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Annual and seasonal home range and distances of movements of released hares (*Lepus europaeus* Pallas, 1778) in Central Poland

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Abstract. Presented here are the results of research on spatial organisation among hares originating from enclosure-type rearing but released into a natural environment for them. The fates of the 60 animals were traced by radiotelemetry in the course of four successive years of research. The mean annual home range size was found to be 1.68 km² in males, significantly greater than that noted for females (0.43 km²). Similar relationships were observed in the case of seasonal ranges. The mean distance of movements noted for hares between successive radio-locations in the first month after release (at 239 m) was significantly greater than that noted for the second month (103 m) or the third (116 m). The mean distance of movement within individual annual home range for the males hares was 335 m and was significantly greater than that for females (226 m). Similar findings were obtained for seasonal ranges.

Key words: brown hare, release, radiotelemetry, home range, movements

Introduction

The goal of protecting, saving and rebuilding populations of endangered animal species is being pursued worldwide using a very wide range of methods. The drastic decline in numbers of brown hares (*Lepus europaeus*) across Europe (also in Poland) has given rise to a situation in which many states have sought to take measures to protect and then rebuild the ever-declining populations of the species. In recent years, brown hare has been added to Annex III of the Berne Convention. In turn, in Norway, Germany, Austria and Switzerland the species has now been entered in Red Books as Near-Threatened or Threatened (Boye 1996, Pfister et al. 2002, Reichline et al. 2006, Roedenbeck & Voser 2008).

In Poland, activity in the name of conservation has first and foremost sought to increase the biodiversity of hunting areas, as well as to reduce numbers of predators. In recent years, the goal of saving the brown hare has also been pursued by way of releases to supplement depleted populations, using hares from various different types of cage- or enclosure-based raising facilities (Dziedzic 2007). This type of activity is embarked upon where a population has

fallen to a critically low level, and there is only now a very limited possibility of spontaneous population recovery. What is then applied is the method of so-called reinforcement or restocking of local populations by means of the release of individuals originating in captivity or translocated from other populations (Paullin 2004). It is considered that such measures may have a major role to play in the animal species conservation, being capable of increasing genetic diversity, as well as ensuring a return of threatened populations to demographic equilibrium, thereby raising their chances of long-term survival.

There are only scanty data on the effectiveness of restocking hare population and their spatial organisation in new environment after release. Some researchers have made use of radiotelemetry, but with a few notable exceptions (Marboutin et al. 1990, Angelici et al. 1999, Angelici et al. 2000), this kind of work has only been continued with for a very brief period, not exceeding 12 months.

Existing data on home ranges and movement behaviours of brown hares concerned wild animals. Presented here results are the very first data concerned the spatial organisation of a group of hares

originating in captivity but released into their natural habitat. Specifically, the aim of this research was the determination of individual home range sizes in released hares, in annual and seasonal terms, as well as the assessment of the degree to which released hares were sedentary or inclined to move around. The presented study is part of larger brown hare project that includes studies of population dynamic, spatial organisation and habitat use of released hares.

Study Area

The research was carried out over the four years between November 2005 and November 2009, Central Poland (Mazowia), on the territory of the community of Maciejowice (51°45' N, 21°26' E). This study area (approx. 18 km²) is located c. 60 km south of Warsaw. More than half (c. 53 %) of the study area is covered by cultivated fields. Windbreaks, hedges and areas of planted trees in the middle of fields together account for some 10 % of the area, while the land within flood banks accounts for 8 %. The forest within the study area (taking some 18 % of it) forms part of a larger complex. Orchards and meadows in turn cover c. 3 % of the area, while areas that are not suitable for hares (e.g. roads, built-up areas and rivers) account for c. 8 % (for a detailed description of the study area see Misiorowska & Wasilewski 2008, 2012). The mean autumn population density of hares in the study area over the four years was c. 10 individuals per km².

