Why males incur a greater predation risk than females in juvenile European sousliks (*Spermophilus citellus*)

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Abstract: Leaving a familiar area is assumed to involve an increased vulnerability to predation, yet rarely are movement patterns and mortality monitored directly. For this reason we examined the locomotor patterns and activity of 41 juvenile European sousliks (*Spermophilus citellus)* in relation to their individual fates. We investigated whether mortality risk increases with distance from the natal burrow, and we also attempted to distinguish sex-differential locomotor and anti-predator behaviours explaining the female-biased sex ratio among non-juveniles. During three years, weaned juveniles inhabiting a 4 ha plot in a recreation area north of Vienna, Austria, were equipped with radio collars. Nearly 76% of the tagged juveniles were killed by cats or disappeared with unknown fates. Only 5% (two females) permanently departed from their natal area and survived, that is to say, dispersed successfully. Survival of females more than doubled the male percentage and was independent from distance from the natal burrow, whereas most of the surviving males were philopatric. The major finding of this study was that nonsurviving juveniles had moved faster than survivors, with individual speed resulting in sex-differential mortality. Males tended to move faster than females, incurring a greater risk of predation when remote from their natal burrows. Further analyses of behaviour provided evidences that male-biased mortality could arise from sexually different patterns of time allocation to predator avoidance and vigilance. We conclude that among juvenile *Spermophilus citellus*, males perform an unfavourable trade-off in surface activity allocated to locomotion and vigilance.

Keywords: European souslik, *Spermophilus citellus*, ground squirrel, Austria, radio telemetry, natal dispersal, predation risk, survival, sex difference, locomotion.

Introduction

It is a common demographic trait of ground-dwelling squirrel populations that sex ratio is balanced among juveniles at emergence from their natal burrows, but female-biased among older animals (Boag & Murie 1981, Sherman & Morton 1984, Sauer & Slade 1987, Michener 1998). The proximate causes of this phenomenon are not as well documented. Although a wealth of information exists on sex-differential locomotor and exploratory activities (Holekamp 1984a, Holekamp 1984b, Michener 1989, Wiggett & Boag 1989, Shriner & Stacey 1991, Waterman 1995, Olson & Van Horne 1998, Byrom & Krebs 1999), virtually no explanation is given why these behaviours should be risky (Schmutz et al. 1979).

Similar to North American *Spermophilus*, sex ratios of European sousliks *(Spermophilus citellus)* are balanced at litter emergence and develop a skew towards females until the subsequent season (Hoffmann et al. 2003a). European sousliks are obligate hibernators with a pronounced endogenous annual cycle (Hoffmann 2002). The active season sets off with the emergence of reproductive males in early March and ends in late September, when the last juveniles immerge into hibernation (Millesi et al. 1999b). Mating is restricted to early spring, and females give birth 27–31 days later (Huber et al. 2001). Juveniles emerge from their natal burrows between the end of May and the beginning of July (Millesi et al. 1999b), 30–34 days after parturition, and are weaned at four to nine weeks of age (Millesi et al. 1999a, Huber et al. 2001). Fewer males than females are recruited into the yearling age class (Hoffmann 2003a), with most losses having occurred during the juvenile summer (Millesi et al.

1999b). To date, information on behaviour of juvenile European sousliks is sparse (Hoffmann 1995, Hoffmann 2002), and virtually nothing is known about behavioural sex differences in spacing and vigilance. We thus projected a detailed examination of movement patterns and concurrent activities during the juvenile summer as a first step to elucidate the origins of the skewed sex ratio among non-juveniles.

The purpose of our study was to track juvenile fates, and to detect sex-specific differences and possible risks associated with movement patterns, as has been described for North American members of the genus *Spermophilus* (Dobson 1981, Holekamp & Sherman 1989, Wiggett & Boag 1993). To this end, we radio-tracked locomotor behaviour of juvenile European sousliks in the field and investigated possible behavioural interactions with sex and mortality.

