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Home ranges of European Ground Squirrels (*Spermophilus citellus*) in two habitats exposed to different degrees of human impact

Domovské okrsky sysla obecného (*Spermophilus citellus*) ve dvou biotopech s odlišnou intenzitou antropogenního vlivu

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Abstract. Because of habitat loss and alteration, European ground squirrel populations in Austria are increasingly restricted to isolated fragments, where, however, they can reach conspicuous densities. To investigate potential effects of habitat alteration and population density on space use, we radio-collared comparable numbers of individuals at two different study sites; a secondary steppe with relatively low anthropogenic influence and a highly altered, isolated alfalfa meadow. Subsequently, individual movements were recorded during approximately one week. Home ranges were compared between the two study sites and sex and age differences were examined. Juveniles covered larger areas in the secondary steppe, where population density was relatively low. In ≥1year-old individuals, mean home ranges did not differ between the two habitats, although they exhibited high individual variation in the secondary steppe. In either of the study sites, no sex difference in home-range size was found. In addition, minimal and maximal distances moved were calculated. One yearling male with scrotal testes in the secondary steppe dispersed from its original home range, moving about 750 m. We conclude that habitat characteristics affect space use in juvenile individuals. Since juveniles are the ones benefiting most from selective foraging to promote growth and fattening, quality and distribution of food resources probably accounted for differences in home-range size in the two study sites. Furthermore, variances in population density and predator presence could have contributed to the observed movement patterns.

Key words. *Spermophilus citellus*, home range, radiotelemetry, habitat alteration, space use.

INTRODUCTION

Over the past decades there has been a dramatic change in European ground squirrel abundance in Austria and the species that was considered an agricultural pest during the first half of the 20th century has been listed as endangered since 1984 (Bauer 1989). Urbanisation and habitat destruction have restricted ground-squirrel aggregations to isolated habitat fragments, which increasingly lack corridors allowing movements between those patches (Spitzenberger & Bauer 2001). At the same time, however, populations in anthropogenically shaped areas have reached extraordinarily high densities (Millesi et al. 1999). These developments have heightened the need for a better understanding of how habitat modifications caused by humans affect population dynamics and behavioural traits of ground squirrels. Since space use is strongly linked to habitat structure, it represents a key aspect in assessing the influence of anthropogenic alteration on this species and hence, in developing concepts for its conservation (Caro 1999).

Several studies on home-range size have been carried out in North American ground squirrels, using either direct observations (e.g. Murie & Harris 1978, Michener 1979, Festa-Bianchet & Boag 1982, Boellstorff & Owings 1995) or radiotelemetric techniques (e.g. Ortega 1990, Shriner & Stacey 1991, Hubbs & Boonstra 1998, Harris & Leitner 2004) to locate animals. So far, however, there has been little research on movement patterns in *Spermophilus citellus*.

Those studies that involved radiotelemetric techniques were aimed at assessing circadian rhythms or aboveground activity patterns by using light-sensitive transmitters (Hut et al. 1999, Hoffmann et al. 2004a) or at investigating sex differences in predation risk of juveniles (Hoffmann et al. 2004b), and did not focus on determining individual home-range size. In another study that examined space use in European ground squirrels, data were obtained exclusively by direct observation with a binocular (Huber 1996). The present study is the first one published to provide information on home-range size of European ground squirrels obtained with radiotelemetric methods.

Different degrees of isolation and fragmentation together with other, possibly associated, environmental factors such as availability and distribution of food resources and predation pressure may generate variances in movement behaviour across populations. At the individual level, sex, age, body condition and reproductive state may affect an animal's space use. In this paper, we present results on home-range sizes of juvenile and older European ground squirrels in two habitats exposed to different degrees of anthropogenic influence. We aimed at determining effects of habitat characteristics and population density on movement behaviour in European ground squirrels and examined potential sex and age differences.

MATERIAL AND METHODS

Study areas

The study was conducted from late March to early August 2008 and involved two populations of European ground squirrels in eastern Austria. The distance between the two study sites is about 58 km, and human activities have subjected them to different degrees of disturbance.