Material and Methods

The research was based on around 60 hares raised in 20 ha open-field enclosures within Świebodzin Forest District that had been radio-collared with radio-transmitters and were released into the field in three groups (of 29, 15 and 16) in 2005, 2006 and 2007 respectively (Table 1). Releases took place in autumn, at the end of November. All animals were born in open-field enclosures. They were harvested by nets, next their sex was defined and individuals were put into single wooden cages. The same day, hares were transported to the place of release. The next morning hares were weighed, radio-collared and released directly into the field. In the first year of study animals were released in three different sites within the study area, and only in a single location the next two years. The mean weight of females was 3.7 kg (range: 2.7-4.9) and males 3.8 kg (range: 2.7-4.8). The exact age of the released hares was not known. Based on the existing data on body weight increments during hares lifespan, the age of individual hares could be assumed as younger than six months in individuals less than 2.7

kg. Unfortunately, the body weight increments of the hares raised in open-field enclosures were not been studied till now. Therefore, the age of released hares was not considered in presented paper. Moreover, from 60 released radio-collared hares, the only two individuals (one female and one male) weighing 2.7 kg, survived only one day and eight days respectively so they have been excluded from the analysis on spatial organisation. The average weight of the all other hares was near 4 kg, which indicates their adulthood. Hunting did not occur in the study area.

Table 1. Characteristics of the hares released in successive years.

Gender	Year			Total
	November 2005	November 2006	November 2007	
Females	18	11	10	39
Males	11	4	6	21
Both	29	15	16	60

Radiotelemetry

Radiotelemetry was used to study the spatial organisation of the released hares. Animals were collared with radio-transmitters outfitted with internal antenna and with “active” mortality sensors (models TXP-1 and TXP-R, 40 and 55 g; Televilt, Sweden). The lifespan of the radio-transmitters was c.18 months. Hares were monitored over a period of four years, between November 2005 and November 2009. The locations of given individuals were determined by means of triangulation (Harris et al.1990, Kenward 1993, R  he 1999), and such readings were obtained 2-3 times (mean 2.8 ± 1.3 times) per week, both in the day and at night. The analyses of obtained data were made using the TRACKER 1.0 program (Radio Location System AB, Hudding, Sweden). A more detailed description of the radiotelemetry is provided by Misiorowska & Wasilewski (2012).

Estimation of home ranges, size of annual home ranges Annual home ranges were determined for individuals that managed to survive through a full year (between January 1st and December 31st). The first month after release (December) was treated as an adaptation period, and no account in the analysis of annual home range sizes was taken of data collected then. Where a given hare lived through two full years, the home ranges for each year separately were determined. Annual home ranges were determined by the traditional method of the minimum convex polygon (MCP) – Stickel 1954, Kenward 1993, with account

taken of 95 % of the location points located closest to the centre of the home range. This method has been resorted to most often when home ranges for hares and other mammal species had to be determined (White & Garrot 1990, Marboutin & Aebischer 1996, Kunst et al. 2001, R  he & Hohmann 2004).

Sizes of seasonal home ranges

For the purposes of the research into spatial organisation among hares released, a division of the year into seasons was adopted, involving: (1) spring-summer (from March 1st through to August 31st), as well as: (2) autumn-winter (September 1st to February 28th). This division arose first and foremost in line with the breeding season in hares, which extends from March through to September (Pielowski 1979, Broekhuizen & Maaskamp 1981). In the seasonal analyses of the home ranges, only data obtained in spring-summer and the second autumn-winter were included. The data recorded in the first autumn-winter (subsequent to the release) were not included into the analyses.

Seasonal home ranges were only determined for those individuals surviving for a minimum of 16 months after release, that is a complete spring-summer and autumn-winter sequence, in order to make it possible for a comparison of locations that are representative and similar to be made. The sizes of the two seasonal home ranges for each individual were determined, the MCP 95 % method being used in the estimation.

Overlap of seasonal home ranges

The degree of overlap of the seasonal home ranges of given individuals was determined using the following formula:

$$Ov = \frac{2Sc}{(Sa + Sb)} \cdot 100[\%]$$

where Ov is degree of overlap; Sa, Sb are the (km²) areas of home ranges of the same individual in the spring-summer and autumn-winter seasons, Sc is the (km²) area common to both seasonal home ranges for a given animal and hence overlapping.

Estimation of distances moved

Distances moved by hares were determined on the basis of data for successive radio-locations of animals. The time intervals between the successive locations of all individuals were assumed as three days randomly at morning, afternoon, evening or night. For the further analyses, only animals with complete, same days

location in established time intervals were selected. The distances moved by hares between successive location were determined on the basis of the formula presented below, which characterises the Euclidean distance between two points on a plane.

$$O = \sqrt{((X_1 - X_2)^2 + (Y_1 - Y_2)^2)} [m]$$

where O is the distance between two consecutive radio-locations, X₁ and Y₁ are the coordinates for the first location, X₂ and Y₂ are the coordinates for the second location.

