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Do European Ground Squirrels (*Spermophilus citellus*) in Austria adjust their life history to anthropogenic influence?

Odráží se vliv člověka na změnách biologie sysla obecného (*Spermophilus citellus*) v Rakousku?

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Abstract. While the European ground squirrel in Austria is sometimes near to extinction in its natural habitat, aggregations in altered habitats often achieve exceptional densities. In an effort to clarify this phenomenon, we compared demographic and life-history variations of five focal populations exposed to different environmental conditions. The respective habitat types were: secondary steppe, semi-arid grassland, a meadow renaturated from arable land, a wine-growing area, and a meadow altered by alfalfa. The study plots also differed in the degree of inclination, fragmentation and isolation. The populations were examined in 2006–2008 from April to July of each year by capture-mark-recapture and observation. At initial capture, each ground squirrel was categorised (sex, age, reproductive state), marked with hair dye, tattooed and/ or equipped with a PIT tag. Body mass, head length and gonadal development were recorded continuously. Our results indicate that population densities increased with anthropogenic influence (range: 9–43 individuals/ha), whereas sex ratios varied inconsistently among study plots. Each focal population contained reproductive yearling males. Their highest and lowest percentages, respectively, occurred on the alfalfa meadow (83%) and in the vineyards (40%), indicating that habitat alteration might either delay or accelerate puberty. We conclude that anthropogenic influence may have beneficial effects on European ground squirrels in terms of population growth. However, this conclusion is ambiguous in short terms. Thorough analyses of our data will provide information not only on the species' habitat requirements, but also on the artificial constraints it is yet able to cope with.

Key words. *Spermophilus citellus*, life history, habitat alteration, demography, population density, population size

INTRODUCTION

The recent distribution of European ground squirrels in Austria is confined to the Pannonian zone in the country's easternmost states (Spitzenberger & Bauer 2001), which is equivalent to the south-western periphery of the species' distribution range (Kryštufek 1999). This region originally consisted of primary and secondary steppe, with local anthropogenic shaping going back over centuries (Holzner 1986). Hence, the modern landscape includes all kinds of arid grassland on a gradient from nearly natural to strongly altered environments, and is fragmented by intensive agriculture, urban sprawl and major roads. Consequently, European ground squirrels occur mainly in isolated habitat patches (Leitner 1986, 1988, Spitzenberger & Bauer

2001), a pattern that is characteristic for relict populations (BEGON et al. 1990). Sometimes near to extinction in their natural habitat, aggregations of ground squirrels in a close spatial association with humans often achieve exceptional densities (MILLESI et al. 1999), though exhibiting significant fluctuations (HOFFMANN et al. 2003a). Determining the causes and consequences of this unsteady state has not been accomplished to date, therefore information is insufficient to assess whether the altered areas are optimal habitats or suboptimal refuges. Interdependencies of habitat fragmentation, quality and preference with ground-squirrel abundance have to be elucidated. Knowledge on demographic attributes and life-history strategies of populations exposed to different levels of human alteration is required to reveal causal relationships with environmental conditions.

Ground-dwelling sciurids are generally classic subjects for research on variations in life-history traits and population dynamics (e.g., ARMITAGE 1991, BOAG & MURIE 1981, DOBSON 1995, DOBSON & KJELGAARD 1985, FESTA-BIANCHET & KING 1991, HOFFMANN 2002, MICHENER 1998, OLI et al. 2001). SHERMAN & RUNGE (2002) describe the collapse of an Idaho ground-squirrel population, likely due to anthropogenic habitat disturbance acting on life-history parameters. In the European ground squirrel, the degree of interaction with human environments goes beyond that previously described for other sciurids. At the same time, comprehensive information on abundance patterns of European ground squirrels in Austria is sparse. Moreover, there has been virtually no scientific research on interrelations of population density, demography and life history. It is well known that life-history traits differ in their potential to influence population dynamics, with some demographic variables affecting changes in population size more profoundly than others (cf. OLI & DOBSON 2001). Therefore, this study is aimed at comparing demographic and life-history adaptations of populations exposed to different degrees of habitat alteration. It may provide essential information about how endangered species cope with changing environmental conditions, in particular with the constraints imposed by modern landscapes. On top of this, it might serve as a model for other small mammal species that, while being endangered, have increasingly settled in anthropogenically shaped environments (e.g., the European hamster *Cricetus cricetus*, FRANCESCHINI 2002, FRANCESCHINI & MILLESI 2001).

