0.05$).

Variation in number of overlapping animals explained 56% of variation in percentage of overlap ($F_{1,137}=175.4$; $p<0.0001$; $R^2=0.56$).

Site fidelity of mountain hares, measured as an individual's percentage seasonal overlap, was $33\pm 11\%$ ($n=125$; range; 2–59%). There was no effect of between-seasons comparisons on degree of site fidelity (between-season index $F_{3,120}=1.33$, $p=0.27$). In the final model, only the factor area was significant (area $F_{1,123}=18.8$, $p<0.01$), with higher site-fidelity in SG (site fidelity mean±SD, SG = 36 ± 9 ; VZ = 28 ± 12).

Discussion

Home range size

The use of different field methods and home range size estimators in studies of spacing patterns reduces the reliability of between-study comparisons (e.g., Marboutin 1997; Wauters et al. 2001). Therefore, we tried to limit our comparisons to studies that used similar time periods and range-size estimators to our study. However, because few results are available throughout the species' range, we also included some home range estimates obtained with minimum convex polygons (100% or 95% MCP). In our areas, MCPs and 95% KDE estimates were strongly correlated (100MCP, $r=0.59$, $df=117$, $p<0.01$; 95MCP, $r=0.89$, $df=117$, $p<0.01$).

Average home range size (95% KDE) of mountain hares in our two areas (SG, males 63 ha, females 46 ha; VZ, males 52 ha, females 60 ha) was smaller than in Scandinavian populations (Sweden, males, 219 ha, females, 66 ha, Dahl 2005b; Dahl and Willebrand 2005; Finland, both sexes, 206 ha, Kauhala et al. 2005), but within the range of populations in different habitat types in Scotland (95% MCP, males, 22.0 ha, females, 14.9 ha; 100% MCP males, 113 ha, females, 89 ha; Hewson and Hinge 1990; Hulbert et al. 1996; Rao et al. 2003). In Ireland, median (100% MCP) of 46 ha for males and 21.5 ha for females

were recorded (Wolfe and Hayden 1996). In our study areas, there were no differences in home range size between the sexes or between areas, despite higher densities at SG than VZ.

Compared with other alpine populations, home ranges in this study were on average larger than in a nearby site (about 100 km) in the Swiss Alps (38 ha, Genini-Gamboni et al. 2008), but much smaller than in the Austrian Alps (National Park Hohen Tauern), where an average home range size of 551 ha was reported (Slotta-Bachmayr 1998). These comparisons must be considered with care as: (a) only eight hares were monitored for about 1 year in the Swiss study, and (b) there is no information on possible temporal variation of range size in the Austrian study. In Austria, most of the tagged hares made regular movements of more than 1 km, covering in some cases an elevation range of more than 400 m, within 24 h. We reported this behavior for only one of our tagged hares in VZ area. Since home range size in Lagomorphs tends to be negatively correlated with food supply (Boutin 1984), the differences between alpine habitats could be related to habitat related variation in food productivity among the study areas. However, the cited studies did not give details on habitat structure and/or productivity, prohibiting useful comparisons.

Weather conditions in the Alps are more similar to Scandinavia than to the British Isles, with long cold winters with permanent snow cover for several months. If weather affects space use, we would expect home ranges to be more similar to Scandinavian than to Scottish populations, but this was not the case. Larger ranges in Finland could be related with poor habitat productivity (unproductive barren heath, Kauhala et al. 2005). Moreover, where habitat structure is a mosaic of patches of different quality, in terms of availability of suitable resting and foraging sites, as reported in Scotland (Hewson and Hinge 1990; Hulbert et al. 1996; Rao et al. 2003), we suggest that space use is strongly related to habitat structure.

In agreement with studies in Northern Europe (Kauhala et al. 2005; Dahl and Willebrand 2005), we found significant differences in autumn home range compared to home range size in the other seasons. In autumn, hares have just finished a period of high energy expenditure due to breeding activity, and in other populations, the end of the breeding season is the period of the year when hares have the lowest body mass (Van der Merwe and Racey 1991). Hence, they might reduce

activity and space use to decrease their energy expenditure. An alternative but not mutually exclusive hypothesis is that reduction of home-range size in autumn is an anti-predatory strategy. Small ranges in autumn could be related to hares being in mid-moult (Flux 1970b), becoming completely white in November–December. Hence, lack of snow cover in November–early December could force hares to reduce space use to decrease predation risk.

