Reproductive strategies of male European sousliks (*Spermophilus citellus*) at high and low population density

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Abstract: The spring population density of European sousliks (*Spermophilus citellus*) in a suburban area near Vienna, Austria, changed from 60 to 6 individuals/ha from 1991 to 1998. The decline occurred during the active seasons of 1994 and 1995. In order to investigate effects of population density on reproduction we examined male mating effort and success. Male home-range size, intrasexual aggression, mass loss during the mating period, and individual reproductive success changed with population density. Home-range size increased with density decline, whereas aggression and mass loss decreased. High densities were characterized by more intense male-male competition and a skewed distribution of mates per male. Mate numbers in low-density situations were normally distributed and all males were able to acquire at least one mate. At low density, all yearling males were reproductively active compared to only 13% in the high-density years. Mature yearlings had lower growth rates than non-reproductive ones. Analyses of cortisol secretion indicated high stress levels at low density throughout the season. These changes could be viewed as a facultative response to changes in mate availability and the distribution of reproductive success. On the other hand, the costs of reproduction could be amplified by precociousness associated with population density changes.

Keywords: population dynamics, mating effort, cortisol, growth patterns, *Spermophilus.*

Introduction

In seasonal-breeding animals, reproduction is limited by energetic and temporal constraints. These constraints are even more pronounced in hibernating species (Heaney 1984). As a result, in many of these species mating is restricted to a short period in spring and females produce only one litter per year (Michener 1984). These patterns of reproduction are part of an animal's life-history strategy, which arises from trade-offs in time and energy allocation for different seasonal processes. Energetic demands of developmental processes like structural growth or prehibernatory fattening often compete with those associated with reproduction (Emlen & Oring 1977, Clutton-Brock 1988). Environmental bottlenecks associated with seasonal activity in hibernators intensify the effects of these interactions. Patterns of reproduction must then be adapted to environmental and social circumstances. However, these parameters may exhibit spatio-temporal variations within the same species. Selection should favour strategies, which specifically regulate the allocation patterns while adapting to changing demands of an animal's environment. In small mammals, density changes can result in populations, which remain stable or fluctuate to only a minor degree for long periods while others show marked fluctuations, which may occur as regular cycles of growth and decline (Feldhamer et al. 1999). Population density can affect different aspects of an individual's life history, such as intrasexual competition, reproductive effort and success, or even survival.

Age at the onset of sexual maturity is an im-

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portant life-history trait, which can reflect this adaptability (Daan & Tinbergen 1997). Precociousness shortens the latency to reproduce and thereby can prolong the overall time span for reproduction. On the other hand, individual mating success, which may interact with age, is highly dependent on mating effort (Emlen & Oring 1977). This in turn is directly related to mate availability and factors like the operational sex ratio (Emlen & Oring 1977). High intrasexual competition and/or low female availability have been proposed to delay puberty in males (Clutton-Brock 1988). Deferred maturity allows males to allocate more energy to growth and thereby increase their competitive ability (Kenagy et al. 1989). Longevity plays an important role here, in that this strategy necessitates survival over a number of breeding periods. These trade-offs can be extremely complex. Nevertheless, they have been documented in a number of species (Emlen & Oring 1977, Clutton-Brock 1988, Daan & Tinbergen 1997). We have been able to study these trade-offs over the course of a long-term field study (1991-1998) on European sousliks (*Spermophilus citellus*) (Millesi et al. 1998, Millesi et al. 1999, Hoffmann et al. 2003). During 1991-1993 population density in the study area was high (57 animals/ha) and remained quite constant until 1994 (Hoffmann et al. 2003). The numbers of sousliks decreased during 1994 and 1995 in a stepwise manner. This drop seemed to be mainly caused by a lack of immigration probably due to the loss of dispersal corridors and low local survival rates (Hoffmann et al. 2003). The density decrease was even more pronounced in males compared to females. Thereafter, the number of individuals in the area was much lower (about 8 individuals/ha) but remained stable during 1996-1998. This situation enabled us to compare male reproductive strategies at high population density with those in a low-density situation. In this report we analyzed effects of population density on male reproductive effort, age at puberty and subsequent individual consequences. Endocrine parameters, testosterone and cortisol were measured to gain information on gonadal and adrenal activity in both situations. In addition, behavioural observations enabled us to compare intrasexual aggression, home-range size and foraging at high and low density.