MATERIAL AND METHODS

Five locally distinct European ground squirrel populations were selected to compare their demographic attributes and life-history strategies. Their habitats are exposed to different levels of human alteration, and also vary in inclination, fragmentation and isolation (Table 1). One of them is situated west of Lake Neusiedl near Trausdorf (TD), one in Vienna south of the Danube at a former radio station (RS), and three are near (Gerasdorf Badeteich) or in Vienna (Stammersdorf, Falkenberg) north of the Danube (GB, ST, FB). The five habitats were ordered a priori by their aspect, i.e., the apparent degree of human alteration, from low to high:

1. TD (47°48'N, 16°33'E, 164 m a. s. l.) is a secondary steppe of nearly 100 ha, and was a grassy airport, until the area was rededicated as a pasture in the 1990s. TD itself is hardly fragmented, and encircled by dust roads, small fields and vineyards, all of which provide connections and corridors to numerous adjacent ground-squirrel habitats. Ground squirrels were captured on a study plot of approx. 7 ha.

2. RS (48° 09' N, 16° 24 'E, 236 m a. s. l.) consists of semi-arid grassland that merges with vineyards and fallows in the south and east. Ca. 50 ha contain patches of suitable ground-squirrel habitat. The site borders on an urban area and a forested park in the north and west. Fragmentation is moderate, but isolation is substantial, since any connection is inhibited in at least two directions. The area of the study plot was approx. 4 ha.

3. GB (48° 18' N, 16° 28' E, 151 m a. s. l.) is a lawn restored from an approx. 6 ha arable land in 2003/04. Conceived for sunbathers, it was soon occupied by ground squirrels, presumably immigrants from the banks of an adjacent pond and a nearby irrigation canal. Visitors feed the animals near the pond, especially during summer, which results in a considerable exchange of ground squirrels between the pond and the lawn. Due to intensive agriculture and urban sprawl, the surrounding habitat is extremely fragmented, but dispersal into and out of patchily distributed colonies in the farer environs seems possible. We captured ground squirrels on approx. 3 ha of the lawn.

4. ST (48° 19' N, 16° 25' E, 199 m a. s. l.) is situated within >250 ha of a wine-growing area intermingled with grassland and small fields. The vineyards are farmed differently every few meters; most of them have ground vegetation, some get scarified and just a few get ploughed regularly. Only a small oak wood and some access roads intercept the landscape, and isolation is moderate, caused by a settlement in the south and two major roads in the west and east. The study plot was ≥1 ha.

5. FB (48° 18' N, 16° 22' E, 318 m a. s. l.) is an approx. 5 ha area of formerly dry grassland that was altered by sowing alfalfa (*Medicago sativa* L.) some years ago. At about the same time, in 2001, 118 ground squirrels were translocated from a site nearby; a small aggregation has been already extant before. An adjacent wood, a huge conventional vineyard, arable fields and a transmitting station cause both substantial fragmentation and considerable isolation of the habitat. Ground squirrels were captured on >1 ha of the area.

Capture-mark-recapture was performed in 2006–2008 from April to July of each year at least once per week and site using the Tomahawk live traps. We included data from a pilot study carried out at RS in 2004 and 2005. At initial capture, each ground squirrel was categorised (male/ female, juvenile/ nonjuvenile, reproductive/ nonreproductive), tattooed with dot codes on the skin between anus and hind legs, and marked with commercial hair dye for recognition in the field. Recaptured individuals received PIT tags (Datamars Comp.), facilitating identification and age determination in subsequent years. At each capture, body mass, head length and gonadal development (Millesi et al. 1999) was recorded. We measured head length with a digital calliper as the distance between occipital bone and tip of the nose. Detailed description of the capture technique appears in Huber et al. (1999) and Millesi et al. (1999). Population density was determined annually as the number of nonjuvenile individuals observed and/or captured on each study plot.

We conducted statistical analyses with SPSS 15.01 for Windows. After performing the Shapiro-Wilk tests for distribution, we applied parametric tests for normally distributed samples; otherwise nonparametric tests were carried out. Samples were checked for an equal distribution with χ^2-tests. Statistical significance was set at $p<0.05$.