Materials and methods

Radio collars

We developed small-sized radio transmitters and collars for European sousliks, adapting circuit diagrams as described in Kenward (1987) and Naef-Daenzer (1993). Technical details appeared in Hoffmann (2002). The tag was shaped to fit a ground squirrel neck and was embedded in a latex collar with Velcro fasteners (figure 1). The collar could be adjusted to neck sizes between 8 and 10 cm and hence be suitable for juvenile and older sousliks. Compared to conventional radio collars, this design had several advantageous features: 1. the species-specific shape of the tag, 2. a total mass of maximum 4 g (<4% body mass of a weaned juvenile), 3. the elastic latex collar did not cut into the neck, and to a certain degree, expanded with juvenile growth, 4. the risk of strangling was minimised, because the animal was able to slip out and/or the Velcro fastener opened, 5. latex disintegrates and, in case the animal was not recaptured, the collar fell off.

Transmitter life was 15–30 days, after which the power cell could be replaced, enabling the re-

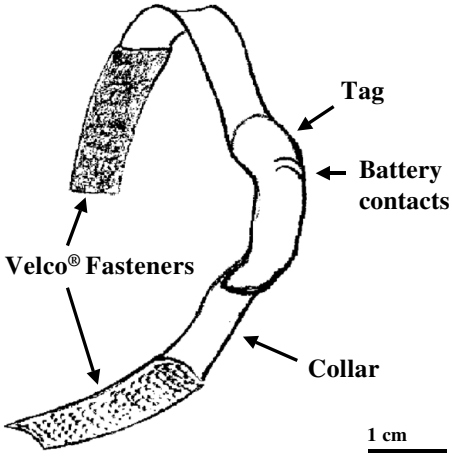

Figure 1. Radio collar for European sousliks (simplified representation).

utilisation of the transmitter. The relatively small signal range (400 m) was compensated for by mobile bearing, that is, following weak signals or searching lost signals on foot. The range and life span of the transmitters proved workable in the field and enabled us to track sousliks virtually without disturbing their natural patterns of behaviour.

Field study

We investigated European sousliks dwelling on a 4 ha plot in a recreation area (48°31' N, 16°36' E) north of Vienna, Austria. Detailed descriptions of the capture technique appear in Hoffmann et al. (2003a, b) and Millesi et al. (1999a, b). From 1996–1998, we consecutively equipped 41 weaned juveniles (29 males, 12 females) with radio collars. Between 25 June and 21 August, we followed each of the tagged individuals for a minimum of 5 days, unless its fate was known before. A programmable receiver (Telonics TR2+TS1) connected to a hand-held H-antenna and earphones was used to locate each tagged squirrel in 30-minute intervals daily between 8 a.m. and 2 p.m. At the same time we recorded whether the animal was seen aboveground. In 15 of the tagged animals (8 males, 7 females), we additionally monitored vigilance behaviour

(bipedal postures). Locations were determined either visually by scanning the area with binoculars in the direction of the strongest signal, or acoustically by reference to the animal's preceding position. The individual bearings were transformed into x-y coordinates of a 15-m grid overlaying a 1:2000 field map. When a signal was received from outside the study site, it was followed on foot to check the location and state of the tagged animal. Kills were observed either directly during radio-tracking sessions or indirectly, when we recovered the radio collar and found evidence for predation (carcass, intestines, blood, etc.). Juveniles that disappeared after their radio collars had been removed had left the field site undetected, either actively as emigrants or passively as prey. Kills and disappearances were combined to nonsurvivors, if not mentioned otherwise. We used two estimates of survival: 1. until hibernation: juveniles known to be alive after 31 August (Millesi et al. 1999a), or 2. until the following year: individuals recaptured after hibernation.