Materials and methods

Study area and trapping techniques

The study was carried out in a recreation area in Langenzersdorf (48°18’ N, 16°22’ E), near Vienna, Austria from 1991-1998. The area was characterized by 8 ha meadowland with scattered trees, mainly robinia (*Robinia pseudoacacia*), alder (*Alnus glutinosa*) and ash-tree (*Fraxinus excelsior*). Human residences surrounded the study area, offering small patches of suitable habitat for sousliks. In the analyses of behavioural and physiological parameters only data from 1991-1993 (high density) and 1996-1998 (low density) were used. The years 1994 and 1995 were excluded from this report because population density appeared to be very unstable and none of the juveniles born in 1994 could be recaptured in 1995. Individuals were delegated to three age classes: juveniles (<1 year), yearlings (1 year, juveniles of the preceding year), and adults (≥2 years). For comparisons only individuals with known age and reproductive status were used. Sousliks were observed and captured from spring emergence until the last individual had immerged into hibernation. Live trapping was conducted with Tomahawk traps baited with peanut butter on five days per week for 4-8 hours depending on weather conditions and seasonal activity changes of the squirrels. Trapping techniques and frequency as well as observation methods did not differ among the years included in this study. For permanent identification of the animals a transponder chip (PIT tag, Indexel or Data Mars) was subcutaneously injected in the neck. In addition, the fur was painted with a commercial hair dye in an individually recognizable pattern. Females were marked with brownish-red colour and males with black. The sousliks were weighed (±0.5 g, Sartorius laboratory scale) and head length was measured using a calliper (maximal length of skull) at each capture.

The area was scanned at periodic intervals on a daily basis. In earlier studies we have shown that by scanning 1 ha five times per day, >90% of marked individuals could be identified (Millesi et al. 1999). Checklists that were maintained daily from the beginning until the end of surface activity expanded the scan data. In these checklists all sightings of marked individuals (during scans, captures or from other observations) were registered. Population density was defined as the number of individuals present during the mating period. The premating phase was defined as the period between the first male and the first female emergence. The mating phase started with female emergence and ended one week after the last female had emerged. Thereafter, all females showed signs of gestation or lactation and no male sexual behaviour was observed (S. Steurer, unpublished data). Postmating was defined as the period from the end of the mating phase until the onset of moult.

Behavioural parameters

To determine the reproductive success of individual males, male-female interactions were observed from the onset of the mating period until all females had signs of gestation and male testes regression started. When females went into oestrus interactions like genital inspection, grooming and spatial cohesion were observed. Earlier studies had shown that spatial proximity with a male and a decrease in female aggression towards males occurred simultaneously and preceded mating. Non-oestrous females do not tolerate male proximity (Millesi et al. 1998). Copulation occurred underground, in the female's burrow. Therefore, mating was defined as synchronous burrow use by a male and a female in bouts longer than 5 minutes. Positions of males and females above ground were recorded using scan sampling every 30 minutes. Whenever a male and female were seen together (within one body length distance) the observation of the interaction continued and burrow use was registered. We had previously noted that synchronous burrow use with a male was very limited during the mating phase and hence can be taken as a marker for receptivity and copulation (Millesi et al. 1998). As shown earlier, common use of the female's burrow was only seen with one individual male/female (Millesi et al. 1998). Comparable behavioural data sets were available for 1992 and 1993 for high density, and for 1996 and 1998 for low density. Individuals were repeatedly observed 2-10 times per phase. Focal protocols were done in periods where the animals were most active (morning and afternoon). Aggressive interactions (spatial displacements of other individuals, chases and fights) between the focals and other individuals were counted and recorded as units/30 s-interval. At the same time, individuals within 15 m of the focal were noted at 30 s-intervals. This distance was used because observations had shown that animals at larger distances were never attacked. For analysis the number of interactions/focal protocol was divided by the average number of close individuals (within 15 m from the focal animal) /protocol (Smith & Dobson 1994). This method was used to correct conflict frequencies for individual density. During protocols, locations of focal individuals were recorded every 30 s in a 3.75 m sector network. From these point locations, movement (locomotion) was quantified and range size determined using the method of outer polygonal analysis (Kenward 1990). The range was summed over each phase. Foraging behaviour was expressed as a binary variable (1 = yes, 0 = no) per time unit.