Studies exploring age effects on spatial behavior (juveniles, subadults, and adults) of mammals have found different age-dependent responses in relation to study species, population density, habitat type, and sex (Wauters and Dhondt 1992; Wooding and Hardisky 1994; Forsys and Humprey 1996). Usually, adults have well-defined behavioral tactics: they know where to find preferred resources and how and where to find mates. In contrast, behavior of subadults may gradually change with age: Their home range could resemble that of adults or completely change in size and location over time. In our study, subadults (<13 months old) had larger home ranges than adults. Young hares may make major exploratory movements to gather information about the habitat (patches with good shelter and food), a behavior not necessary for adults, which have already knowledge of the surrounding area. Another possible explanation is that adults behave aggressively against subadults, forcing them to roam over larger areas.

Overlap and site fidelity

In Northern Europe, the mountain hare is documented as a non-territorial species (Flux 1970b; Hewson 1976; Hewson 1988; Hewson and Hinge 1990; Dahl 2005b), and seasonal home ranges of mountain hares in the present study overlapped considerably, indicating a lack of territorial behavior in both males and females. The degree of overlap was higher in SG than VZ, where densities were also higher (winter densities in SG and VZ respectively 12 and four hares per square kilometer, our unpublished data). Thus, higher densities did not cause a reduction in home range size of hares (no effect of study area on home range size), but resulted in higher degrees of range overlap (see also Swihart 1986). This tendency was confirmed by percentage overlap increasing with number of overlapping individuals.

In mammals, reproductive investment differs between the sexes, and the type of mating system affects spatial behavior (Ostfeld 1990). Consequently, male space use patterns tend to be mainly determined by distribution of potential mates, while female spacing is mainly affected by distribution of food resources or safe shelter for nursing young. In this study, we found that intersexual overlap in males (thus with females) was larger than intrasexual overlap in each sex. This could be related to male mating

behavior, males trying to overlap with several oestrous females over the breeding season (Flux 1970a; Angerbjörn and Flux 1995). In fact, females were more strongly overlapped by males in the breeding season than in autumn.

Mountain hares in our study areas did not shift their home ranges completely from one season to the next or from 1 year to the next. Hence, site fidelity remained high over the different seasons (Fig. 2) and years, suggesting that distribution of food resources and shelter did not vary throughout the year in our alpine habitats. In contrast, hares in boreal forest used different areas in different seasons in relation to distribution of resources (Dahl 2005b). This long-term (year to year) site fidelity agrees with the hypothesis proposed by Dahl and Willebrand (2005) that the knowledge of an intensively frequented area is an important element of habitat quality.

Strong site fidelity and a lack of long distance movements in subadult hares suggest that the species depends strongly on local habitat structure and/or productivity. This implies that management of mountain hare populations in the Alps should be based on monitoring of local hare densities in different areas/habitats, using standardized indices (e.g., counts of hare signs on line transects, our unpublished data) that correlate with true numbers. Since space use data suggest a limited capacity to colonize new areas, unmanaged hunting with no consideration to population size estimates might increase risk of local extinction of mountain hares in habitats where they occur at low densities.

Our data suggest that habitat structure, density, and availability of mates all interact in affecting mountain hare space use. Home range size was larger than in most Scottish studies (populations with relative high hare densities and productive habitats) and smaller than in boreal forests

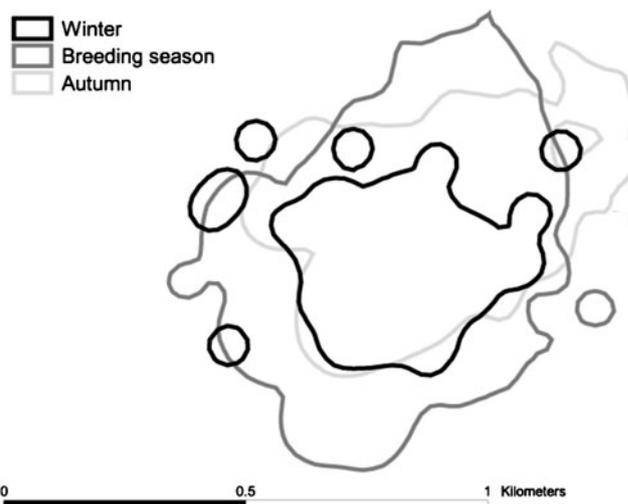


Fig. 2 Examples of an individual's winter, breeding season, and autumn home ranges (KDE 95%, ha)

where food availability is believed to be lower than in our alpine sites. Unfortunately, quantitative measures of food abundance are generally lacking, but detailed data on habitat structure and composition can be obtained for most studies. Hence, comparative studies exploring resource selection of mountain hares, over differently structured landscapes and habitat types, will be necessary to understand how this species adapts its space use to available habitat types and resources.