We applied RANGES-V Software (Kenward & Hodder 1996) to analyse locations and to calculate locomotor attributes. We computed length of line between an animal's natal burrow and its location at specified times, and used this linear distance in meters (m) as an estimate of ranging behaviour. We related linear distances between locations to the time span within they had been covered, and thus calculated speed in meters per hour (m/h), which served as an approximation of mobility. As an average measure, its magnitude was influenced by both continuous running (temporal acceleration) and intermittent behaviour (deceleration). To examine developmental variations in movement patterns and their interactions with sex-specific survival and behaviour, we pooled individual data over 10-day periods (decades) post emergence from the natal burrow. Retreat into a burrow lowers predation risk even if not intended as anti-predator behaviour. Hence we regarded underground activity as predator avoidance and quantified it with the number of tracking intervals a focal individual was seen aboveground. Vigilance was measured with the number of observation intervals a focal animal spent in bipedal postures. Data sets were analyzed with non-parametric and parametric statistics, respectively, after performing Shapiro-Wilk tests for data distributions. *P*-values are outcomes of two-tailed tests.

Results

Most of the tagged juveniles were killed by house cats, and less than a third survived their first summer. The remainders' fate was unknown because their radio collars had been removed before they disappeared. Local survival of females more than doubled the male percentage, and >75% of the males were killed or disappeared with unknown fate, but only half of the females (table 1). Considering only juveniles with a known fate, 67% of the males died compared to 45% of the females (χ^2=9.1, df=1, P<0.01).

At nine weeks of age (during decade 4 after litter emergence), juveniles started to depart from their birth sites, travelling significantly farther distances than before (figure 2). Subsequently they either kept on with forays or shifted their home ranges. The period following the logistic incline (figure 2) coincided with the time of monitored predations. All kills involved juveniles during decades 4–7 after natal emergence at 9–14.5 weeks of age.

Table 1. Fates of radio-tagged juvenile European sousliks until hibernation. A significantly higher percentage of females than of males survived (χ^2 =14.4, df=1, P<0.001).

	Sample	% survived (n)	% killed (n)	% disappeared (n)
Males	29	24.1 (7)	48.3 (14)	27.6 (8)
Females	12	50.0 (6)	41.7 (5)	8.3 (1)
Total	41	31.7 (13)	46.3 (19)	22.0 (9)

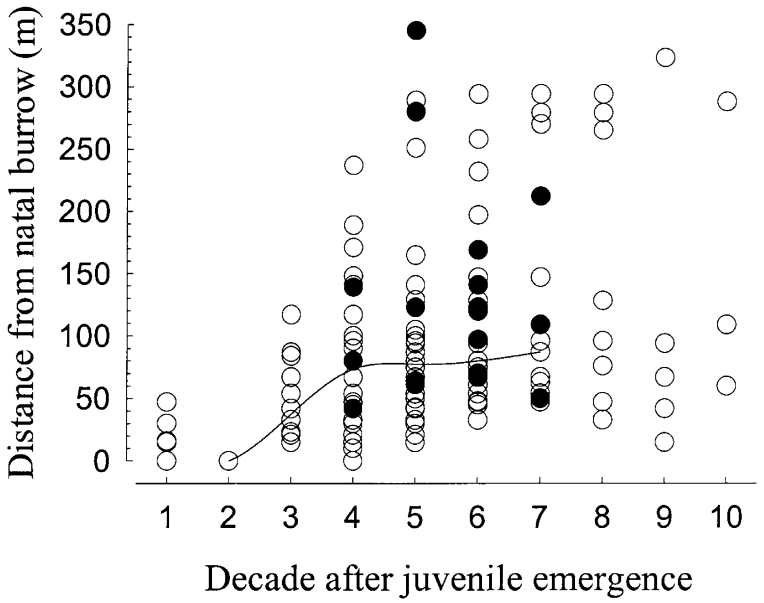

Figure 2. Association between age (10-day intervals post emergence) of juvenile European sousliks and maximum distance from their natal burrows. Distances in decade 3 were shorter than in decades 4 (n=11, P=0.005, Wilcoxon Z=-2.8), 5 (n=8, P=0.028, Z=-2.2) and 6 (n=7, P=0.028, Z=-2.2). During decade 7, juveniles travelled farther than during decade 4 (n=8, P=0.025, Z=-2.2). Median (*mdn*) ranging behaviour as a function of time (decades 1–7) is best fitted with a logistic regression (r^2>0.99). Black symbols indicate the timing of kills and the preceding maximum distance. Data points from decades 1, 2 and 10 are derived from visual localisations.