RESULTS

We captured a total of 419 individual European ground squirrels at the five study sites (231 non-juveniles, 188 juveniles; Table 1). Nonjuvenile population densities did not differ among years (Friedman test, $\chi^2=2.80$, $p>0.24$), therefore we pooled the data for further comparisons. Densities (Table 1, Fig. 1) differed among sites (One-way ANOVA, $F=22.77$, $p<0.001$) and increased with anthropogenic influence (Pearson, $r=0.91$, $p<0.001$). They were lowest in TD and RS (LSD post-hoc tests: each $p\leq0.005$ vs. all other sites) and highest in FB (LSD post--hoc tests vs. TD, RS: each $p<0.001$; vs. GB: $p=0.001$; vs. ST: $p>0.05$). Densities in GB were intermediate and marginally lower than in ST (LSD post-hoc test: $p=0.08$).

Sex ratios (males per female, Table 1) did not deviate significantly from an equal distribution in any of the study plots (each $\chi^2<0.93$, each $p>0.33$). In 2007, we found significant male biases among juveniles in RS (21 males/10 females, $\chi^2=3.90$, $p=0.048$) and FB (26 males/13 females, $\chi^2=4.33$, $p=0.037$), but we did not recapture any yearlings in 2008 in RS, and in FB, nonjuvenile sex ratio was again balanced in 2008.

Table 1. Habitat characteristics and demographic attributes of the study sites
Tab. 1. Vlastnosti stanoviště a demografické parametry na sledovaných lokalitách. Vysvětlivky zkratek viz Materiál a metodika (Material and methods)

field name	Trausdorf	Radiostation	Gerasdorf Badeteich	Stammersdorf	Falkenberg
abbreviation	TD	RS	GB	ST	FB
type	secondary steppe	semi-arid grassland	renaturated lawn	vineyards	alfalfa meadow
inclination	–	SE	–	S	S
fragmentation	minimal	moderate	considerable	minor	substantial
isolation	minimal	considerable	moderate	minor	substantial
initial captures	106	75	80	77	81
nonjuveniles	60	42	46	39	44
juveniles	46	33	34	38	37
nonjuveniles/ha	9.3	11.9	25.9	33.8	42.6
males per female					
nonjuveniles	1.1	0.8	0.8	1.0	1.
juveniles	0.8	2.3	1.0	1.7	1.8
% reproductive / all yearling males (n)	72.7 (8/11)	57.1 (4/7)	60.0 (6/10)	40.0 (2/5)	83.3 (5/6)

The percentages of immature yearlings in the whole male population ranged between 4.2% in FB and 20.0% in GB and ST. In other words, most of the males captured during spring had descended testes. Considering only yearling males, the majority of them was reproductive except in ST (Table 1). The highest percentages occurred in TD and FB, the least and the most altered sites.

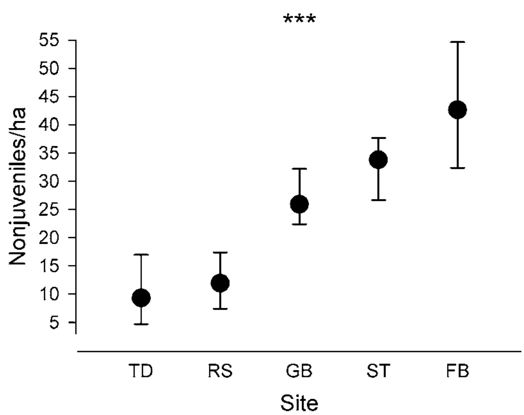

Fig. 1. Population densities of ≥1-year old European ground squirrels in the five study sites (mean, range).
Obr. 1. Populační hustota syslů na pěti sledovaných lokalitách (průměr, rozsah). Zahrnuta jsou jednoletá a starší zvířata.

