DIPLOMARBEIT

EFFECTS OF ANTHROPOGENIC HABITAT ALTERATION ON HOME RANGES OF EUROPEAN GROUND SQUIRRELS *(SPERMOPHILUS CITELLUS)*

Effekte anthropogener Habitatsveränderung auf die Aktionsraumgröße Europäischer Ziesel (*Spermophilus citellus)*

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CONTENTS

1 Effects of anthropogenic habitat alteration on animal space use

1.1 Landscape fragmentation

In modern landscapes, human activities have altered the natural environment, modifying habitat characteristics, which has led to changes in plant and animal communities. Habitat loss or its reduction to single fragments isolated from one another is one of the major threats to biodiversity and hence has been a dominant issue in conservation biology since its inception (SOULÉ 1987). Landscape fragmentation restricts organisms to small areas that provide limited connections to other suitable terrain and conspecifics. Thus, they face a variety of problems: Homozygosity and inbreeding depression represent severe problems; furthermore small populations are increasingly vulnerable to stochastic effects and catastrophes. Hence, as human-induced landscape alteration will continue, the long-term survival of many endangered species will depend on their capacity to cope with anthropogenically shaped habitats.

Since habitat and population characteristics strongly influence space use in animals, anthropogenic changes can cause variances in this parameter across populations exposed to different degrees of human impact. Studies on space use in response to human influence operate at the interface between behavioural ecology and conservation, possibly providing knowledge for successful conservation measurements (CARO 1999). Different movement patterns between sites may reflect direct consequences of anthropogenic habitat alteration or disturbance, or they may result from altered life-history traits or demographic changes. Space use can be measured at different levels: in terms of dispersal patterns, home-range size, or spacing.

1.2 Dispersal

In conservational contexts, much attention has been paid to animal dispersal because of its relevance for metapopulation dynamics (e.g. HANSKI 1998, WOODROFFE 2003). A metapopulation consists of several subpopulations connected by dispersing individuals. Enabling gene flow between colonies, dispersal may counteract the typical problems associated with small and isolated populations: high levels of inbreeding, high genetic drift (i.e. the stochastic change of allele frequencies from one generation to the next causing eventual disappearance of alleles), and, consequently, high levels of homozygosity and loss of genetic diversity which means reduced possibility to adapt to environmental changes. Thus, in fragmented landscapes, where suitable habitat patches are embedded in a more or less hostile matrix, the degree to which individuals still move between subpopulations and to unoccupied patches may decide on the fate of small colonies.

The resistance of a species to habitat fragmentation can be influenced by several parameters. Findings from the long-term “Biological Dynamics of Forest Fragments Project” conducted in the Amazon rain forest, where fragments of different sizes where left intact but the rest of the habitat was deforested, emphasize the roles of the character of the matrix surrounding the fragments and the readiness of the animals to use it (LAURANCE et al. 2002). Furthermore, the ability of an animal to percept the presence of high-quality habitat in the surrounding area, as has been investigated in some sciurid species (ZOLLNER 2000), presumably plays a role for movements from one patch to another.

The evolutionary causes of dispersal involve variations in the non-social environment (habitat quality, breeding sites, food availability, parasites, and predation), the social environment (competition), and the genetic environment (inbreeding avoidance on the one hand, presence of co-adapted genes on the other hand; CLOBERT et al. 2008). Who disperses and when varies greatly between species. In general, *natal dispersal* can be found in prereproductive individuals, and *breeding dispersal* in reproductive individuals (GREENWOOD 1980). Natal dispersal tends to be dimorphic among birds and mammals: it is usually female-biased in birds, whereas in mammals males are the ones that usually disperse further from their birth sites than females (LAWSON HANDLEY & PERRIN 2007). Sciurid species are apparently no exception to this pattern (HOLEKAMP 1984), though in the European ground squirrel sex-differences in dispersal have at present only been shown for travel speed but not for distance from the natal burrow (HOFFMANN et al. 2004a).

1.3 **Home-range size**

In this study, space use was investigated in terms of home-range size. The concept of an animal's home range was established by BURT (1943), who defined it as the area where "normal activities of food gathering, mating, and caring for young" occur, but argued that occasional excursions outside this area should not be considered as part of the home range. During time, individuals can shift their home ranges in such a way that the new home range is still overlapping with the former one, or they can departure permanently from their original home range, i.e. disperse. Moving behaviour accounts for the animals' dispersion, their socially mediated spatial arrangement. Spacing behaviour is usually associated with the degree of sociality in a species (territorial or not) and influences parameters such as population density and home-range overlap (STENSETH & LIDICKER 1992).