Statistical methods

Data were analysed using parametric tests – analysis of variance (ANOVA) and the t-test, as well as a non-parametric tests in the form of the Mann-Whitney U test. Differences were deemed significant where $p \leq 0.05$, highly significant where $p \leq 0.01$.

Results

Characterisation of home ranges, annual home ranges

Annual home range sizes were determined in the case of 21 hares. However, for some animals it was possible to determinate theirs home ranges for two consecutive years. For the final analysis the total of 25 home ranges were delineated (16 for females and 9 for males). The mean number of radio-locations used in determining home range size was 95 (range: 45-110).

Home range sizes in males were between 0.5 and 5.22 km² (mean 1.68 km²), and were significantly larger than those determined for females, at 0.07-0.92 km², and 0.43 km² on average (Mann-Whitney U test, U = 12, $p < 0.01$) (Table 2, 3).

Seasonal home ranges

The material collected allowed to determine the sizes of home ranges in different seasons (i.e. in the spring-summer and autumn-winter periods) for 16 hares (10 females and 6 males). In total, 32 seasonal ranges were therefore subject to analysis (Table 2, 3).

The spring-summer home ranges of males covered between 0.28 and 4.91 km², the average being 1.80 km² and were significantly larger than in females (Mann-Whitney U test, U = 7, $p < 0.05$). Specifically, females in this period used areas covering between 0.06 and 0.73 km², the average being 0.30 km².

In the autumn-winter period, males had home ranges covering between 0.24 and 0.98 km² (average 0.52 km²), and this was again a significantly larger than

Table 2. Annual and seasonal home ranges of females (F) and overlap between the seasonal home ranges. (a – second annual home range for on individual which survived more than one year).

Females	Annual	Size (MCP 95 %) of home range (km ²)		Overlap to the seasonal home ranges	
		Seasonal: spring-summer	Seasonal: autumn-winter	Common area – average (km ²)	Degree of overlap – average (%)
F00	0.18				
F01	0.93	0.14	0.16	0.12	78
F02	0.73	0.73	0.19	0.19	41
F02a	0.64				
F03	0.07	0.06	0.05	0.04	75
F04	0.34				
F05	0.17	0.10	0.21	0.01	64
F09	0.77				
F10	0.42	0.34	0.28	0.18	58
F10a	0.30				
F14	0.28	0.35	0.25	0.14	46
F18	0.42				
F19	0.45	0.38	0.17	0.15	54
F27	0.42	0.36	0.31	0.21	64
F30	0.34	0.18	0.38	0.18	63
F32	0.40	0.38	0.11	0.01	40
Mean	0.43 (± 0.23)	0.30 (± 0.19)	0.21 (± 0.10)	0.14	58
Range of values	0.07-0.93	0.06-0.73	0.05-0.38		

Table 3. Annual and seasonal home ranges of males (M) and overlap to the seasonal home ranges. (a – second annual home range for the individual which survived more than one year).

Gender	Annual	Size (MCP 95 %) of home range (km ²)		Overlap to the seasonal home ranges	
		Seasonal: spring-summer	Seasonal: autumn-winter	Common area – average (km ²)	Degree of overlap – average (%)
Males					
M16	5.22	4.91	0.30	0.30	12
M17	0.60				
M23	2.61	2.28	0.85	0.52	33
M23a	1.34				
M24	0.61	0.66	0.47	0.47	83
M26	2.21	1.70	0.98	0.64	48
M29	0.98	0.97	0.30	0.30	47
M29a	1.10				
M33	0.50	0.28	0.24	0.13	51
Mean	1.68 (± 1.51)	1.80 (± 1.69)	0.52 (± 0.32)	0.39	46
Range of values	0.50-5.22	0.28-4.91	0.24-0.98		

those of females, whose home ranges were 0.05-0.38 km² (0.21 km² on average) (Mann-Whitney U test, $U = 8$, $p < 0.05$). Mean sizes of the home ranges of males did not differ significantly from one season to another (U test, $U = 32$, $p > 0.05$), and the same kind of relationship applied to females (Mann-Whitney U test, $U = 36$, $p > 0.05$) (Table 2, 3).