The six directly observed predation incidents occurred at a median (*mdn*) distance of 110 m from the natal burrow. This was significantly farther than the average movements of eight juveniles during decades 4–7 (*mdn*=38 m) that survived to the following year (P=0.028, Mann-Whitney U=7.0). Five of the six directly observed kills involved males. We therefore could not test statistically for sex-differential distances of fatal encounters; the female victim, however, was less remote from the natal burrow (97 m) than the males (*mdn*=123 m).

When we compared ranging behaviour of nonsurvivors and survivors (last distance recorded before predation, before transmitter removal or in decade 7), we found sex-dependent differences (figure 3a). Males that survived had remained more philopatric than nonsurviving males, and marginally nearer to their natal burrow than nonsurviving females. There were no other group differences in distances travelled (each P>0.11), in other words, survivorship among females was independent of travel distance.

None of the tagged males departed from his birthplace successfully to establish a new home range. Two females, however, dispersed and survived, one even to reproductive maturity. For a further investigation of the possible causes of such sex-dependent vulnerability to predation, we analysed speed, as it is the second dimension of locomotion. The ontogenetic development of mobility was comparable to that of ranging behaviour, but slightly less of the variation was explained by time (logistic regression: r^2<0.93), and hence, temporal effects were not as pronounced (Friedman ANOVA: ns). The logistic incline occurred from decades 2 (*mdn*=0.0) to 3 ($\bar{x}$=20.0 m/h), implying that average running speed increased earlier than travel distance and remained on similar levels thereafter (=20.3–32.6 m/h). !In contrast to ranging behaviour, we