The significance of home-range size has been less integrated in conservation issues compared to dispersal patterns. Hence, knowledge on the plasticity of individual ranging behaviour in dependence of anthropogenic habitat changes may yield insights on a species' response to the challenges imposed by human activities (CARO 1999, APPOLONIO et al. 2003). For example, knowing the average spatial requirements of a species and relating it to habitat patch size might help predicting how animal populations are affected by habitat reduction, as well as assessing the likelihood of colonization and extinction at patches of a given size. If individual home ranges are small relative to the patch size, population viability might be less threatened than when they are large. This ratio also determines the proportion of the population exposed to the habitat border, which may play a role in species that are vulnerable to edge effects (WOODROFFE & GINSBERG 2000).

Certainly, the extent to which the space at disposition tends to be covered by more than one individual is crucial. This factor strongly interacts with a species' social organisation and mating system. Home ranges may overlap to different degrees, or they can be distinct from one another if the individuals defend perpetual or spatiotemporal territories (e.g. MURIE & HARRIS 1978, FESTA-BIANCHET & BOAG 1982). Movement behaviour and territoriality may vary between sexes, and the home range of one individual may encompass those of several others, especially when a male monopolizes several females. In addition, individuals do not equally use all parts of the home range, but movements are concentrated to a main activity area (DIXON & CHAPMAN 1980, HARRIS et al. 1990).

Variances in home-range size between individuals and between populations of the same species may reflect different parameters:

(1) First, home-range size may be influenced by individual traits, like sex, age, condition or reproductive state (e.g. ORTEGA 1990). It is a general rule that home-range size increases with body weight and energy requirements (MCNAB 1963, HARESTAD & BUNELL 1979), across species as well as within species, though this relationship does not seem to be linear (KELT & VAN VUREN 1999).

(2) Secondly, population characteristics may have an effect on home-range size, like population density (ERLINGE et al. 1990, OSTFELD 1986), sex-ratio, oestrus synchrony, and the degree of intrasexual competition (MURIE & HARRIS 1978, MILLESI et al. 1998).
(3) Finally, environmental factors affect home ranges, like habitat patch size (IMS et al. 1993), habitat structure, distribution, abundance and the nutrient value of food resources (OSTFELD 1986, MARES & LACHER 1987, HUBBS & BOONSTRA 1998, HARRIS & LEITNER 2004), the distribution of other resources (e.g. breeding or resting sites), and predation pressure (HUBBS & BOONSTRA 1998).

Human activities may alter a species home-range size in different ways, either directly in terms of human disturbance and spatial limitation, or indirectly, for example, through effects on population demography or resource availability. From an experimental study with root voles (*Microtus oeconomus*), IMS et al. (1993) deduce three scenarios of space use responses to habitat fragmentation, depending on the social behaviour of the individuals as an intrinsic factor, and patch size as an extrinsic factor.

(1) *Fusion response*: In animals without aggressive behaviour, individuals may congregate on habitat patches in a way that their home ranges overlap to a high degree.
(2) *Fission response*: In aggressive animals, individuals may minimize their home ranges and keep home range overlap at a minimum.
(3) *Expansion response*: If home ranges are sufficiently large in relation to patch size and inter-patch matrix, individual home ranges could cover more than one habitat patch.

2 Study system: The European ground squirrel

2.1 Geographic range and endangerment

The European ground squirrel (*Spermophilus citellus* (L. 1766), Scuridae), is a middle-sized, diurnal rodent that typically inhabits steppe and open grassland in eastern and south-eastern Europe, to which it is endemic (KRYŠTUFEK 1999). In Austria, this habitat type can be found only in the pannonian zone, confining the ground squirrel occurrence to the country's easternmost regions of Vienna, Lower Austria and Burgenland. Austrian ground squirrel populations hence represent the western periphery of the species' geographic range (LEITNER 1988). A European-wide, small-scaled map of the species' distribution, however, is currently inexistent.