The overlap of seasonal home ranges

In the case of females, there was c. 60 % overlap between the spring-summer and autumn-winter home ranges, the corresponding figure for males being at the level of 46 %. These differences between the sexes

did not achieved statistical significance, however (Mann-Whitney U test, $U = 19$, $p > 0.05$) (Table 2, 3). The marked overlap in seasonal home ranges in both sexes attests to the fact that introduced animals made use of the same areas in spring-summer and autumn-winter.

Distances moved by released hares

Over the course of the four years, all the tagged and released hares moved around within a c. 18 km² area. This was determined by reference to the most distant locations obtained for released individuals, and was thus seen to fall entirely within a single Hunting District.

Distances moved in the first three months after release
In the course of the relocating of released hares, it became clear that the individuals under study moved large distances in the first month after release, most likely because they were seeking out a suitable place in which to reside. In the light of this, a comparison was made of distances between consecutive radio-locations separately in each of the first three months after hares were released, in order to determine if there were any differences between successive months. The analysis thus concerned the displacements between successive radio-locations noted for 19 females and 11 males.

The two-factor (month after release and sex) analysis of variance indicated a significant effect on movement behaviour in the first three months after release (ANOVA, $F = 9.15$, $p < 0.001$), however the time after release was much more important (ANOVA, $F = 23.28$, $p < 0.001$). The influence of the sex only on movement behaviour in the first three months was not significant (ANOVA, $F = 0.14$, $p = 0.705$). The mean distances moved by hares in the first month after release were significantly greater than those recorded in the later (second and third) months. However, only in the first month after release males moved significantly larger distances than females. In the two next months the differences in moved distances between sexes were not significant (Table 4).

Detailed statistical analysis made for each hare separately showed that there are significant differences

in the mean distances moved by individual hares of the same sex (ANOVA, $F = 9.78$, $p < 0.001$).

Distances moved within annual home ranges

The analysis took account of distances moved in the case of 19 hares (13 females and 6 males – all were located at the same time). Mean distances moved within annual home ranges between successive radio-locations were significantly larger in males than in females (ANOVA, $F = 55.03$, $p < 0.01$).

Mean distance covered by female hares was 226 (± 206) (no. of analysed cases of distance moved $n = 1281$), for males 335 (± 343) ($n = 581$). Range of values for sizes of moves for female hares was 0-1358 m, and for males 0-4187 m, respectively. There was high variability of movement between individual hares during study. Detailed statistical analysis, made individually for each hare shown that there were significant differences in the mean distances moved by individuals of the same sex (ANOVA, $F = 6, 72$, $p < 0.001$).

Distances moved within seasonal home ranges

The data on distances moved between successive locations were analysed for 16 hares (10 females and 6 males) within the home range in the spring-summer and autumn-winter periods (Table 5). The influences of season and gender on mean distances between successive radio-locations were determined using two-factor analysis of variance.

Table 4. Mean distance (m) separating successive locations for hares in the first three months after release and ranges (m) of values (min-max) for displacements between successive locations in females and males, and in successive months following release. (l – no. of analysed cases of distance moved by hares).

Month	Female (19)		Males (11)		All (30)
	Mean size of displacement from one radio-location to the next	Range of values reported for distances moved	Mean size of displacement from one radio-location to the next	Range of values reported for distances moved	Mean size of displacement from one radio-location to the next
1	188 (l = 270)	0-1879	289 (l = 147)	0-4242	239 (l = 417)
2	133 (l = 179)	0-575	74 (l = 89)	0-706	103 (l = 268)
3	150 (l = 151)	0-917	81 (l = 88)	0-862	116 (l = 239)

Table 5. Mean distances between successive radio-locations of hares within the two seasonal home ranges (m). (l – no. of analysed cases of distance moved by hares).

Gender	Spring-summer home range		Autumn-winter home range	
	Mean distance (m)	Range of values (m)	Mean distance (m)	Range of values (m)
Females (n = 10)	235 (± 201) (l = 450)	0-1358	224 (± 195) (l = 445)	0-1166
Males (n = 6)	427 (± 502) (l = 274)	0-4187	327 (± 313) (l = 295)	0-2514

Table 6. Comparison of individual home range sizes in hares reported in published studies (TEL-radiotelemetry).