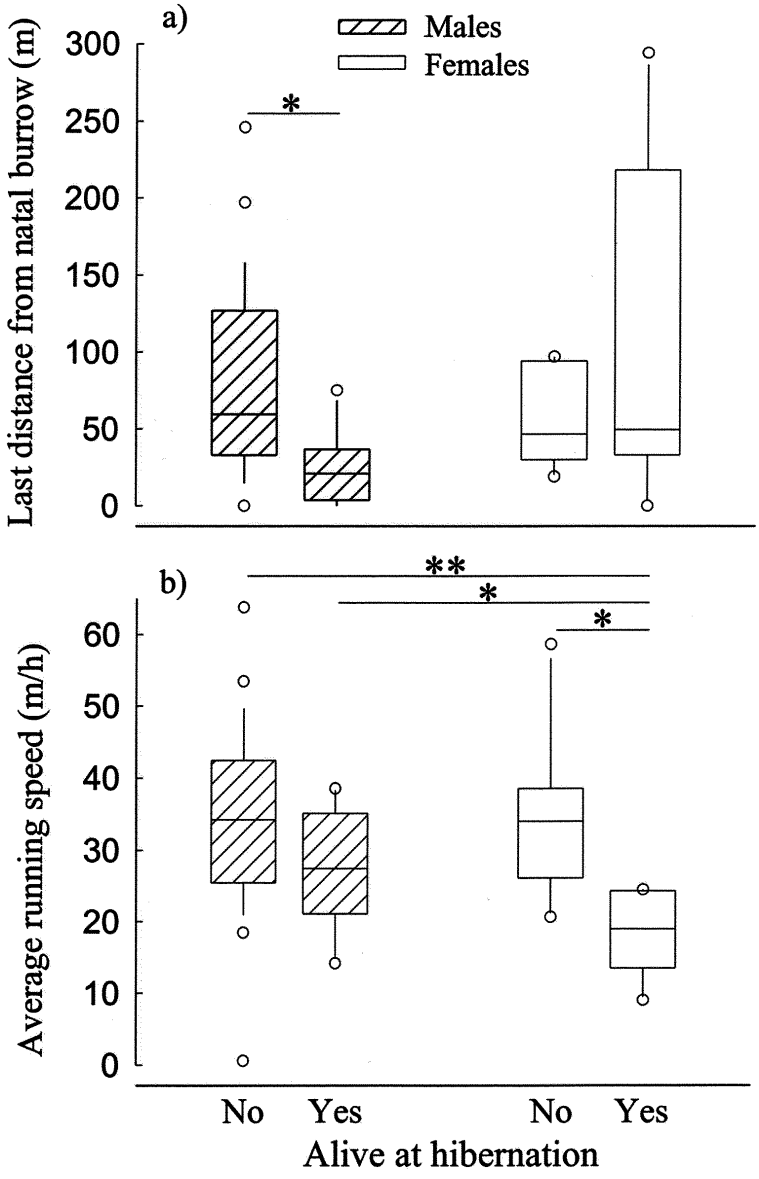

Figure 3. Sex-differential effects of distance from the natal burrow (a) and travel speed (b) on survival of juvenile European sousliks until hibernation. a. Surviving males had remained nearer to their natal burrows than nonsurvivors (males: P=0.014, Mann-Whitney U=29; females: P<0.1, t=1.8). b. Surviving females had moved slower than surviving males (P<0.05, U=7) and nonsurvivors (males: P=0.005, U=16; females: P=0.018, t=2.8). Each box-plot represents the median, quartiles, 5% and 95% percentiles, and outliers; see table 1 for sample sizes. Differences between samples indicated by horizontal lines and marked with * P<0.05, ** P<0.01.

found sex differences in two stages: males moved faster than females in decades 5 (20 males, $\bar{x}$=37.3 m/h versus nine females, $\bar{x}$=22.2 m/h; P=0.011, t=-2.7) and 7 (nine males, $\bar{x}$ =25.4 m/h versus six females, $\bar{x}$=12.7 m/h; P=0.014, t=-2.8).

Maximal travel speeds of juvenile European sousliks during decades 4–7 after natal emergence exceeded 500 m/h. Juveniles that were directly observed to be killed had moved significantly faster ($\bar{x}$=262.4 m/h) than year-to-year survivors in the critical time span $\bar{x}$=115.8 m/h; post-hoc LSD, P=0.009). The killed males had travelled with an average maximum of 287.0 m/h, which was more than twice the maximal speed of the female victim (134.2 m/h). Analyses of average mobility revealed consistent results: during the critical time span (decade 4–7), killed

and/or disappeared juveniles had been significantly faster ($\bar{x}$=34.3 m/h) than summer survivors ($\bar{x}$=23.2 m/h; P=0.008, t=2.8). When we took into account the sex (figure 3b), it turned out that surviving females had moved the slowest. No speed difference was found among the three rapid groups.

Note that results are somewhat reversed compared to ranging behaviour (figure 3a), where survival of males, but not of females was affected. In other words, surviving males had remained philopatric, despite of moving faster than surviving females, some of which dispersed. Females with male-like mobility were killed or disappeared, just like the males that departed from their natal burrows. Consistent with these sex-differential effects, we found no significant correlations between our measures of distance and speed (each P>0.14, each Spearman r_s<0.21), except in nonsurviving males. This group moderately decelerated with increasing distance from the natal burrow (r_s=-0.475, P=0.025, n=22).