Acknowledgements We wish to thank the Sondrio Province personnel Andrea Vanotti, Maria Ferloni, and all the game wardens; the Stelvio National Park personnel Luca Pedrotti, Alessandro Gugliatti, and all the game wardens; Alessandro Bianchi for the veterinary support; A. Guizzardi, P. Bertoglio, L. Perlasca, L. Tarengi, E. Trizio, F. Ossi, and C. Rota for assistance with fieldwork. Peter Lurz and Annabel Harrison reviewed the text and constructive comments by two reviewers greatly helped to improve the manuscript. The study was part of the Mountain Hare Research (MoHaRe) project, carried out by University of Insubria, Varese and Istituto Oikos, Milan. Financial support was provided by the Wildlife Service of the Province of Sondrio and the Stelvio National Park.

References

- Angerbjörn A, Flux JEC (1995) *Lepus timidus*. Mamm Species 495:1–11
- Boutin S (1984) Effect of late winter food addition on numbers and movements of snowshoe hare. *Oecologia* 62:393–400
- Conner M, Plowman B, Leopold BD, Lovell C (1999) Influence of time-in-residence on home range and habitat use of bobcats. *J Wildl Manage* 63:261–269
- Couturier M (1964) *Le gibier des montagnes francaises*. Arthaud, Grenoble
- Dahl F (2005a) Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. *Eur J Wildl Res* 51(3):163–169. doi:10.1007/s10344-005-0095-y
- Dahl F (2005b) Life and death of the mountain hare in the boreal forest of Sweden. Dissertation, Swedish University of Agricultural Sciences, Umea, Sweden
- Dahl F, Willebrand T (2005) Natal dispersal, adult home ranges and site fidelity of mountain hares *Lepus timidus* in the boreal forest of Sweden. *Wildl Biol* 11:309–317
- Eckert CG, Samis KE, Loughheed C (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol Ecol* 17:1170–1188. doi:10.1111/j.1365-294X.2007.03659.x
- ESRI Inc. (1999) Using ArcView GIS version 3.2. Environmental Systems Research Institute, Inc., Redlands, CA, USA
- Flux JEC (1970a) Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. *J Zool (Lond)* 161:75–123
- Flux JEC (1970b) Colour change of mountain hares (*Lepus timidus scoticus*) in north-east Scotland. *J Zool (Lond)* 162:345–358
- Forys EA, Humprey SR (1996) Home range and movements of the lower marsh rabbit in a highly fragmented habitat. *J Mammal* 77(4):1042–1048
- Genini-Gamboni AS, Bisi F, Masseroni E, Nodari M, Preatoni DG, Wauters LA, Martinoli A, Tosi G (2008) Home range dynamics of mountain hare (*Lepus timidus*) in the Swiss Alps. *Hystrix It J Mammal* 19(2):77–83
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8:461–467. doi:10.1111/j.1461-0248.2005.00739.x
- Hanski IK, Stevens PC, Ihalempia P, Selonen V (2000) Home range size, movements and nest-site use in the Siberian flying squirrel, *Pteromys volans*. *J Mammal* 81(3):798–809
- Hewson R (1976) A population study of mountain hares (*Lepus timidus*) in North-East Scotland from 1956–1969. *J Anim Ecol* 45(2):395–414
- Hewson R (1988) Spacing and habitat preference of mountain hares in Shetland. *J Appl Ecol* 25(2):397–407
- Hewson R, Hinge MDC (1990) Characteristics of the home range of mountain hares *Lepus timidus*. *J Appl Ecol* 27(2):651–666
- Hiltunen M (2006) The ecology of the mountain hare (*Lepus timidus*) in managed boreal forests: habitat associations at different forest scales. Dissertation, University of Helsinki, Helsinki, Finland
- Hiltunen M, Kauhala K, Linden H (2004) Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. *Acta Theriol* 49(4):479–490
- Holt R, Keitt T (2005) Species' borders: a unifying theme in ecology. *Oikos* 108:3–6
- Hulbert IAR, Iason GR, Elston DA, Racey PA (1996) Home range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. *J Appl Ecol* 33(6):1479–1488
- IPCC (2001) Climate change 2001: the scientific basis. Contribution of Working Group I to the Third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Isakovic I (1970) Game management in Yugoslavia. *J Wildl Manage* 34:800–812
- Kauhala K, Hiltunen M, Salonen T (2005) Home ranges of mountain hares *Lepus timidus* in boreal forests of Finland. *Wildl Biol* 11(3):193–200
- Kenward RE, Clarke RT, Hodder KH, Walls SS (2001) Density and linkage estimators of home range: nearest-neighbour clustering defines multinuclear cores. *Ecology* 82:1905–1920
- Lurz PWW, Garson PJ, Wauters LA (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels, *Sciurus vulgaris* L. *J Zool (Lond)* 251:167–178
- Marboutin E (1997) A note on home range size in the European hare (*Lepus europaeus*). *Gibier Faune Sauvage* 14(3):349–357
- Van der Merwe M, Racey PA (1991) Body composition and reproduction in mountain hares (*Lepus timidus scoticus*) in North-East Scotland. *J Zool (Lond)* 225:676–682
- Mitchell-Jones AJ, Amori G, Bogdanowicz W, Krystufek B, Reijnders PJH, Spitzenberger F, Stubbe M, Thissen JMB, Vohralik V, Zima J (1999) Atlas of European mammals. Academic, London
- Nams VO (2006) Locate III user's guide. Pacer Computer Software, Tatamagouche
- Nodari M, Masseroni E, Preatoni DG, Wauters LA, Tosi G, Martinoli A (2005) Live-trapping success of the mountain hare (*Lepus timidus*) in the southern Italian Alps. *Hystrix It J Mammal* 16:143–148
- Ostfeld RS (1990) The ecology of territoriality in small mammals. *Trends Ecol Evol* 5:411–415
- Pearson GA, Lago-Leston A, Mota C (2009) Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *J Ecol* 97:450–462. doi:10.1111/j.1365-2745.2009.01481.x
- R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rao SJ, Iason GR, Hulbert IAR, Racey PA (2003) The effect of establishing native woodland on habitat selection and ranging of moorland hares (*Lepus timidus*), a flexible forager. *J Zool (Lond)* 260:1–9. doi:10.1017/S0952836903003534