Country	Sample size (n)	Mean size of home range (km ²)	Males	Females	Home range estimation method	No. of readings	Method	Period (months) over which home range determined	Author	Origin of hares
Poland	45	3.30	-	-	Size of circle embracing all successive places of capture	Several recaptures over several seasons	Mark-recapture	Several seasons	Pielowski 1979	Wild
Netherlands	10	0.26	-	-	MCP(< 100 %)	40 (19)	TEL+ night observations	1-6.5	Broekhuizen & Maaskamp 1982	Wild
Netherlands	3	0.39	-	-	MCP(< 100 %)	27 (12)	TEL+ night observations	0.75-4	Broekhuizen & Maaskamp 1982	Wild
New Zealand	5	0.53	-	-	MCP (90 %)	> 600	TEL	12	Parkers 1984	Wild
England	15	0.38	-	-	harmonic means (90 %)	78 (54)	TEL	1-7.0	Tapper & Barnes 1986	Wild
Hungary	6	0.37	-	-	MCP (100 %)	65 (11)	TEL	4-7.0	Kovacs & Buza 1992	Wild
Hungary	6	0.45	-	-	MCP (100 %)	86 (23)	TEL	3-5.0	Kovacs & Buza 1992	Wild
France	6	1.23	-	-	MCP (100 %)	221 (14)	TEL	9.0-10.0	Reitz & Léonard 1994	Wild
France	6	1.09	-	-	Kernel (100 %)	221 (14)	TEL	9.0-10.0	Reitz & Léonard 1994	Wild
France	6	0.54	0.54 (n = 5)	0.33 (n = 1)	Kernel (95 %)	221 (14)	TEL	9.0-10.0	Reitz & Léonard 1994	Wild
France	14	0.60	0.62 (n = 11)	0.54 (n = 3)	Kernel (95 %)	179	TEL	6 (summer + autumn)	Reitz & Léonard 1994	Wild
France	20	1.90	-	-	MCP (95 %)	195 (53)	TEL	5	Marboutin & Aebischer 1996	Wild
France	20	0.72	-	-	MCP (95 %)		TEL	daily (01.05-15.07)	Marboutin & Aebischer 1996	Wild
France	20	0.53	-	-	MCP (95 %)		TEL	daily (15.07-15.09)	Marboutin & Aebischer 1996	Wild
France	20	0.92	-	-	MCP (95 %)		TEL	nocturnal (01.05-15.07)	Marboutin & Aebischer 1996	Wild
France	20	0.89	-	-	MCP (95 %)		TEL	nocturnal (15.07-15.09)	Marboutin & Aebischer 1996	Wild
France	20	0.92	-	-	MCP (95 %)		TEL	daily (01.05-15.09)	Marboutin & Aebischer 1996	Wild
France	20	1.38	-	-	MCP (95 %)		TEL	nocturnal (01.05-15.09)	Marboutin & Aebischer 1996	Wild
Netherlands	6	1.42	-	-	MCP (100 %)	204 (32)	TEL	10	Kunst et al. 2001	Wild
Netherlands	6	0.43	-	-	MCP (95 %)	204 (32)	TEL	10	Kunst et al. 2001	Wild
Netherlands	6	0.55	-	-	Kernel (100 %)	204 (32)	TEL	10	Kunst et al. 2001	Wild
Netherlands	6	0.44	-	-	Kernel (95 %)	204 (32)	TEL	10	Kunst et al. 2001	Wild
Germany	38	0.21			MCP (95 %)		TEL	2	Rühe & Hohmann 2004	Wild
Italy	15	-	0.18-0.29	0.11-0.45	MCP		TEL + GPS	3	Zaccaroni et al. 2009	Wild
France	?	-	0.23 (at high density)	0.37 (at high density)	?	?	?		in: Bray et al. 2007	Wild
France	?	-	0.64 (at low density)	0.39 (at low density)	?	?	?		(Bray Y. – unpublished) in: Bray et al. 2007	Wild
France	?	-							(Bray Y. – unpublished)	Wild

In both the spring-summer and autumn-winter seasons, the mean distances between successive radio-locations were significantly greater for males than females (ANOVA, $F = 83, 56, p < 0.01$).

It was possible to note significant seasonal differences between the mean sizes of the distances moved by male hares (ANOVA, $F = 11, 78, p < 0.01$). Successive locations obtained for males were separated by greater distances in the spring-summer season than in autumn-winter. No similar relationship could be observed for females (ANOVA, $F = 0.6, p > 0.05$), for which similar mean displacements of position between successive locations were noted, irrespective of season.