Physiological parameters

Emergence body mass was measured in animals captured within three days after their emergence from hibernation. Mass loss during mating (mean g/day) was determined in males, which were captured at least at the beginning, in the middle, and at the end of the mating period.

The reproductive condition of individual males was determined at capture by measuring testis width externally with a calliper (Millesi et al. 1998). Reproductively active males had descended testes and scrotal pigmentation at emergence from hibernation. Testis regression started at the end of the mating period but scrotal pigmentation was evident until moult had been completed in late June (Millesi et al. 1998).

At capture, 100 µl blood was taken from the femoral vein. The blood samples were collected in heparinized capillaries, centrifuged in the field, and plasma was stored at –20°C until analysis. Plasma testosterone levels were analyzed in duplicate after a diethylether extraction (85% recovery rates) using a biotin-streptavidin enzyme-immuno-assay according to Palme & Möstl (1993). Testosterone was used as standard, the assay showed cross-reactions with testosterone (100%), 5α-androstane-17ß-ol-3-one (23%) and 5ß-androstane-17ß-ol-3-one (12%). Inter- and intra-assay variation was less than 10%. Adrenal activity was determined by measuring cortisol metabolites in faecal samples collected during captures. For each sample 0.5 g faeces were used; extraction was done in 4 ml of 90% methanol. Analysis was done using standard biotin-streptavidin enzyme-immuno-assays (Palme & Möstl 1997). Inter- and intra-assay variation was less than 12%.

Results

Density changes

Population density changed from 1991-1998. From spring 1991-1993 densities were high and quite stable (table 1). In the years 1996-1998 population density was significantly lower than in the first three years (Chi-square test, $P<0.001$) but stabilized at this level (table 1). No significant differences in spring density were found within high and low-density years. Adult sex ratio changed with animal numbers. Sex ratios of reproductive individuals were female biased in all years but decreased from 37% males on average at high densities to 15% at low density (*t*-test, $P<0.01$, table 1).

Table 1. Numbers of reproductive animals/ha and sex ratio. Individuals present in the study area during the mating period were the basis for comparisons. Sex ratio is expressed as proportion of males in the breeding population.

	Males	Females	Sex ratio
High density			
1991	19	39	0.32
1992	22	34	0.39
1993	24	36	0.40
mean	22	36	0.37
Low density			
1996	1	8	0.11
1997	1	7	0.12
1998	2	7	0.22
mean	1	7	0.15

Sexual maturity and mate numbers

At high density, most yearling males (82.6%, n=34) were reproductively immature. Only a small number of yearlings had descended testes (1991: 12.5%, n=8; 1992: 7.7%, n=13; 1993: 30.8%, n=13). This proportion changed at low density where all male yearlings trapped in the study area during the mating period were sexually mature. Scrotal pigmentation was present in all reproductively active males and remained until even after complete testis regression. Developmental processes in yearling males differed between the two situations. We had shown earlier that non-reproductive yearling males continued growth in their second season (Millesi et al. 1999). Precocious yearlings terminated growth after their first hibernation. We compared head length of reproductive and non-reproductive yearlings at the end of the active season. The latter were significantly larger than the precocious males (means ± SD; 52.6 mm ± 2.0, n=12 versus 49.4 mm ± 61.8, n=8; *t*-test, $P<0.05$). Non-reproductive males entered hibernation with a significantly higher body mass than mature yearlings (388.2 g ± 34.5, n=10 versus 297.6 g ± 31.2, n=7; *t*-test, $P<0.001$).

We compared numbers of mates acquired by males at high and low density to determine whether the increased female availability at low density affected individual reproductive success in males (figure 1). At high density the distribution was skewed (Wilk-Shapiro test, $P<0.04$). A high percentage of the males in the focal area had only one or even no mate. Some males were quite successful and had up to four mates. The few reproductive yearlings in high-density years were never observed to acquire a mate. At low density all males were able to acquire at least one female (figure 1) and mate numbers/male were normally distributed (Wilk-Shapiro test, $P>0.3$).