The first study area, a secondary steppe (47° 48' N, 16° 33' E), is located west of Lake Neusiedl at an elevation of 164 m a. s. l. It encompasses about 100 ha; data were collected on a focal area of 7 ha. The area was used exclusively as a pasture until the 1930s, when it was turned into an airfield and grazing was subsequently reduced. In the 1990s, flying activities were shut down, and for about 10 years human activities have been restricted to mowing the dry grassland once in summer and occasionally letting sheep graze on it in winter. Surroundings of the grassland are hardly fragmented; dust roads, small fields and vineyards provide connections and corridors to numerous adjacent European ground squirrel habitats. There are occasional disturbances by cars and walkers with dogs, but mainly at the edge of the area. Hence, we considered this area as nearly natural.

The second study site, an alfalfa (*Medicago sativa* L.) meadow, is located at Falkenberg in the north of Vienna (48° 18' N, 16° 22' E) at an elevation of 318 m a. s. l. The study was carried out on a focal area of 1 ha that was part of a ca. 5 ha habitat fragment with substantial human impact. The fragment is bordered by woodland; a huge conventional vineyard, arable fields and a transmitting station cause further isolation of the focal ground squirrel colony. The plant composition of the former grassland was severely altered some years ago when a farmer sowed the alfalfa. Even though the meadow is mown repeatedly, this element has dominated the vegetation ever since. Moreover, the area belongs to a region popular for recreational excursions and hence presence of humans, often with dogs, is almost permanent.

Population density (N/ha) was determined by the total number of nonjuveniles captured and/or observed per area. It was about 9 individuals/ha in the steppe and 43 individuals/ha in the alfalfa meadow.

Field study

In both study sites, animals were captured with Tomahawk life traps or with self-made tube traps, the latter were preferably used for juveniles. The traps were baited with hazelnut cream, peanut butter, carrots and/or maize. Because of the high vegetation in both study areas, especially in midsummer, it was not feasible to distribute the traps evenly across the sites but set them at observable locations. The traps were checked at 15 min-intervals and for all captured ground squirrels body mass, age, sex, and reproductive state were recorded. We classified individuals born in the year of the study as juveniles, older individuals were classified as nonjuveniles. Males were categorised as reproductive when testes were scrotal and as nonreproductive when testes were abdominal. In females, size of the vulva and the teats were used to determine whether they were pregnant or lactating, i.e. reproductively active (Millesi et al. 1999). Of all collared nonjuveniles, only one male in the steppe was nonreproductive. Since this individual dispersed from its original home range during the radiotracking period, it was excluded from the home-range analysis.

After capture, nonjuvenile as well as juvenile ground squirrels were equipped with ATS radiocollars weighing about 3 g, which even for pups was less than 2% of the animals' body mass. Original nitrile collars were cut, and latex was inserted to prevent strangling and to ensure that in case of no recapture or of signal loss the latex would disintegrate and the collar would fall off. Additionally, ground squirrels were marked individually with conventional hair dye (Hair Culture intensiv). Subsequently they were located with a portable receiver (Telonics TR2+TS1, AVM LA12-Q) connected to a handheld H-antenna and earphones. In the alfalfa meadow, direct observation with a 10×40 binocular additionally allowed to record movements of the animals, whereas in the steppe, the size of the area and the pronounced height of the vegetation usually disabled individual recognition from the distance. From late March to mid May we fitted 12 nonjuveniles (8 males and 4 females) with transmitters in the steppe, and 8 nonjuveniles (5 males and 3 females) in the alfalfa meadow. In July, juveniles were radiocollared: 8 individuals (4 males and 4 females) in the steppe and 9 individuals (5 males and 4 females) in the alfalfa meadow.

After being collared, each individual was radiotracked for several hours on successive days until the mean percentage home-range size began to stabilize. Signal range varied intensively with height and density of the vegetation as well as with weather conditions, and was between 30 and 200 m, also depending on the position of the collared animal (above- or underground). Intervals between subsequent bearings were about 30 minutes. Within this period ground squirrels should be able to traverse their entire home ranges, a criterion recommended by White & Garrot (1990) for independency of two fixes. In both sites, coordinates of locations were obtained on a 15×15 m grid to the nearest 4 m. In the alfalfa meadow, topographic features such as the adjacent wood, paths or bushes made additional landmarks obsolete, but in the steppe coloured wooden stakes were placed at 60 m intervals with the help of a GPS (Garmin etrex) where no other structures for orientation were available.

On average, the animals were recaptured after 9.3±3.4 days and their collars were removed. Since battery life was about 30 days, one transmitter could be used for several trials. On average, 69.5±22.2 locations were recorded for nonjuveniles and 56.8±10.3 for juveniles, the minimum number was 16 and the maximum number was 104. One male individual from the alfalfa meadow that was not radiocollared but frequently spotted with the binocular and identified by its individual fur mark was also included in the analysis.