Since ground squirrels inhabit burrows, they require well drained soil (KRYŠTUFEK 1999). The massive reduction of dry grassland, the species' prime habitat, due to agrarian use, human settlement and establishment of industrial zones during the past decades, has caused a rapid decline of ground squirrel abundance in Austria (LEITNER 1988, HOFFMANN 2002, HOFFMANN et al. 2003a). Hence, the species is listed as endangered since 1984 (BAUER 1989) and classified IUCN vulnerable (KRYŠTUFEK 1999). The current situation dramatically differs from that during the first half of the 20^{th} century, when ground squirrels were regarded an agricultural pest and rural communities paid rewards for their ears and tails (SPITZENBERGER & BAUER 2001, pers. comm. of local residents at one of the study sites). The decrease of ground squirrel abundance is apparently linked to an increase of urbanisation which restricted ground squirrel populations in Austria to isolated fragments, where altered environmental conditions appear to affect individual life history traits as well as population dynamics (HOFFMANN 2002, HOFFMANN et al. 2008). Thus, though in suburban environments ground squirrel aggregations commonly exhibit conspicuous densities (MILLESI et al. 1999, HUBER 1996) it is assumed that those areas represent rather suboptimal refugees than optimal habitats. Although anthropogenic influence virtually has beneficial effects, like the possible provision of additional food resources, increased attraction of predators due to high density and population isolation may lead to a higher vulnerability of these colonies (HOFFMANN et al. 2008).

Fig. 1: The European ground squirrel (*Spermophilus citellus*), a middle-sized, diurnal rodent.

2.2 Biology

European ground squirrels live in loosely structured colonies or “aggregations” (sensu ARMITAGE 1981). They undergo a pronounced endogenous annual cycle with 6-7 month of hibernation. Body mass is dimorphic between sexes, and strongly depends on age and annual cycle, varying from 150 g for yearling females after emergence from hibernation to >400 g for males at the end of the active season. The active period sets off with the emergence of adult males in early March, and yearlings of both sex classes emerge together with adult females (MILLESI et al. 1999). Since the latter, in contrast to other *Spermophilus* species (MICHENER 1984), are the first to start hibernation in autumn, they have a longer hibernation period and higher overwinter mass loss than males. The last to immerge are the juveniles, which have a lower body mass than adults at the onset of their yearling season, but catch up with them until the end of the summer (MILLESI et al. 1999). The ground squirrels’ diet is predominantly vegetarian, with different herbal species, but occasionally includes also small insects (SPITZENBERGER & BAUER 2001, pers. obs.).

Females typically reproduce as yearlings showing signs of gestation and lactation (HUBER et al. 1999, MILLESI et al. 1999), whereas in males, sexual maturity can be delayed to the following year, as indicated by non-descending testes. In contrast to other ground squirrel species, it is assumed that females only mate with a single male (MILLESI et al. 1998). Mean litter size has been described to be about 4, and females have only one litter per year (MILLESI et al. 1999). Maximum life span was found to be about 3 years for males and 5 years for females (MILLESI et al. 1999). The plasticity of the life-history adaptations has been shown to be remarkable in this species (HOFFMANN 2002), and some characteristics are apparently density-dependent (HOFFMANN et al. 2003b).

2.3 Research aims

This study was part of a 3-year research project entitled *European ground squirrels in Cultivated Landscapes: Ecological, Behavioural and Genetic Adaptations in an Endangered Species,* led by Ilse E. Hoffmann (Department of Behavioural Biology, University of Vienna). The project aimed at providing information on the dynamics of free-ranging ground squirrel aggregations in Austria and their interdependencies with human-induced environmental changes, necessary for an effective conservation of this species. To investigate the ground squirrels’ response to anthropogenic habitat usage and degradation, five focal populations, inhabiting different habitats on a degree form nearly natural to strongly altered, were studied over a 3-year-period in an interdisciplinary approach, including ecological, demographical, physiological, genetic and behavioural analysis. As part of this project, a study on home ranges of European ground squirrels was conducted in the two most extreme habitats to investigate potential effects of habitat alteration on space use. Data on home-range size were collected during the field season in 2008 using radiotelemetric methods.