We examined some behavioural parameters, which have been shown in previous studies to be related to reproductive effort and success (Millesi et al. 1998; table 2). Aggression among males was an important parameter to investigate. We found that more aggressive encounters occurred during the mating period at high densities even when corrected for potential recipients. Aggression in the premating and postmating period did not differ significantly between the two density situations. It was consistently low. Agonistic interactions during mating often resulted in injuries. We correspondingly found differences in the proportion of males that had been injured during this period. Most of the high-density males (90.7%, $n=65$) trapped during mating or shortly thereafter had injuries, in the low-density years only 25% of the males had been injured ($n=12$). Home-range size increased significantly during mating in both situations but in line with the spatial distribution of individual females, males had larger ranges at low than at high density (table 2). Another important parameter was the time an individual spent foraging especially during the mating phase. Males in a situation with high competition spent less time feeding during the mating period than those at low densities (table 2).

Physiological parameters

An important parameter of reproductive effort was body mass loss during the mating period. At high density mass loss during mating was higher than at low density (t-test, $t=2.97$, $P<0.01$), and was positively correlated with mate number ($r_P=0.84$, $P<0.01$, figure 2). This significant relationship was not found in the low-density situation ($r_P=0.21$, $P=0.52$).

We compared endocrine parameters associated with gonadal and adrenal activity before, dur-

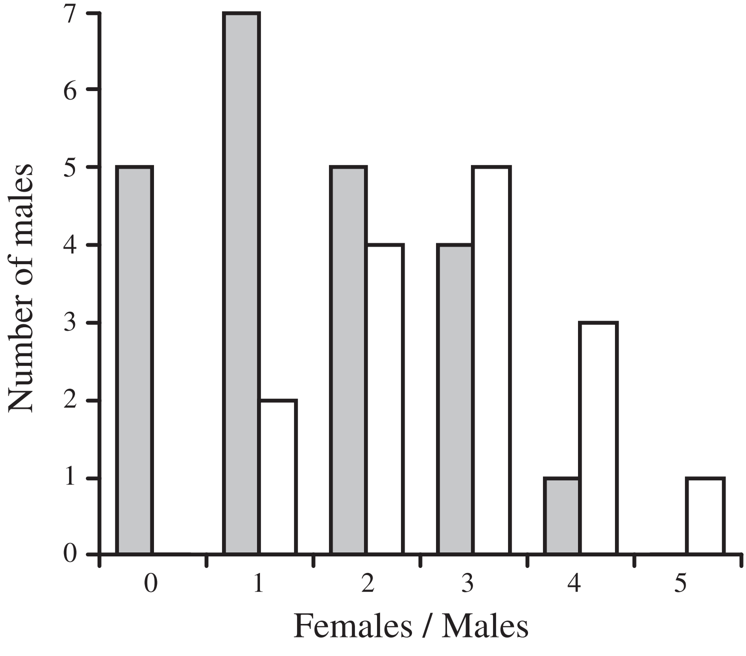

Figure 1. Distribution of acquired mate numbers of focal males at high (1992-1993; hatched bars) and low density (1996-1998; open bars).

Table 2. Seasonal changes in behavioral parameters of focal males at high and low population density. Male aggression is expressed as frequency/protocol, range size (ha) and foraging as percentage of time units/protocol in which the animal showed feeding behaviour. Medians and quartiles are shown, sample sizes per phase are 8/12/7 at high density and 6/6/5 at low density; (Mann-Withney *U*-tests, ** *P*<0.05, ns: not significant).

	High density	Low density	Significance
Male aggression			
Premating	0.0 (0.0, 0.2)	0.0 (0.0, 0.1)	ns
Mating	0.8 (0.6, 1.2)	0.5 (0.3, 0.6)	**
Postmating	0.4 (0.3, 0.6)	0.3 (0.3, 0.5)	ns
Range size			
Premating	0.05 (0.03, 0.08)	0.07 (0.06, 0.11)	ns
Mating	0.16 (0.12, 0.29)	0.38 (0.33, 0.48)	*
Postmating	0.06 (0.03, 0.09)	0.13 (0.08, 0.21)	ns
Foraging			
Premating	82.8 (66.2, 91.0)	67.3 (61.3, 79.7)	ns
Mating	17.7 (16.8, 33.1)	40.2 (38.2, 48.9)	*
Postmating	55.9 (51.6, 66.5)	47.5 (37.4, 63.8)	ns