The analysis of home-range size was carried out using RANGES6 software (Kenward et. al. 2003), and home ranges were calculated with 100% minimum convex polygons (MCP). In spite of its tendency to overestimate home-range sizes, we chose this method because of its comparability with other studies and relative robustness when operating with low sample sizes (Harris et al. 1990). Since the bearings were not obtained continuously but for several hours daily and therefore the outlying locations did not necessarily lie beyond the main activity area of an individual, all locations where individuals were radio-tracked, trapped or observed during the collared period were used. Capture or observation data from other periods

Table 1. Mean home ranges of European ground squirrels [ha] in two habitats during periods of about one week duration from March to July 2008. Bonferroni-corrected level of significance: *P*=0.008
Tab. 1. Průměrná velikost domovských okrsků sysla obecného ve dvou biotopech zjištěná v období od března do července 2008 během přibližně týdenního sledování. Hladina významnosti upravená pomocí Bonferroniho korekce: *P*=0.008

	steppe		alfalfa		statistics	
	mean±SD	n	mean±SD	n	U	P
both sexes	0.448±0.332	19	0.175±0.081	18	74	0.003
juvenile	0.518±0.296	8	0.183±0.100	9	7	0.005
nonjuvenile	0.397±0.361	11	0.166±0.060	9	31	0.160
males	0.435±0.322	11	0.205±0.091	11	28	0.033
juvenile	0.436±0.213	4	0.232±0.115	5	4	0.142
nonjuvenile	0.435±0.387	7	0.182±0.069	6	10	0.116
females	0.465±0.368	8	0.127±0.018	7	12	0.064
juvenile	0.600±0.377	4	0.123±0.023	4	0	0.021
nonjuvenile	0.330±0.300	4	0.132±0.010	3	6	1.000

were excluded from the analysis to avoid overestimation of home-range size in cases of individuals that had shifted their home range during the active season, particularly with regard to the fact that we frequently located animals by sighting throughout the season in the alfalfa meadow but could hardly obtain observational data in the steppe. Hence, the calculated home ranges represent the space covered by ground squirrels at a certain time interval. In addition to home-range size, home-range span, i.e. the maximum distance between any two locations obtained for one individual, was analysed.

Statistical procedures

Statistical procedures were carried out using SPSS (Release 15.0, © SPSS Inc. Chicago/USA, 2006) software. Differences in home-range size and span between groups were examined for significance by using Mann-Whitney U tests. The p-value was corrected for multiple comparisons using the Bonferroni adjustment: We applied a corrected significance level of p=0.008 for tests between sites and p=0.01 for tests within sites. All tests were two-tailed. Means±SD are given.

RESULTS

Animals in the steppe differed in their movement behaviour from those in the alfalfa meadow: In the nearly natural habitat, home ranges were significantly larger compared to that with higher anthropogenic influence (Table 1). This difference disappeared when sexes were analysed separately, but separate tests for the two age classes revealed that the general site effect arose from a significant difference within juvenile individuals, while nonjuvenile individuals had similar home ranges in the two study sites (Table 1, Figs 1, 2). In juveniles, the difference between study sites disappeared when the sample was restricted to one sex (Table 1). When we examined differences between age groups within each site, we found that home ranges did not differ in size between juvenile and nonjuvenile individuals, in the alfalfa meadow (*P*=0.965, *U*=40) as well as in the steppe (*P*=0.160, *U*=27).

In either of the two study sites, home ranges of males and females did not differ significantly, neither when all animals were included in the analysis, nor when age classes were analysed

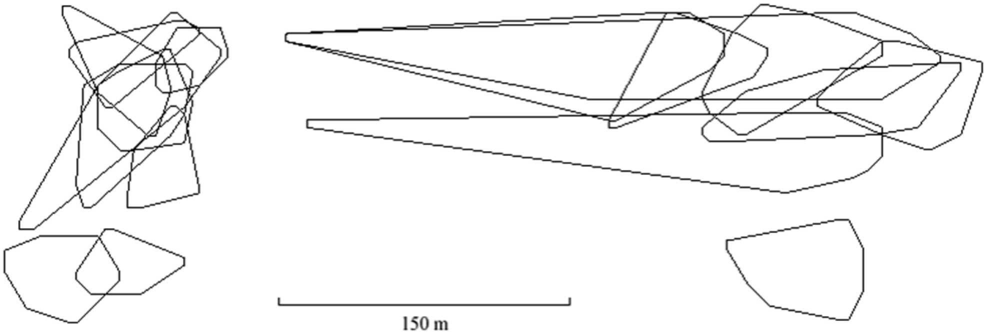

Fig. 1. Home ranges of nine juveniles in the alfalfa meadow (left) and eight juveniles in the steppe (right).
Obr. 1. Domovské okrsky devíti mláďat na vojtěškovém poli (vlevo) a osmi mláďat v druhotné stepi (vpravo).