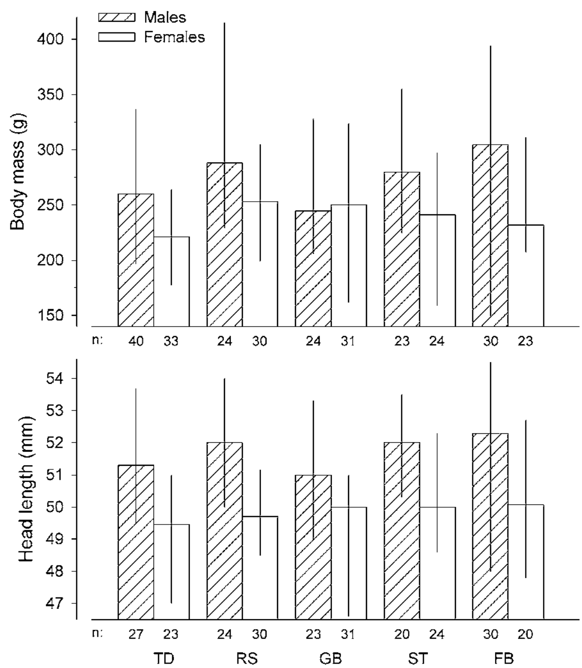

Fig. 2. Body mass and head length of ≥1-year old European ground squirrels in the five study sites (median, range). Variations in both measures were significant among the sites (body mass: Kruskal-Wallis tests, males: χ^2=41.90, p<0.001; females: χ^2=16.74, p=0.002; body size males: Kruskal-Wallis test, χ^2=22.87, p<0.001; females: Oneway ANOVA, F=3.10, p=0.031).
Obr. 2. Hmotnost těla a délka hlavy syslů ve věku od 1 roku zjištěná na pěti sledovaných lokalitách (medián, rozsah). Rozdíly mezi lokalitami byly v obou parametrech signifikantní (hmotnost těla: Kruskal-Wallisův test, samci: χ^2=41.90, p<0.001; samice: χ^2=16.74, p=0.002; velikost těla samci: Kruskal-Wallisův test, χ^2=22.87, p<0.001; samice: Oneway ANOVA, F=3.10, p=0.031).

We focussed further analyses on two important individual life-history traits: body mass and body size of yearlings and adults. Both measures varied significantly among sites, in males as well as in females (Fig. 2), and were significantly, but weakly, correlated with anthropogenic influence (Spearman correlations, each $r_S \leq 0.356$, each p≤0.038). Male body mass in GB and TD was significantly lower than at the other sites (Mann-Whitney tests, each U >96.0, each p≤0.003). Males in FB had the highest body mass; they were also significantly heavier than in ST (Mann-Whitney test, U=201.0, p=0.01). When we examined age structure, we found that FB was the only site where we had recaptured ≥3-year old males. We used head length as a measure of body size. Differences were consistent with the body mass data, i.e., the light males of TD and GB were also significantly smaller than those at the other sites (Mann-Whitney tests, each U>115.0, each p≤0.021). In contrast to mass differences, the sizes of males in FB and ST were similar (U=251.0, p>0.33). Body mass varied among sites also in females. In contrast to males, this difference was based on the low weights from TD only (vs. RS: U=226.0, p<0.001; vs. GB: U=300.5, p=0.005; vs. ST: U=258.0, p=0.026; vs. FB: U=205.0, p=0.004). Differences among the other sites were not significant. Interestingly, females at RS were heavier during the pilot study (2004/05, n=14) than afterwards (n=16, Mann-Whitney, U=63.0, p=0.042). In GB, female body mass turned out to be similar to that of males (U=363.0, p=0.879). Differences in head length were significant between small TD-females and large females in ST (LSD post hoc, p=0.003) and FB (LSD post hoc, p=0.036). In addition, females in ST were significantly larger than in RS (LSD post hoc, p=0.038). In ST, only one female was recaptured as a yearling in a subsequent year.

DISCUSSION

This study provides evidence that European ground squirrels exhibit a notable plasticity in their life-history adaptations. The underlying mechanisms can be categorised as intrinsic (e.g., behavioural and genetic attributes) or extrinsic processes (e.g., changes in environmental conditions), all of which may act synergistically. The potential range of life-history variation has evolved during natural selection, whereas individual strategies within this range are triggered by internal and external conditions (Hoffmann 2002).

The most conspicuous finding was that populations were sparse in nearly natural and dense in strongly altered environments. Remarkably high densities under semi-natural conditions have also been reported for North-American ground-squirrel populations. E.g., densities of *S. armatus* in an artificial habitat (lawns) were 82 ind./ha compared to only 16 ind./ha in a natural habitat (Slade & Balph 1974). Dense populations in close association with humans are nowadays a typical characteristic of European ground squirrels (Golub 1988, Hoffmann et al. 2003a, b, Millesi et al. 1999, Ružic 1978, Spitzenberger & Bauer 2001), but to date, it has not been stated explicitly that undisturbed populations may exhibit significantly low densities.