Anti-predator behaviour may influence both vulnerability to predation and locomotion. We therefore analysed surface activity and vigilance, assuming that survivors allocated a greater portion of their aboveground activity to bipedal postures than nonsurvivors. Of the 15 focal juveniles (eight males, seven females), seven were killed (four males, three females), two disappeared (two males), and six survived until hibernation (two males, four females). Vigilance behaviour of survival- and sex groups was not significantly different. However, a correlative approach revealed that the number of bipedal postures increased with time allocated to surface activity (figure 4; r_s>0.89, P<0.0001). Correlations were stronger among females (r_s>0.90, P=0.005) than among males (r_s=0.83, P=0.011), and slightly weaker in survivors (r_s>0.81, P=0.050) than in nonsurvivors (r_s>0.84, P=0.004). Linear regressions of bipedal vigilance against surface activity (log scale) clarified variations between two groups (figure 4): The essential difference between nonsurviving males and surviving females is reflected not in the slopes, but in the intercepts, which are closer to 0 in the female (-1.16) than in the male (-3.42) group. The regression line of male nonsurvivors thus intersects the abscissa at a higher x-value (more surface activity) than that of female survivors, corresponding to a smaller number of bipedal postures in the male group. That is to say, compared to nonsurviving males, surviving females spent less time aboveground or allocated more time to vigilance behaviour, both resulting in lower travel speed when covering a given distance.

Discussion

European sousliks started to expand or shift their home ranges 30–40 days post natal emergence at about nine weeks of age. This timing coincides with the definitive end of weaning (Huber et al. 2001), and matches the onset of natal dispersal (the permanent departure of prereproductive individuals from their place of birth, Lidicker 1975) in many North American ground squirrel species (Holekamp 1984a). Our results indicate that the departure of juveniles from their natal burrows involved an increased risk of predation (figure 2), which depended on behaviour associated with locomotion (figure 3). It is evident that males were more vulnerable than females (table 1), which is also supported by sex differences in year-to-year survival of juveniles (Hoffmann et al. 2003a). The relatively high proportion of unknown fates (22.0%) might partly have been due to undetected dispersal, but the fact that virtually no immigration occurred during this study (Hoffmann et al. 2003a) suggests that most of the potential dispersers (88.9% male) were killed. Increased male vulnerability to predation is also reflected in sex differences in year-to-year survival of juveniles (Hoffmann et al. 2003a). Sex-specific comparisons of distance and speed were significant on a higher level when based on year-to-year instead of summer survival, indicating continued male-biased mortality after the onset of hibernation. Sex-differential predation pressure is also supported by findings on adrenal activity of yearling males, which suggest an in-

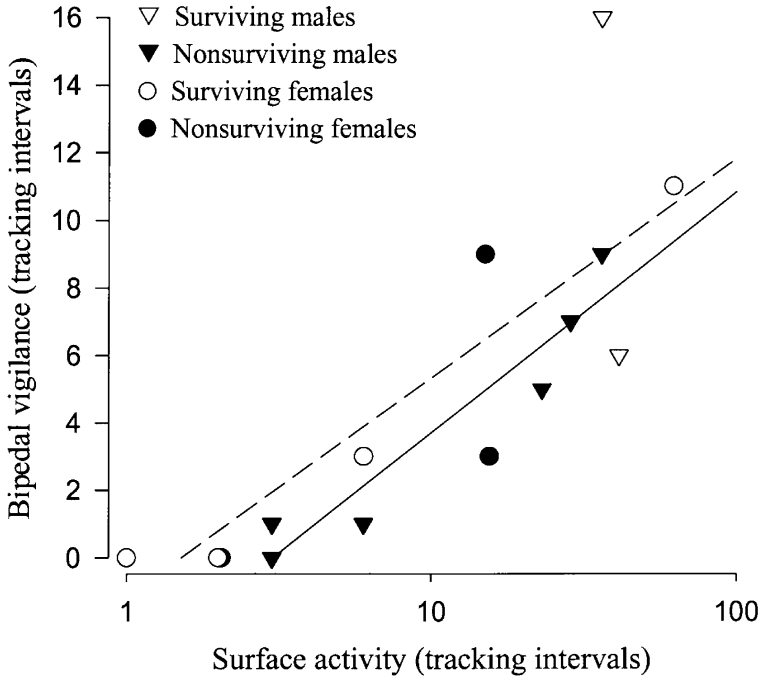

Figure 4. Association between surface activity (sum of tracking intervals each individual was observed aboveground) and vigilance (sum of tracking intervals with bipedal postures). Regression lines are shown for nonsurviving males (solid; y = -3.42 + 7.13x; r^2>0.91, n=6) and for females known to be alive shortly before hibernation (dashed; y = -1.16 + 6.49x; r^2>0.96, n=4). Because of small sample sizes, no regressions were performed for surviving males and killed females.