European ground squirrels represent a beneficial model organism to study behavioural responses to habitat changes. The species represents a typical faunal element of the pannonian region, but as a consequence of anthropogenic land use, has increasingly settled in suburban areas, where it is exposed to a range of human-induced limiting factors of gradual effectiveness towards which populations are highly sensitive (HOFFMANN 2002). Hence, different populations apparently exposed to varying degrees of environmental changes can be found. Insights gained from studies on ground squirrels can serve as models for other small mammals, for example, European hamsters (*Cricetus cricetus*). Like ground squirrels, they have increasingly settled in close association with humans and their ability to deal with the challenge of modern landscapes will be crucial for the species’ future fate. Conclusion from studies on habitat fragmentation are applicable across taxa, e.g. evidence for space use responses to habitat fragmentation of root voles (*Microtus oeconomus*) were used as a model for a bird species, the capercaillie grouse (*Tetrao urogallus*; IMS et al. 1993). Furthermore, ground squirrels are rather easy to trap and handle (which is especially important when operating with small radiotransmitters that have limited batteries and must be taken off in time), and their diurnal activity facilitates field work, allowing extensive data acquisition feasible on time scales amenable for field research. Lastly, the European ground squirrel is a “flagship species” with a public appeal.

Ground squirrels dwelling on anthropogenically influenced small habitat patches face a variety of interrelated conditions capable of interacting with their movement behaviour: When habitat patches are restricted in size, space becomes a limited resource. This might, predominantly via an increase in competition, influence not only the socially mediated distribution, but also the home-range size of animals. Secondly, the aforementioned elevated population densities commonly found in ground squirrel populations in suburban environments presumably increase space limitation and competition for resources and mates, but at the same time also the number of possible mates in close proximity. A male mating tactic that is successful when females are loosely scattered might be less feasible in high-density populations, afflicting the size of the males’ home ranges. If the habitat is saturated, high densities should promote dispersal (STENSETH & LIDICKER 1992), but if the habitat is isolated and a dispersing individual has nowhere to go, saturation dispersal is possibly hindered. Another factor involved with high densities is an elevated attraction of predators. Though per capita predation pressure may not be higher than in populations with lower densities (DEHN 1990), the mere presence of predators may motivate animals to limit the time they are exposed to them by reducing aboveground movements. Presence of humans or cars may have a similar effect, generating a trade-off between ‘predator’ avoidance and resource use (GILL & SUTHERLAND 2000).

Though the ground squirrels’ diet is not very specific, different food resources may vary in their nutritional value (BENNET 1999). Anthropogenic activities may alter the habitat’s plant composition and distribution of food resources, either facilitating or complicating the allocation of high-quality food. In European ground squirrels, as hibernating small mammals, the limited active season causes additional energetic and temporal constraints. Mating, gestation and weaning of the young have to occur in a limited time period allowing juveniles to complete growth and fattening prior to hibernation.

To yield insights on the potential effects of habitat changes on the animals’ space use, we studied home ranges of European ground squirrels in the two most extreme study sites; the nearly natural one, a secondary steppe, and the one with the highest anthropogenic impact, an alfalfa meadow, subjected to isolation, fragmentation of the surroundings, alteration of the vegetation and presence of humans. Home ranges were compared between the two habitats and sex and age differences were examined.

3 Field study: Home ranges of European ground squirrels (*Spermophilus citellus*) in two habitats exposed to different degrees of human impact

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3.1 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. At 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 at the two study sites. Furthermore, variances in population density and predator presence could have contributed to the observed movement patterns.

3.2 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. 2004b) or at investigating sex differences in predation risk of juveniles (HOFFMANN et al. 2004a), 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.

3.3 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 (Fig. 2); 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 (Fig. 2) 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.

Fig. 2: Aerial views of the two study sites (defined by the red line), the secondary steppe (left) and the alfalfa meadow (right).

Field study. At 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 (NORBURY et al. 1998).

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. At 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 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.

3.4 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 at the two study sites (Table 1, Figs. 3, 4). 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).

At 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 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).

	Steppe	Alfalfa	Statistics	
Both sexes	0.448 ± 0.332 (n = 19)	0.175 ± 0.081 (n = 18)	U = 74	**P = 0.003**
juvenile	0.518 ± 0.296 (n = 8)	0.183 ± 0.100 (n = 9)	U = 7	**P = 0.005**
nonjuvenile	0.397 ± 0.361(n = 11)	0.166 ± 0.060 (n = 9)	U = 31	P = 0.160
Males	0.435 ± 0.322 (n =11)	0.205 ± 0.091 (n = 11)	U = 28	P = 0.033
juvenile	0.436 ± 0.213 (n = 4)	0.232 ± 0.115 (n = 5)	U = 4	P = 0.142
nonjuvenile	0.435 ± 0.387 (n = 7)	0.182 ± 0.069 (n = 6)	U = 10	P = 0.116
Females	0.465 ± 0.368 (n = 8)	0.127 ± 0.018 (n = 7)	U = 12	P = 0.064
juvenile	0.600 ± 0.377 (n = 4)	0.123 ± 0.023 (n = 4)	U = 0	P = 0.021
nonjuvenile	0.330 ± 0.300 (n = 4)	0.132 ± 0.010 (n = 3)	U = 6	P = 1.000