Our findings are consistent with the results of a multiyear-study on Arctic ground squirrels in Canada that emphasised the importance of food availability and predator presence for population density (Karels et al. 2000): the latter increased when supplemental food was provided or predators were excluded, primarily through changes in reproduction and body condition. In the steppe, we found the lowest population density (9 ind./ha) and the lightest animals. Consistent with Karels et al. (l.c.), reduced body mass at TD might be attributable to poorer quality of food and interactions with predation risk: we saw avian and mammalian predators on many occasions, and increased per-capita predation risk due to the sparse distribution of individuals (Dehn 1990) may promote predator avoidance, to the detriment of foraging. Thus, the ground squirrels are continuously facing a trade-off between foraging and anti-predator behaviour (Lima & Dill 1990), which might affect body mass and size. On the other hand, the population may perceive the habitat as size-neutral (Begon et al. 1990), which would explain that mainly light and small animals are able to constitute a colony of at least 900 nonjuveniles. One might hypothesize that this corresponds to the intrinsic target value of a continuous population, independent of habitat size (Dittami, pers. comm.). Given that the target population size acts as a kind of internal carrying capacity, population densities should adjust in such way that population size approaches this value (logistic equation, Feldhamer et al. 1999).

The semi-arid-grassland population was similarly sparse (12 inds./ha), but occupied a patchy habitat. High male body mass could indicate senescence, and the male-biased juvenile sex ratio in 2007 preceded a year without any yearling recaptures. Both may be symptoms of instable population dynamics (Boonstra 1994, Hoffmann et al. 2003a), probably promoted by isolation effects at the edge of the habitat, which might imply an increased mortality risk (Hoffmann et al. 2003b). These symptoms, and the temporal difference in female body mass within five years, suggest that identifying causal relationships requires long-term monitoring of populations.

On the lawn, males were light and small, indicating a high proportion of yearlings. The fact that GB was the only site without a sex difference in body mass supports this assumption: usually, the sexual dimorphism in body mass is pronounced among European ground squirrels of the same age, but adult females may be as heavy as yearling males (Millesi et al. 1999). The renaturated meadow may have represented a dispersal sink (cf. Pulliam 1988), preferably for yearling males: because of the intermediate population density (26 ind./ha), competition was probably low (Millesi et al. 2004), and access to resources like food and burrows, but also to females, was facilitated. Consistently, 60% of the yearling males captured in spring were reproductive.

In the vineyards, we observed a relatively high population density (34 ind./ha) and the largest proportion of immature yearling males (60%) compared to the other sites. Both might be attributable to low predation: from the ground squirrels' point of view, vine provides cover from above while not obstructing sight near the ground. Hannon et al. (2006) emphasise the role of shrubs in protecting Uinta ground squirrels from attacking predators. The same applies for grapevines. Thus, mortality risk was reduced, which may have enhanced survival, specifically of juvenile males that did not reproduce as yearlings. The presence of nonreproducing yearling males in turn contributes to dense populations, at least in altered habitats (Hoffmann et al. 2003a, Millesi et al. 1999).

Inter-year recaptures indicate that the female population at ST contained a high percentage of adults, which could explain the large head size of females. Such, the habitat in some way favoured large females, probably acting via enhanced longevity. One could hypothesize that females at ST benefited from foraging on wine grapes, which contain polyphenols: a considerable body of literature supports the contribution of dietary polyphenols in the prevention of oxidative stress in the pathogenesis of age-related human diseases (Scalbert et al. 2005). A study on selective foraging and food composition is required to investigate this topic.

On the alfalfa meadow, we found a couple of traits that might be related to habitat alteration. The most conspicuous fact was that the male population mainly consisted of heavy individuals. Indeed, FB was the only site with some males recaptured at a minimum age of three years. The habitat is a fragment, and the surroundings seem to inhibit dispersal, which might explain why males tended to remain resident. The male bias among juveniles in 2007 was not significant among nonjuveniles in 2008. This indicates poor survival of juvenile males, resulting in a low number of yearling males. As it is likely that mainly juveniles in good condition had survived, most of the yearling males were reproductive.