creased stress response (Millesi et al. 2005), maybe due to both carryover effects from the preceding year and current hazards. Consistently, juvenile male arctic ground squirrels (*Spermophilus parryii plesius*) showed endocrine characteristics indicative of a prolonged period of stress in mid-August (Boonstra et al. 2001).

Surprisingly, distance from the natal burrow did not depend on sex (figure 3a). This finding is in contrast to North American ground squirrels (Dobson 1981, Waterman 1986, Holekamp & Sherman 1989, Byrom & Krebs 1999). The magnitude of the observed ranges (figure 2, figure 3a) was smaller than those reported for dispersing juvenile *Spermophilus columbianus* (Wiggett & Boag 1989, Wiggett & Boag 1993). No tagged squirrel, including individuals that departed from the central study site, actively left the 8-ha recreation area, which is surrounded by suburban terrace houses. We propose that dispersal beyond the monitored distances was inhibited by extrinsic factors like predation (this study) and landscape fragmentation (Hoffmann et al. 2003b). Thus potential sex differences in dispersal distance might have been concealed.

Our results indicate that the sex-differential mortality (table 1) and hence, the female bias among yearlings (Millesi et al. 1999a, Hoffmann et al. 2003a) were mediated by concurrent behaviour interacting with locomotion. Kenagy & Hoyt (1989) suggested that golden-mantled ground squirrels (*Spermophilus saturatus*) run fast to reduce exposure to predation. In European sousliks, surviving males were faster than surviving females, but nonetheless both moved slower than nonsurvivors. The maximum speed recorded in our study (553 m/h, equivalent to 9.2 m/s) was higher than what has been reported for nonjuvenile members of European souslik and other *Spermophilus* species except *Spermophilus leptodactylus* (Trombulak 1989). In *Spermaphilus beldingi*, natal dispersal was temporally correlated with high levels of locomotor and exploratory activity, and after having escaped into a burrow, males reappeared more rapidly than did females at four to ten weeks of age (Holekamp 1984a). Time allocated to antipredator behaviour (bipedal postures and/or

retreat into a burrow) instead of locomotion evidently affects mobility and hence, running speed is accelerated when vigilance and predator avoidance are reduced (cf. Ydenberg & Dill 1986). Male European sousliks were less vigilant than females while spending the same or even more time aboveground, indicating an unfavourable trade-off in surface activity allocated to vigilance and locomotion. Only two of the focal males were known to be alive shortly before hibernation, one of which had been extremely vigilant. Females apparently pursued one of two different strategies: they either minimised surface activity, vigilance thus becoming negligible, or when aboveground more often, they allocated a considerable amount of time to bipedal postures, resulting in low travel speed. Among the killed females, one behaved male-like in allocating too little time to bipedal postures, the other two died despite of following each of the female strategies. The second strategy could explain the difference between surviving and nonsurviving females in proportional surface activity as an observation bias: among the total of tagged females, survivors supposedly were bipedal more often, resulting in better visibility than nonsurvivors. Philopatric male European sousliks were familiar with the burrow systems in their surroundings and presumably still associated with some of their kin. Due to the dilution effect (Dehn 1990) and nepotistic vigilance of their kinship group (Desportes et al. 1991, Hoffmann 1995), reduced anti-predator behaviour was not as detrimental as for males departing from their birth site. Nonsurviving females had apparently behaved like males, moving as fast as the dispersers and marginally farther than the philopatrics. It is probable that they reduced vigilance in favour of speed while leaving their natal site. Fifty percent of the females obviously accomplished a beneficial trade-off in time allocation between locomotor activity and anti-predator behaviour, and survived even when dispersing.