ing and after the mating period. Patterns of testosterone secretion in plasma did not differ between high and low densities (figure 3). Males emerged from hibernation with elevated androgen levels independent of age and density. Levels decreased significantly after mating when males started testes regression (Mann-Whitney *U*-test, mating versus postmating, *P*<0.001 in both situations). Adrenal activity was monitored by documenting contents of cortisol metabolites in faecal samples (figure 4). The analyses showed that low-density males had higher cortisol levels in all three phases (high versus low density, Mann-Whitney *U*-test, premating: *P*<0.01, mating: *P*<0.05, postmating: *P*<0.05).

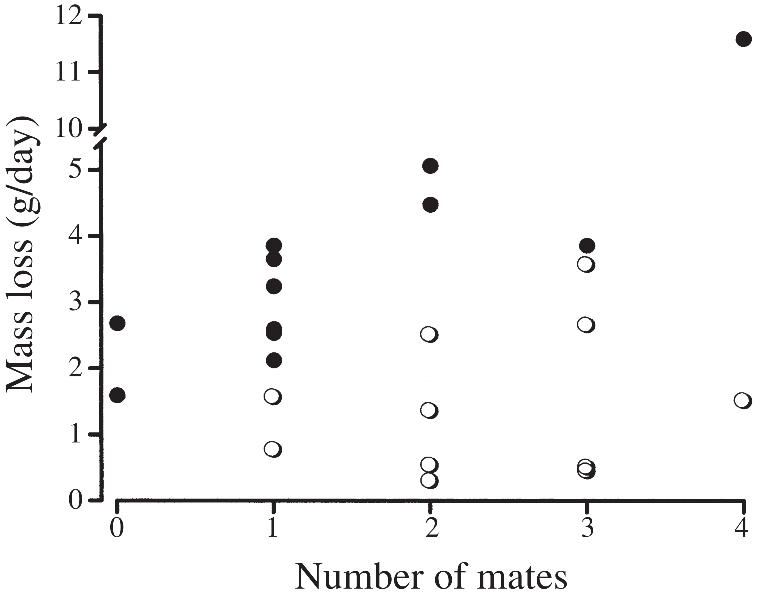

Figure 2. Mass loss and mating success of focal males at high (closed symbols) and low density (open symbols) during the mating period (high density: *n*=15, low density: *n*=10).

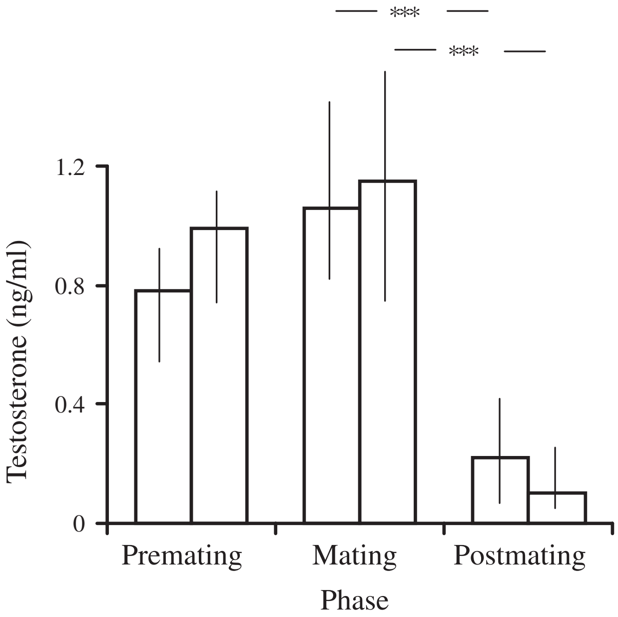

Figure 3. Patterns of androgen secretion in focal males during the premating, mating and postmating period at high (hatched bars) and low density (open bars). Medians and quartiles are plotted; sample sizes per phase are 11/16/8 at high density and 8/12/7 at low density. Significant differences are labelled ***.