Discussion

Individual home ranges (annual and seasonal)

There are very limited data on spatial organisation on brown hares. Moreover, the majority of them concern free living population. While the oldest studies are based on mark-recapture methodology (Pielowski 1979), a majority of studies carried out since the early 1980s have utilised radiotelemetric methodologies. Numbers of radio-collared animals used in determining parameters like home range size or distances moved by hares in location have ranged from 3 to 38. However, periods over which studies were conducted were brief, often not exceeding a few months (mostly 1-9). Most research was also carried out in the late summer and autumn periods (e.g. Tapper & Barnes 1986, Kovacs & Buza 1992, Reitz & Léonard 1994, Marboutin & Aebischer 1996), with spring and summer (the hare breeding season) or else winter only being chosen more rarely (Kunst et al. 2001, R  he & Hohmann 2004, Zaccaroni et al. 2009). The above circumstances have ensured that there are considerable disparities in the available data on individual home ranges (see Table 6), with figures supplied ranging from 0.2-1.9 km² (Broekhuizen & Maaskamp 1982, Parkers 1984, Tapper & Barnes 1986, Kovacs & Buza 1992, Reitz & Léonard 1994, Marboutin & Aebischer 1996, Kunst et al. 2001, R  he & Hohmann 2004, Bray et al. 2007, Zaccaroni et al. 2009). It is noticeable from unpublished data that the duration of the period over which observations were made, plus the seasons of the year involved, had a decisive influence on determining differences in home range sizes among hares.

Furthermore, only a few researchers have determined individual home range sizes for females and males separately (Reitz & Léonard 1994, Bray et al. 2007, Zaccaroni et al. 2009), and in relation to the influence

on home range size of population densities of hares differing from one area to another (R  he & Hohmann 2004, Bray et al. 2007).

In this paper the home range sizes were analysed over a full 12-month (January-December) period, as well as during two designated six-month seasons.

Annual home range sizes determined for released hares were on average of 0.43 km² or more in the case of females, up to 1.68 km² among males. The significant male-female differences in home range sizes confirm findings in other studies (Reitz & Léonard 1994 reported figures of 0.33 km² for females and 0.54 km² for males, Bray et al. 2007 had females 0.39 km² and males 0.64 km², Misiorowska & Wasilewski 2008 females 0.5 km² and males 1.3 km², Zaccaroni et al. 2009 females 0.2-0.3 km² and males 0.1-0.5 km²). Nevertheless, the mean sizes of individual home ranges reported here are towards the upper size limits. The considerable length of time for which the research was continued may have had an influence on this, and such a hypothesis was advanced by Reitz & Léonard (1994), who i.a. justified the fact that the home ranges they obtained were larger than those cited by other authors (Broekhuizen & Maaskamp 1982 and Kovacs & Buza 1992) by reference to the longer duration of the studies carried out.

Differences in individual home range sizes are also influenced by densities of hare populations. Sp  th (1989), R  he & Hohmann (2004), and Bray et al. (2007) indicated that greater densities of population are associated with smaller home ranges. Similar relationships between home ranges and densities of population have also been observed in many studies on other mammal species (e.g. roe deer, Kjellander et al. 2004, red fox, Trehwella et al. 1988 and weasel, J  drzejewski et al. 1995). The density of the population of hares in the study area was rather low (between 10 and 15 individuals/km²), this enabled released individuals to occupy greater areas. These two elements (longer duration of research plus the lower density of the hare population) may explain why the annual home ranges reported in this study were large.

The work carried out on seasonal ranges aimed to compare habitat use in the breeding period, as well outside it (in the months from September through to late February). The results obtained show how mean home range sizes were similar in the two seasons for females, but not males. In the latter case, mean home range size in spring-summer was significantly greater than that in autumn-winter. This perhaps enables to males penetrating and occupying larger areas in the

course of the 6-month breeding season than at other times of the year. Similar observations were made by Reitz & Léonard (1994), as well as by Kunst et al. (2001). These authors noted that home range size in hares is smaller in winter than in spring-summer, and this finding indicates that availability of food can be a determining factor (Hulbert et al. 1996). Kunst et al. (2001) confirm that the larger areas occupied in spring and summer may link up with the breeding season, while the smaller sizes of winter home ranges reflect more limited activity, the smaller distances moved by hares, and in general the more frequent likelihood of animals remaining largely immobile. The latter strategy safeguards against excessive loss of energy in periods of the more limited accessibility of food and unfavourable weather conditions (Thirgood & Hewson 1987).