Tab. 1: Mean (± SD) home ranges of European ground squirrels [ha] in two habitats during periods of about one week duration from March to July in 2008. Bonferroni-corrected level of significance: P = 0.008.

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.

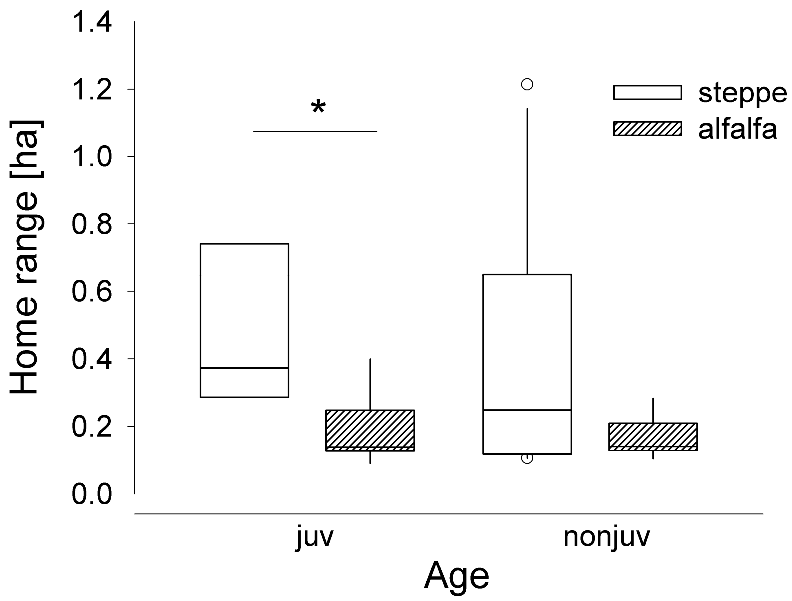

Fig. 3: Differences in home-range size between habitats within age classes. Juvenile individuals at the secondary steppe used more space than individuals at the alfalfa meadow, whereas home ranges of nonjuveniles were similar between study sites (* p < 0.008, for details see Tab. 1).

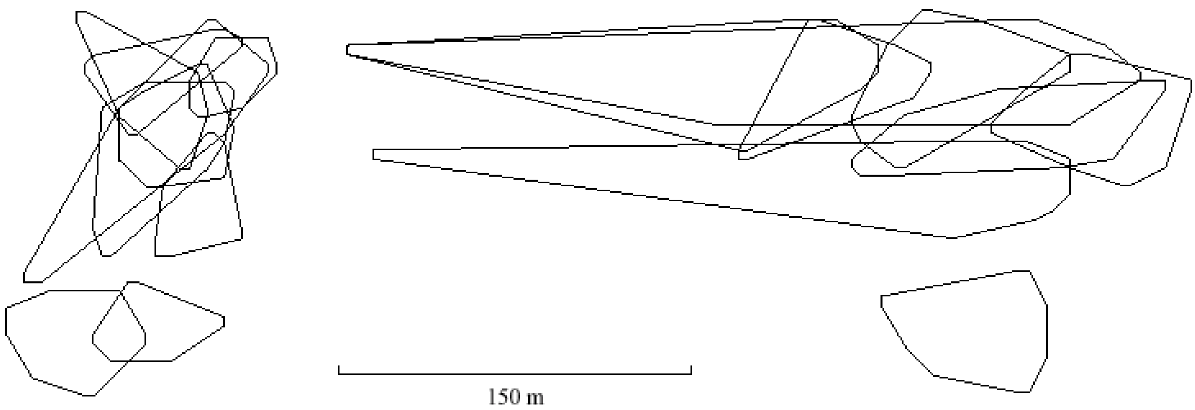

Fig. 4: Home ranges of nine juveniles at the alfalfa meadow (left) and eight juveniles at the steppe (right).