Discussion

The comparison of male mating strategies, reproductive effort and success demonstrated differences between high and low population densities. In the high-density situation, intrasexual competition was high and evident in frequent displacements and fights. The sparse reproductive yearlings captured during the high-density years were not able to compete with older and heavier males. None of them was observed to acquire a mate and most disappeared at the end of the mating period. Non-reproductive yearlings were not attacked by older males (Millesi et al. 1998). They were able then to dedicate one complete active season to growth and preparation for hibernation. At high density with high frequencies of intra-male aggression an appropriate body condition may be considered as a pre-requisite to successfully compete for females. Mass-dependent delayed maturity among males of the genus *Spermophilus* has been described or proposed for a number of species including *Spermophilus beldingi*, *armatus* and *townsendii* (review in Michener 1984). As in *Spermophilus citellus*, the sexual maturation processes have been shown to be affected by trade-offs with growth patterns (*Spermophilus saturatus*, Kenagy et al. 1989) and potential mating success (*Spermophilus beecheyi*, Boellstorff et al. 1994). Kenagy et al. (1989) postulated that deferred maturity in yearling males is facultative in that some males forego testicular development and reproductive chances in one year to allocate more energy to growth. This kind of trade-off has been documented in *Spermophilus citellus* under certain circumstances (Millesi et al. 1999, Hoffmann et al. 2003).

In the low-density years, age at puberty in males changed (Hoffmann et al. 2003). All yearling males that emerged in the study area were reproductively mature. In contrast to the high-density situation, even yearlings with relatively low emergence body mass (<180 g) went through puberty in their first hibernation. Due to the wider distribution of females and strongly female-biased sex ratio, intra-sexual aggression was lower and locating oestrous females seemed to be more important for reproductive success than mate guarding. Therefore, mature yearlings had larger home-ranges and fewer agonistic encounters. All low-density males could acquire at least one mate and in contrast to high-density years, mate numbers were normally distributed among males. The

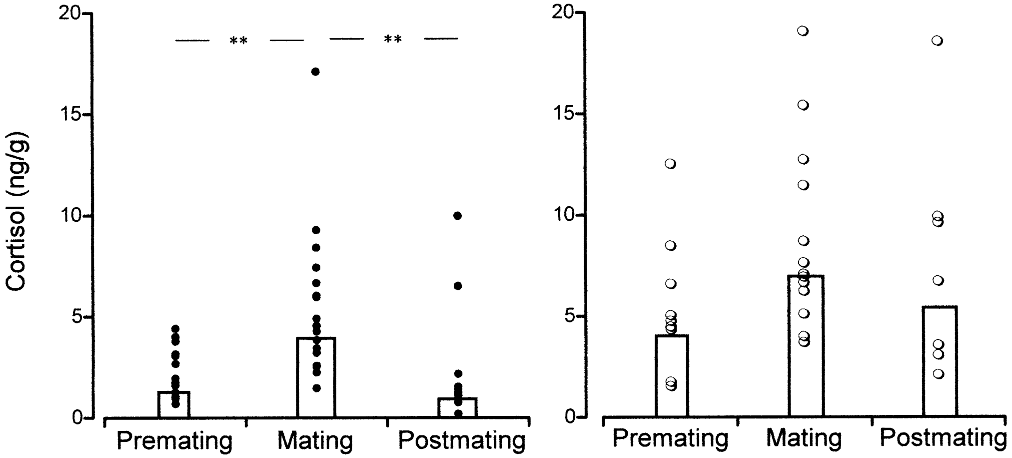

Figure 4. Cortisol metabolites in focal males during the premating, mating and postmating period at high (closed symbols) and low density (open symbols). Medians and individual values are plotted; sample sizes per phase are 11/16/8 at high density and 8/12/7 at low density. Significant differences are labelled ***.

behavioural results indicate that the energetic costs of mating were lower at low density. This is also reflected in the higher amount of time the animals could spend foraging and the lower proportion of mass loss during mating.

Adult male European sousliks immerge into hibernation with regressed gonads and emerge from their hibernacula with fully developed testes and elevated plasma testosterone levels in spring (Millesi et al. 1998). Testes growth and the onset of spermatogenesis hence occur in the burrow, during periodic arousals and/or after termination of torpor before vernal emergence, as has been shown for other *Spermophilus* species (Barnes 1986). Body condition before hibernation has been shown to be an important factor determining puberty in young males. Nonetheless, low density with high female availability was associated with precociousness in yearlings, apparently circumventing the body-mass constraint. Causes and effects here are still hypothetical. Different factors like the access to specific nutritional resources, suitable hibernacula and social interactions are affected by density and may have been critical in causing the changes (Florant 1998, Millesi et al. 1999, Bruns et al. 2000).