separately (steppe both age classes: P=0.869, U=42, juveniles: P=0.773, U=7, nonjuveniles: P=0.450, U=10, alfalfa meadow both age classes: P=0.026, U=14, juveniles: P=0.08, U=3, nonjuveniles: P=0.197, U=4, n=9, Table 1). As home ranges were similar between sites in nonjuveniles, data from the steppe and the alfalfa meadow were pooled for a comparison of males and females, which was not significant (males: 0.318±0.085, n=13, females: 0.245±0.102, n=7, P=0.191, U=29).

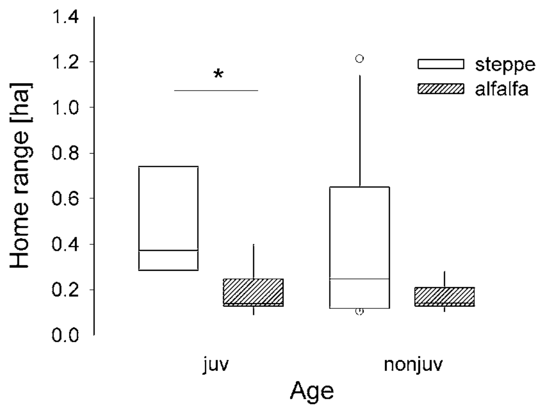

Fig. 2. Differences in home-range size between habitats within age classes. Juvenile individuals in the secondary steppe used more space than individuals in the alfalfa meadow, whereas home ranges of non-juveniles were similar between study sites (* p<0.008, for details see Table 1).
Obr. 2. Rozdíly ve velikosti domovských okrsků ve sledovaných biotopech mezi jednotlivými věkovými kategoriemi. Mláďata (juveniles) v druhotné stepi využívají větší plochu než mláďata ve vojtěškovém poli, zatímco velikosti domovských okrsků dospělých jedinců jsou na obou lokalitách podobné (* p<0.008, podrobnosti viz Tab. 1).

In the steppe, the minimum home-range span was 71 m in juveniles and 39 m in nonjuveniles, and the maximum home-range span was 338 m in juveniles and 203 m in nonjuveniles. In the alfalfa meadow, home-range span ranged between 40 m and 136 m in juveniles and between 45 m and 93 m in nonjuveniles. Differences between groups were consistent with the home--range size data, i.e. when all individuals were included in the analysis, it turned out that in the steppe ground squirrels moved longer distances than in the alfalfa meadow (P=0.001, U=68, steppe: n=19, alfalfa meadow: n=18). Separate tests for age classes were significant for juveniles (P=0.005, U=7, steppe: n=8, alfalfa meadow: n=9), but not for nonjuveniles (P=0.063, U=25, steppe: n=11, alfalfa meadow: n=9). In the steppe, we were able to document one dispersal event in a nonjuvenile individual: one nonreproductive male yearling moved about 750 m and subsequently established a new home range at the edge of the grassland close to human settlements, but was directly observed to be killed by a housecat 5 days later. This individual was not included in the home-range analysis, given that it had permanently left its original home range.

DISCUSSION

This research attempted to determine home-range sizes of European ground squirrels and to investigate effects of habitat structure, age and sex. Home ranges of juveniles were larger in the steppe than in the alfalfa meadow, and distances travelled were longer. In nonjuveniles, even though mean home-range size in the steppe more than doubled that in the alfalfa meadow (Table 1), the difference was not significant, due to the high individual variation in the steppe (Fig. 2).