In Montana (USA), ground squirrels invaded alfalfa fields, resulting in yield reduction (Johnson-Nistler et al. 2005, Yensen & Sherman 2003). Hence, alfalfa obviously represented a high-quality food component for the ground squirrels at FB. There is strong evidence that food resources can affect population densities of *Spermophilus* (Davis & Murie 1985, Dobson 1995, Nunes et al. 1997). High densities have also been reported for North-American ground--squirrel populations with supplemented food (Dobson & Kjelgaard 1985, Hubbs & Boonstra 1997, Karels et al. 2000, Michener 1989). In Columbian ground squirrels, population growth was mediated via increased fertility and early sexual maturity (Dobson & Oli 2001), which possibly also applies for the population at FB, as indicated by the high proportion of reproductive yearling males. Quantity and quality of food resources have probably lead to the dense population at FB (43 individuals/ha), acting together with isolation and small habitat size. In other rodents, e.g., eastern chipmunks (*Tamias striatus*, Reunanen & Grubb 2005) and white-footed mice (*Peromyscus leucopus*, Wilder & Meikle 2005), habitat size was also negatively correlated with population density. Whereas chipmunk densities decreased with isolation (Reunanen & Grubb 2005), this was not the case with ground-squirrel densities at FB, most likely because not only immigration, but also emigration was inhibited. Holekamp & Sherman (1989) suggested that philopatry of male *Spermophilus* should be more common in areas with abundant food. In addition, genetic drift initiated by the translocation in 2001 may have enforced male philopatry at FB.

We conclude that anthropogenic influence may have beneficial effects on European ground squirrels in terms of population growth and individual life-history traits. However, this conclusion is not unambiguous: e.g., the low percentage of immature yearling males at FB could be attributable to precocious sexual maturation, but also to high juvenile mortality under strongly altered conditions. On the other hand, timing of male puberty did not vary systematically among the study sites, and may rather depend on other factors than on anthropogenic influence. In addition, certain habitat alterations seem to act differentially on males and females. E.g., the vineyards favoured female body size, whereas mainly males benefited from the alfalfa in terms of body mass. Ground squirrels are often described as relying on open grassland habitats (e.g., Spitzenberger & Bauer 2001). Yet, they appear to be capable of adapting to variations in the structure of the habitat and are likely to thrive as long as minimal habitat requirements are fulfilled. However, the extent and quality of alterations are crucial, as particular habitat conditions may be required to sustain a viable population, such as minimal size, sufficient resource availability, suitable soil structure and a minimal distance to human presence. Ongoing research on time allocation, stress response and population genetics will help to elucidate causal relationships between human interventions and life history as well as population characteristics of European ground squirrels.

SOUHRN

Zatímco ve svém přirozeném prostředí je sysel obecný v Rakousku na některých místech na pokraji vyhynutí, na pozměněných stanovištích dosahují jeho kolonie často mimořádných hustot. Abychom se pokusili vysvětlit tento fenomén, porovnali jsme některé demografické a biologické parametry pěti modelových populací vyskytujících se na lokalitách s rozdílnými podmínkami prostředí. Jednalo se o následující typy biotopů: sekundární step, polosuchou louku, louku vzniklou zatravněním bývalého pole, vinici a kulturu vojtěšky. Studované plochy se lišily také stupněm izolovanosti a fragmentace a dispozicí. Populace byly sledovány v letech 2006–2008 vždy od dubna do června pomocí zpětných odchytů značených jedinců a jejich přímého pozorování. Při prvním odchytu bylo u každého sysla určeno pohlaví, věk a stav z hlediska reprodukce. Poté byla zvířata individuálně označena pomocí barvy na vlasy, tetování a/nebo pomocí aplikace podkožního mikročipu. Při opakovaných odchytech byla u jednotlivých syslů zaznamenávána hmotnost těla, délka hlavy a stav jejich pohlavních orgánů. Výsledky studie ukázaly, že hustota populace se při vzrůstajícím antropogenním vlivu zvyšovala (v rozpětí: 9–43 jedinců/ha), zatímco rozdíly v poměru pohlaví na studovaných plochách byly víceméně náhodné. Na každé modelové ploše se vyskytovali pohlavně aktivní jednoletí samci. Největší podíl těchto samců byl zjištěn ve vojtěšce (83%) a nejnižší ve vinicích (40%), což naznačuje, že změna biotopu by mohla navíc způsobovat opoždění nebo urychlení pohlavního dospívání syslů. Usuzujeme proto, že působení člověka by mohlo mít pozitivní vliv na růst populace sysla obecného. Nicméně tento závěr není vzhledem ke krátkému období výzkumu zcela jasný. Další podrobnější analýzy našich dat by mohly poskytnout nejen informace o biotopových nárocích sysla obecného, ale také o uměle vytvořených omezeních, se kterými je schopen se vypořádat.

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