Mating is energetically costly with subsequent consequences for males. Body-mass loss, feeding decreases and perhaps stress effects of conflict and locomotion combined to initiate an earlier gonadal regression in highly successful males at high density (Millesi et al. 1998). High investment coupled with elevated adrenal activity can undermine maintenance levels of gonadal steroids via negative impacts on the pituitary. This explanation fits with the elevated cortisol levels during the mating period in both situations and the increase of agonistic interactions. High mating effort apparently can have carry-over effects, which are evident in the patterns of subsequent seasonal processes (Millesi et al. 1998). Early maturation, nonetheless, appears to create further difficulties for the males. Here one could assume disadvantageous metabolic and immune changes on the basis of adrenal activity. Negative metabolic effects of mating effort have been reported for some mammal species (Sapolsky 1987, Deutsch et al. 1990, Bronson & Heideman 1994). The results on adrenal activity at low density indicate high stress levels in spite of the apparently low frequencies of aggressive interactions. We propose that these findings might be related to a previously neglected aspect of early sexual maturity. One scenario would be that precocious individuals are more affected by mating effort than older males, producing elevated stress responses (Millesi et al. 2002). This in turn could result in lower survival rates due to decreased immuno-competency or susceptibility to predators. Survival seemed to be affected since at high population density males survived up to four breeding periods compared to a maximum of two seasons at low density. In a situation with high mortality rates especially among young males, selection should favour precocious males because the chance to survive to the next season might be very low.

High predation pressure on the other hand, could lead to increased adrenal activity throughout the season. Although first analyses indicate that the number of observed kills per year did not differ significantly between the two density situations, the individual risk of predation was certainly higher at low density producing higher stress levels for the males (I.E. Hoffmann, unpublished data). This effect would be reflected in elevated cortisol levels of all age and sex groups at low density. The samples analysed do not support this explanation (Millesi et al., unpublished data). We plan further investigations in semi-natural enclosures, which would provide the opportunity of manipulating specific environmental factors while monitoring changes in the males' physiology and behaviour.

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Samenvatting

Reproduktiestrategieën van mannelijke siesels (*Spermophilus citellus*) bij hoge en lage populatiedichtheid

De voorjaarsdichtheid van een populatie siesels (*Spermophilus citellus*) in een suburbaan gebied bij Wenen, Oostenrijk, veranderde van 60 naar 6 individuen/ha tussen 1991 en 1998. De afname trad op tijdens de seizoenen dat de dieren actief zijn in 1994 en 1995. Om de effecten van populatiedichtheid op de reproduktie vast te stellen onderzochten we de reproduktie-inspanning en het reproduktiesucces van de mannelijke siesels. Homerange-grootte van de mannen, intrasexuele agressie, verlies aan lichaamsgewicht tijdens de voortplantingsperiode, en individueel reproduktief succes veranderde met de populatiedichtheid. Homerange-grootte nam toe met een afname in dichtheid, terwijl agressie en verlies aan lichaamsgewicht afnamen. Hoge dichtheden werden gekenmerkt door een sterkere man-man competitie en een ongelijke verdeling van vrouwtjes over de mannen. Het aantal vrouwtjes per man tijdens perioden met lage dichtheden was normaal verdeeld en alle mannen waren in staat om minstens één vrouw te verkrijgen. Tijdens lage dichtheden namen alle eenjarige mannen deel aan de reproduktie, vergeleken met slechts 13% van de eenjarige mannen in jaren met hoge dichtheden. Volwassen eenjarigen hadden een lagere groeisnelheid dan niet-reproduktieve eenjarigen. Analyses van cortisol secreties wezen op hoge stress niveaus gedurende het hele seizoen tijdens perioden met lage dichtheden. Deze veranderingen kunnen gezien worden als een facultatieve reactie op veranderingen in het aantal beschikbare vrouwtjes en de verdeling van reproduktief succes. Daarentegen kunnen de kosten van reproduktie verveelvoudigd worden door het vroeg tot volwassenheid komen, wat is gerelateerd aan veranderingen in populatiedichtheden.

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