Home ranges of adult Arctic ground squirrels (*Spermophilus parryii*) were smaller on food-supplemented grids compared to non-supplemented grids (Hubbs & Boonstra 1998), and a study on eastern chipmunks (*Tamias striatus*), another burrowing sciurid species, revealed similar results (Mares & Lacher 1987). In rock squirrels (*S. variegatus*) the temporal decrease of home ranges met the period in which several plants produced seeds the animals feed on (Ortega 1990). Though mere plant biomass was not obviously different in the two sites in our study, quality and probably distribution of food resources may have affected the ground squirrels' movement behaviour. Mean body mass of nonjuveniles was higher in the alfalfa meadow compared to the steppe (Hoffmann et al., this volume), indicating that alfalfa is a nutritious food source for ground squirrels. This assumption is supported by reports on North American *S. richardsonii* causing substantial damage to alfalfa fields through feeding and burrowing (Yensen & Sherman 2003, Johnson-Nistler et al. 2005), and the finding that the growth rate of juvenile *S. columbianus* was enhanced on sites with higher forb versus grass content in the forage supply (Bennett 1999). We therefore assume that alfalfa motivates ground squirrels to stay where it is abundant, in this way reducing the distance they travel to get to it, which also means reducing the time they are exposed to predators (Lima & Dill 1990). In the steppe, on the other hand, the vegetation was dominated by presumably less nutritious *Poa* spp., and in addition appeared less homogeneous, potentially inducing ground squirrels to move around more in order to exploit different food resources. Some travels of juveniles were directed towards a grain field located west of the grassland (Fig. 1), where nutritious crops were available. Young animals benefit from selective foraging to promote growth and fattening, and thus, additional food resources may be the reason for increased home ranges in the steppe. As body-mass gain is especially crucial for juveniles (Huber et al. 2001), we probably did not observe the same pattern in nonjuveniles.

Population density in the alfalfa meadow was almost 5 times higher than in the steppe. The experimental manipulations of food availability and population density in eastern chipmunk populations suggested that home-range size was determined rather by resource abundance than by density (Mares & Lacher 1987). Hubbs & Boonstra (1998) expect that the same is true for Arctic ground squirrels, although they discuss the possibility that increased density forces animals to reduce their home ranges in order to reduce conflict with conspecifics. Nevertheless, high population densities attract predators. Although not recorded quantitatively, raptors were less frequently observed in the steppe than in the alfalfa meadow, where almost every day after juvenile emergence a kestrel killed a pup. Moreover, in the alfalfa meadowthe numerous visits of people with dogs may alert animals. Altogether, this presumably leads to increased frequency of alarm calls which possibly deters juveniles from covering long distances aboveground. This interpretation conflicts with the study of Hubbs & Boonstra (1998), where predator exclusion had little effect on home-range size. However, this result must be considered with caution since predation by raptors could not be totally inhibited and avian predators were by all means still observable by ground squirrels.

In our study the only individual in which dispersal was observed was a male yearling in the steppe. Since it was not sexually mature, its behaviour falls within Greenwood's definition of natal dispersal as the permanent departure of a prereproductive animal from its birth site (Greenwood 1980, adopted by Holekamp 1984). As far as juveniles are concerned, we attribute the lack of observations of individuals permanently leaving their natal places to relatively short radiotracking periods. Nevertheless, different movement patterns in juveniles recorded at the two study sites may indicate differences in dispersal rates. Although natal dispersal was described to occur within short time periods in some *Spermophilus* species (Quanstrom 1971, Boag & Murie 1981), Holekamp (1984) found that juvenile Belding's ground squirrels (*S. beldingi*) explore their habitat after emergence and gradually expand forays prior to permanently leaving their natal area. A former study by Hoffmann et al. (2004b) indicated similar patterns for *S. citellus*. Given that natal dispersal is not necessarily a single event but presumably rather a process during which a prereproductive ground squirrel gradually expands its home range prior to permanently departing from its natal site, the difference in home-range size of juvenile animals between the two study sites suggests that natal dispersal is less pronounced in the alfalfa meadow compared to steppe. This is in accordance with the findings of low dispersal rates in high-density vole populations (*Microtus* spp., e.g. Sandell et al. 1990, McGuire et al. 1993, Andreassen & Ims 2001).

The loss of suitable habitats in the surrounding landscape could be another factor influencing movement behaviour of ground squirrels in the alfalfa meadow. The population is restricted to a 5 ha habitat fragment that is furthermore bordered by woodland, which hinders animals from leaving in search of other suitable patches. Hence, pronounced one-way movements, like the one observed in the yearling male in the steppe, are hardly possible in the alfalfa meadow.