3.5 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. 3).

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 at 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. 2008), 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. 4), 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). Although HUBBS & BOONSTRA (1998) discuss the possibility that increased density forces animals to reduce their home ranges in order to reduce conflict with conspecifics, they expect that the same is true for Arctic ground squirrels. 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 meadow the 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 in any case, avian predators could still be spotted by the 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. (2004a) 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 the 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 in 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 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 in HUBER'S study 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.

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* (BOELSSTORFF & OWINGS 1995), *S. richardsonii* (MICHENER 1979), *S. columbianus* (females: MURIE & HARRIS 1978, males: FESTA-BIANCHET & BOAG 1982) 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 at 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.

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Zusammenfassung

Moderne Landschaften sind von anthropogenem Einfluss geprägt, welcher zu Veränderungen in der Habitatstruktur und in der Flora geführt hat. Habitatverlust und - -fragmentierung aufgrund menschlicher Aktivitäten stellen die Hauptursachen für die Gefährdung zahlreicher Arten und die weltweite Bedrohung der Biodiversität dar. Populationen werden auf Resthabitatflächen zurückgedrängt und sind dort umso gefährdeter, je kleiner und isolierter diese sind, da stochastische Effekte in Bezug auf die Demographie oder Genetik zunehmen. Wanderbewegungen zwischen Populationen, die diesen Effekten entgegenwirken könnten, werden durch die Fragmentierung der umgebenden Landschaft stark eingeschränkt oder verhindert. Neben dem Wanderungsverhalten kann auch der individuelle Aktionsraum (*home range*) durch menschliche Aktivitäten, welche primär die Umweltbedingungen und sekundär die Populationsdynamik verändern, beeinflusst werden.

In der vorliegenden Studie wurde der mögliche Einfluss anthropogener Habitatsveränderung auf den Aktionsraum des Europäischen Ziesels (*Spermophilus citellus*) untersucht. Diese Kleinsäugerart, die ursprünglich Trockenrasengebiete und Steppen in Ost- und Südosteuropa bewohnte, ist massiv von der Zerstörung ihres natürlichen Habitats betroffen. Zieselkolonien finden sich mittlerweile vermehrt auf anthropogen beeinflussten Flächen wie Erholungsgebieten, Industriebrachen oder Sportfeldern. Die hohen Populationsdichten, welche bisweilen in solchen Kolonien auftreten können, dürfen jedoch nicht über die allgemeine Gefährdung des Ziesels hinwegtäuschen; in den letzten Jahrzehnten wurde ein dramatischer Bestandesrückgang verzeichnet und die einst weit verbreitete Art befindet sich heute auf der roten Liste der gefährdeten Tier- und Pflanzenarten Österreichs.
Mittels radiotelemetrischer Methoden wurden die Aktionsräume von insgesamt 38 Individuen in zwei unterschiedlichen Habitaten erfasst. Dabei handelte es sich einerseits um eine naturnahe sekundäre Steppe südlich von Eisenstadt und andererseits um eine stark anthropogen beeinflusste Luzernwiese bei Wien, wobei letztere durch eine Änderung der natürlichen Vegetationszusammensetzung sowie durch häufige Anwesenheit von Menschen gekennzeichnet ist. Der anthropogene Einfluss kommt außerdem in der Isolierung des Habitats sowie in der Fragmentierung der umgebenden Landschaft zum Tragen. Die Populationsdichten in den beiden Gebieten unterschieden sich stark und betrugen im Untersuchungsjahr 9 Individuen/ha in der sekundären Steppe und 43 Individuen/ha in der Luzernwiese. Die Tiere wurden in Lebendfallen gefangen und, nach der Bestimmung von Geschlecht und Alter (juvenil oder ≥ 1 Jahr alt), mit einem Halsbandsender versehen. Anschließend wurde ihre Position mehrmals täglich über einen Zeitraum von etwa einer Woche aufgenommen.
Zur Berechnung der Größe der Aktionsräume mithilfe des Programms Ranges6 kam die Methode des minimalen konvexen Polygons (MCP) zur Anwendung. Die Aktionsraumgrößen wurden zwischen den beiden Untersuchungsgebieten verglichen und geschlechtsspezifische Unterschiede sowie Unterschiede zwischen den Altersklassen bestimmt. Die Bewegungen von Jährlingen und älteren Individuen schlossen in der Steppe 0.397 ± 0.361 ha ($n = 11$) und in der Luzernwiese 0.166 ± 0.060 ha ($n = 9$) ein, jene juveniler Individuen 0.518 ± 0.296 ha ($n = 8$) in der Steppe und 0.183 ± 0.100 ha ($n = 9$) in der Luzernwiese. Jährlinge und ältere Individuen zeigten in der Größe ihrer Aktionsräume keinen signifikanten Unterschied zwischen den beiden Gebieten und es konnten allgemein keine geschlechtsspezifischen Effekte festgestellt werden. Die