Work by Rühle & Hohmann (2004) analysing home ranges occupied during two-month periods did not take account of the length of the breeding season, a factor that would seem to have had a major influence on home range sizes in this study. No significant differences between males and females could be noted in this respect.

The high degree of season-to-season overlap in hares' ranges revealed in this research confirms that hares use largely the same areas in the autumn-winter period as they do in spring and summer. This reflects rather sedentary lifestyle with no obvious separation of the seasonal ranges.

The mean sizes of home ranges in males were larger than those of females in both the spring-summer and autumn-winter seasons. Assessing the sizes of home ranges occupied for six months, Reitz & Léonard (1994) noted a similar phenomenon for summer-autumn (with females occupying 0.54 km² on average, males 0.62 km²), though these differences were not marked. Zaccaroni et al. (2009) studied wild hares tagged with radio-transmitters over a period of three months between January and the end of March. Significantly larger home ranges were found in males than in females (0.1-0.5 km², as compared with 0.2-0.3 km²). Similar observations indicating larger home ranges in males than in females were made by Bray et al. (2007) (females covered 0.39 km², males 0.64 km²), in the period of the low density of the hare population. Under the circumstances of high population densities, the sizes of female home ranges reported were hardly different (at 0.37 km²), while those of males were distinctly smaller (0.23 km²).

Analyses of differences in individual home ranges of released hares in the period of a year or two

seasons were possible by the relatively large number of released and marked individuals, as well as the lengthy period over which radio contact with a large number of specimens could be maintained ($n = 21$ – annual, $n = 16$ – seasonal).

Distance moved by released hares

Adult hares move around to find suitable and safe places to shelter and rest, to obtain food, to escape danger and to seek out a mate. In relation to each of these objectives, the distances moved may differ markedly, even if they remain within the overall home ranges occupied. Movements made with a view to food being obtained or rest taken almost always entail shorter distances than do, for example, escapes from danger. Breeding-season movements in search of a partner may in turn vary greatly, in relation to a large number of factors, not least gender and population density.

However, activities described above must be distinguished from the juvenile hares dispersal (natal dispersal), a key behavioural process with important consequences of maintaining of the gene flow, colonisation of empty habitats and evolutionary dynamics of animal population (Avril et al. 2011). It should be stressed that in the present study only adult hares were studied, so the phenomenon of the natal dispersal did not occur and was not taken into consideration.

The released animals probably had one more motivation for movements, namely the desire to find and select an optimal place to live in a new and hitherto-unknown environment. Analysis of the distances moved by captive bred hares in the first three months after release showed that these might be influenced by stress, by unfamiliarity with the area, as well as the disorientation that characterises reared animals for ten or more days after they are introduced into the wild. However radiotelemetry data obtained during three consecutive years of my study have shown a very consistent pattern of released hares behaviour. In the first month after release, hares apparently moved considerably greater distances than they did in the next two months (ANOVA). This can indicate that the released hares need approximately one month to adopt to the new, unknown environment and to start to stabilise their home ranges. Similar observations were made by Angelici et al. (1999), these authors recorded significantly greater distances moved by males as opposed to females in the period in question. Angelici et al. (2000) showed that almost all the hares they released moved between 0.4 and 2.8 km away from the release site.

The mean sizes of the displacements between successive radio-locations reported here for hares within their home ranges are similar to those given by other authors (Homolka 1981, Reitz & Léonard 1994, Rühle & Hohmann 2004). At the same time, our results suggested much greater mean distances moved by males than females, a fact that Angelici et al. (1999) also confirmed in their work, as did Rühle & Hohmann (2004). Reitz & Léonard (1994) apparently did not come across this phenomenon, though they attributed this fact to a small sample of hares studied. The work by Hansen (1996) suggested that the greater distances moved by males reflected their devoting more time than females to reconnaissance and full coverage of the area around them. In the breeding season males apparently cover greater distances in search of partners. This phenomenon was noted among the tagged hares of the present study, as well

as in other work (Greenwood 1980, Dobson 1982, Perrin & Mazalov 2000, Rühle & Hohmann 2004).

The results obtained by this study have both scientific and research (cognitive/theoretical) implications and practical (utilitarian) ones. They offer a detailed characterisation of the spatial organisation applying to hares introduced from the semi-free-ranging environment offered by an enclosure. They should at the same time exert an influence on the hunting clubs anticipation, in order that the latter might first and foremost take place on land they themselves lease and manage.

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