Our study did not offer support for sex differences in space use by European ground squirrels. Since it has been reported that reproductive males enlarge their home ranges during the mating period (Huber 1996, Millesi et. al. 1998), potential sex differences in movement behaviour of nonjuveniles might have been concealed in our study because we were not able to analyse seasonal patterns in space use due to limited sample size and short radiotracking periods. In juveniles, male-biased dispersal, common in many related species (Holekamp 1984, Olson & Van Horne 1998, Byrom & Krebs 1999, Devillard et al. 2004), was not indicated by sex differences in home-range size.

Regarding absolute home-range size, ground squirrels in the studied areas used considerably more space than calculated in an earlier study close to one of the field sites (Huber 1996). We assume that these differences are due to the different methods of data collection. Huber (1996) used direct observations and the sample was restricted to a 1 ha focal area, leading to an exclusion of individuals leaving from it, whereas in this study the application of radiotelemetric techniques allowed to follow the animals' movements beyond the focal area. Also in North American rock squirrels, studies involving radiotelemetric methods (Ortega 1990, Shriner & Stacey 1991) revealed that home ranges were considerably larger than reported earlier using direct observation methods (Johnson 1981). However, it cannot be excluded that high food quality provided by the rich meadow and the extraordinarily high population density (up to 100 individuals/ha) could have contributed to reduced home-range size in Huber's study.

Because of different sampling and home-range calculation methods, comparisons between *S. citellus* home-range sizes and those of North American congeners are limited. It appears that absolute home ranges of European ground squirrels resemble those of nonjuvenile *S. beecheyi* (Boellstorff & Owings 1995), *S. richardsonii* (Michener 1979), *S. columbianus* (males: Festa-Bianchet & Boag 1982, females: Murie & Harris 1978) and female *S. mohavensis* (Harris & Leitner 2004), whereas *S. parryii* (on grids without food supplementation, Hubbs & Boonstra 1998), *S. variegatus* (Ortega 1990, Shriner & Stacey 1991) and male *S. mohavensis* (Harris & Leitner 2004) cover larger areas.

We conclude that anthropogenic activities in one study site, namely the alteration of the vegetation and the isolation of the habitat, were the reason for smaller home ranges in juveniles, probably acting through changes in availability of high-quality food and population density. Different frequencies of predator presence may have contributed to the observed patterns. However, further data are necessary to elucidate the effects of habitat fragmentation and isolation on the movement behaviour of European ground squirrels in order to define implications for the species' conservation management. Also, sex differences in home-range size and dispersal rates, as well as changes in space use throughout the season, need to be clarified.

SOUHRN

V práci je hodnocen vliv změny biotopu a populační hustoty na prostorové chování sysla obecného v Rakousku. Ve dvou odlišných biotopech – člověkem relativně málo ovlivněné druhotné stepi a naopak značně pozměněné izolované louce převedené na kulturu vojtěšky – byl označen srovnatelný počet syslů pomocí obojkových vysílaček a následně provedeno jejich telemetrické sledování. Pohyb označených jedinců byl zaznamenáván vždy přibližně po dobu jednoho týdne. Na základě takto získaných dat byly porovnány velikosti domovských okrsků na obou studovaných plochách a zjištěny rozdíly mezi pohlavími a věkovými skupinami. Mláďata v druhotné stepi, kde byla relativně nízká populační hustota, využívala větší domovské okrsky než mláďata ve vojtěškovém poli. Průměrná velikost domovského okrsku zvířat ve věku ≥1 rok se na sledovaných lokalitách nelišila, ve stepním biotopu však byla zaznamenána velká individuální variabilita. Ani v jednom biotopu nebyly zjištěny rozdíly ve velikosti domovského okrsku mezi pohlavími. Spočteny byly také minimální a maximální délky přesunů označených zvířat. Nejdelší přesun byl zaznamenán u pohlavně aktivního jednoletého samce ve stepním biotopu, který opustil svůj původní domovský okrsek a přemístil se na vzdálenost 750 m. Výsledky studie ukazují, že vlastnosti biotopu ovlivňují prostorové chování mláďat sysla obecného. Vzhledem k tomu, že pro mláďata má velký význam selektivní potravní chování napomáhající rychlému růstu a vytváření tukových zásob, byly příčinou rozdílů ve velikosti domovských okrsků na sledovaných lokalitách pravděpodobně kvalita a distribuce potravních zdrojů. Svou roli zde ale mohou hrát také rozdíly v populační hustotě a přítomnost predátorů.

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