We conclude that in European sousliks, like in many other small mammal species, sexually dimorphic losses can be associated differentially with time allocation to conflicting behaviours during aboveground activity (Holekamp 1984b, Wiggett & Boag 1989). Why males tend to perform an unfavourable trade-off between vigilance and mobility remains to be investigated. A hormonal approach might help to settle this issue: during this study all yearling males were reproductively mature (Hoffmann et al. 2003a). Thus it is likely that the onset of male puberty is already initiated during the juvenile summer, coinciding with elevated testosterone levels. These in turn might both mediate dispersal (Nunes et al. 1999) and stimulate quick and unwary locomotion. Further analyses of endocrine aspects are required to elucidate the proximate causes of the sex difference in juvenile mortality.

Acknowledgements: We are grateful to K. Pieta, S. Huber and S. Steurer, who helped to trap and monitor European sousliks over the years. We thank J. Dittami and two anonymous reviewers for constructive comments on a former version of the manuscript. Funding for this study was provided by the University of Vienna (Research Grant GZ. 89/2) and the Austrian National Bank Fund (OeNB, No. 6590). The competent authorities issued a license to capture sousliks (Local Authority Korneuburg: 9-N-90). As radio tagging was possible without anaesthetisation, and the attachment of collars is not considered an animal experiment in Austria, no additional licence was required.

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Samenvatting

Waarom lopen bij juveniele siesels (*Spermophilus citellus*) mannetjes een groter predatie-risico dan vrouwtjes?

Het verlaten van bekend terrein leidt, naar men aanneemt, tot een verhoogde kans op predatie. Toch worden bewegingspatronen en mortaliteit zelden direct waargenomen. Om die reden onderzochten we de bewegingen en de activiteit van 41 juveniele siesels (*Spermophilus citellus)* in relatie tot hun individuele lot. We onderzochten of het mortaliteitsrisico toenam met de afstand tot het geboorteburcht, en we probeerden ook sekse-specifieke verschillen in de bewegingspatronen en het anti-predatiegedrag te vinden die zouden kunnen verklaren waarom er een sexe-ratio ten gunste van de vrouwtjes bestaat bij niet-juveniele dieren. In een 4 ha groot recreatiegebied ten noorden van Wenen (Oostenrijk) werden gedurende drie jaar gespeende juvenielen voorzien van radiozenders. Bijna 76% van de gemerkte dieren werd gedood door katten of verdween met onbekend lot. Slechts twee vrouwtjes (5%) overleefden de natale dispersie van hun geboortegrond met succes. Het overlevingspercentage van vrouwtjes was meer dan twee keer zo hoog als dat van de mannetjes en was onafhankelijk van de afstand tot de geboorteburcht, terwijl de meeste overlevende mannetjes hun geboortegrond trouw bleven. De belangrijkste vondst van dit onderzoek was dat niet-overlevende juveniele dieren zich sneller hadden verplaatst dan overlevende dieren, met snelheden die resulteerden in een per sekse verschillende mortaliteit. Mannetjes neigen zich sneller te verplaatsen dan vrouwtjes en daarmee een groter risico te lopen op predatie wanneer ze zich op afstand van hun geboorteburcht bevinden. Verdere analyse van gedrag leverde sterke aanwijzingen dat de grotere sterfte onder mannetjes veroorzaakt zou kunnen zijn door een per sekse verschillende tijdsbesteding in het vermijden van predatoren en waakzaamheid. Wij concluderen dat onder jonge siesels, mannetjes een ongunstige balans kiezen tussen verplaatsing en waakzaamheid bij activiteit aan de oppervlakte.

Received: 15 October 2004
Accepted: 25 January 2005