Bewegungen juveniler Individuen schlossen jedoch in der sekundären Steppe signifikant größere Flächen ein als in der Luzernwiese.
Vermutlich ist dies vor allem auf die unterschiedliche Qualität und Verteilung von Nahrungsressourcen in den Untersuchungsgebieten zurückzuführen. Obwohl die Nahrung des Ziesels relativ unspezifisch ist, kann der Nährgehalt verschiedener Nahrungsquellen variieren und es gibt aus anderen Untersuchungen Hinweise darauf, dass Luzerne für Ziesel eine Nahrungsquelle hoher Qualität darstellt. Die Abundanz und relative Homogenität der Luzerne im anthropogen beeinflussten Habitat dürfte deshalb zu den verminderten Aktionsräumen in diesem Untersuchungsgebiet geführt haben. Da juvenile Individuen Wachstum und Anlegung von Fettreserven in einer limitierten zeitliche Periode vollenden müssen, können Qualität und Verteilung von Futterressourcen bedeutende Faktoren für das Überleben des Winterschlafes darstellen. Die größeren Aktionsräume in der Steppe werden deshalb auf selektive Nahrungsstrategien zurückgeführt. Diese Interpretation wird von der Beobachtung gestützt, dass in diesem Habitat Bewegungen der juvenilen Individuen mehrfach zu einem am Rand der Steppe gelegenen Weizenfeld führten. Außerdem werden eine erhöhte Anwesenheit von Prädatoren, Menschen und Hunden sowie das limitierte Platzangebot als mögliche Ursachen für kleinere Aktionsradien bei Juvenilen in der Luzernwiese diskutiert. Obwohl anthropogene Einflüsse offensichtlich vorteilhafte Effekte im Sinne der Bereitstellung zusätzlicher Nahrungsressourcen haben können, darf nicht vergessen werden, dass solche Kolonien durch Isolation einerseits und Attraktivität für Prädatoren aufgrund hoher Populationsdichten andererseits dennoch stark gefährdet sind.

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Curriculum Vitae

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08/2005	Dreiwöchige zoologisch-botanische Exkursion nach Panama und Costa Rica mit Aufenthalt in der TROPENSTATION LA GAMBA.
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11/2008	Ausbildung zur Führerin durch die Ausstellung *C'est la Vie* im NATURHISTORISCHEN MUSEUM BERN, Schweiz.

PUBLIKATIONEN UND KONGRESSTÄTIGKEIT:

TURRINI TABEA A., BRENNER MICHAELA, MILLESI EVA, HOFFMANN ILSE E. (2008): *Home ranges of European Ground Squirrels* (Spermophilus citellus) *in two habitats exposed to different degrees of human impact. [Aktionsradien Europäischer Ziesel* (Spermophilus citellus) *in zwei Habitaten mit unterschiedlichen Graden an anthropogenem Einfluss.]* Lynx, **39** (2): 323–332.

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II EUROPEAN GROUND SQUIRREL MEETING (www.groundsquirrel.cz/progr.htm), Sv. Jan pod Skalou, Tschechische Republik, 2008.
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Poster: BRENNER M., TURRINI T., HOFFMANN I.: *Does home-range overlap in European ground squirrels increase with anthropogenic alteration?*

EUROPEAN CONGRESS OF CONSERVATIONAL BIOLOGY (www.eccb2009.org), Prag, Tschechische Republik, 2009.
Angenommenes Poster: TURRINI T., BRENNER M., HOFFMANN I., MILLESI E.: *Anthropogenic habitat alteration influences home-range size of European ground squirrels* (Spermophilus citellus).

EDV- UND FREMDSPRACHENKENNTNISSE:

Sehr gute Kenntnisse: Word, Powerpoint, Excel.
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