- Rühe F, Hohmann 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. doi:10.1007/s10344-004-0049-9
- Sala OE, Chapin FSIII, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774. doi:10.1126/science.287.5459.1770
- Slotta-Bachmayr L (1998) Biologie und Ökologie des Alpenschneehasen (*Lepus timidus varronis* Miller 1901). Verbreitung, Raumnutzung, Aktivität und Habitatwahl in den Hohen Tauern. Dissertation, Paris Lodron Universit, Salzburg, Austria
- Stroh G (1931) Zwei sichere Altersmerkmale beim Hasen. *Berl Tierärztl Wochenschr* 12:180–181
- Swihart RK (1986) Home range—body mass allometry in rabbits and hares (Leporidae). *Acta Theriol* 31:139–148
- Thomas CD, Franco AM, Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends Ecol Evol* 21:415–416. doi:10.1016/j.tree.2006.05.012
- Thulin C-G, Flux JEC (2003) *Lepus timidus* (Linnaeus 1758). Schneehase. In: Niethammer J, F Krapp (ed) *Handbuch der Säugetiere Europas*, Band 3/II, Lagomorpha. Aula Verlag, Wiebelsheim. pp 155–185.
- Wauters LA, Dhondt AA (1992) Spacing behaviour of the red squirrel, *Sciurus vulgaris*, variation between habitats and the sexes. *Anim Behav* 43:297–311
- Wauters LA, Gurnell J, Preatoni D, Tosi G (2001) Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography* 24:525–538
- Wauters LA, Bertolino S, Adamo M, van Dongen S, Tosi G (2005) Food shortage disrupts social organization: the case of red squirrels in conifer forests. *Evol Ecol* 19:375–404. doi:10.1007/s10682-005-8311-5
- Wauters L, Preatoni DG, Molinari A, Tosi G (2007) Radio tracking squirrels: performance of home range density and linkage estimators with small range and sample size. *Ecol Model* 202:333–344. doi:10.1016/j.ecolmodel.2006.11.001
- White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic, San Diego
- Wolfe A, Hayden TJ (1996) Home range sizes of Irish mountain hares on coastal grassland. *Biol Environ Proc Royal Ir Acad* 96B (3):141–146
- Wooding JB, Hardisky TS (1994) Home range, habitat use and mortality of black bears in north-central Florida. *Int Conf Bear Res Manage* 9(1):349–356
- Worton B (1989) Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164–168