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Body mass and timing of the active season in European Ground Squirrels (*Spermophilus citellus*) at high and low population density

Tělesná hmotnost a načasování období aktivity sysla obecného (*Spermophilus citellus*) při vysoké a nízké populační hustotě

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Abstract. In this study we compared timing of the active season and body mass in a colony of European ground squirrels (*Spermophilus citellus*) in years with high and low population density. Data were collected in a suburban area near Vienna, Austria, over a decade. Ground squirrels were live-trapped and censused to determine vernal emergence, immergence into hibernation and body mass in different age and sex cohorts. Among reproductive males, yearlings were generally lighter than older males, but emerged with a slightly lower body mass at high than at low density. Including nonreproductive individuals, yearling males were significantly heavier at emergence in the low compared to the high-density years. Similar to males, yearling females were significantly lighter at emergence at high than at low density. Emergence dates of reproductive females in the high-density period preceded those at low density. Both male and female immergence dates did not differ between the two periods. In juveniles, body mass at natal emergence was similar in both density situations. However, at low density, both male and female juveniles were heavier at immergence than at high density. Juvenile survival rates were lower at low density and most of the yearlings emerging in spring had been born in the study area in the previous year. This was in contrast to the high-density period, in which more than a half of the individuals that were captured after their first hibernation were juvenile immigrants of the previous season. Hence, lower body mass at high density shortly before hibernation may partly reflect the costs of dispersal. In addition, better access to resources and lower social stress at low density could lead to faster growth rates, particularly in juveniles. This may result in a high proportion of reproductive yearlings in the low-density period.

Key words. *Spermophilus citellus*, body mass, population density, seasonal timing.

INTRODUCTION

Population density, defined as the number of individuals per spatial unit, can be highly variable particularly in some small mammals species (reviewed in Feldhamer et al. 1999). Pronounced fluctuations in density can occur as cycles, in more or less regular intervals (Begon et al. 1990, Krebs 1992) or be events due to environmental changes (e.g. Sherman & Runge 2002). The number of individuals living in a colony affects the availability of food resources and mating partners, causing high intraspecific competition at high densities (Armitage 1991, Boag & Murie 1981, Millesi et al. 2004). Thus, high population density can cause increased levels of social stress due to frequent conflict situations. This in turn may lead to decreased reproductive success due to impaired gonadal function and increased mortality rates caused by reduced immune function (BOONSTRA et al. 2001, BRAUDE et al. 1999, CHRISTIAN 1978). On the other hand, living in a large group can reduce individual predation risk via e.g. dilution or vigilance effects (DEHN 1990, HAMILTON 1971). Hence, population density can determine several aspects of individual life history such as the age of puberty, reproductive effort and success, or even survival rates.

During a long-term study on European ground squirrels (*Spermophilus citellus*) at a study site near Vienna, Austria, we observed a dramatic change in population density of the study population (HOFFMANN et al. 2003). During the first years of our study (1990 until spring 1994), the density was relatively high (mean: 56 individuals/ha in spring, range 49–61) compared to other *S. citellus* populations and populations of closely related *Spermophilus* species (BOAG & MURIE 1981, DOBSON & OLI 2001, FESTA-BIANCHET & KING 1991, FRID & TURKINGTON 2001, HUBBS & BOONSTRA 1997, KARELS & BOONSTRA 2000). From 1994 to 1995, density in the study area decreased in a stepwise manner (HOFFMANN et al. 2003). Thereafter, until 2000, population density was low but remained rather stable (mean: 7 individuals/ha in spring, range 6–8). Spring sex ratio also changed from 35% of males at high to 22% at low density (HOFFMANN et al. 2003). This density change was associated with changes in several demographic aspects. Litter size was larger at low density and juvenile sex ratio was male-biased. In addition, the age of puberty in males varied with population density (HOFFMANN et al. 2003, MILLESI et al. 2004). Low density with high female availability was associated with precociousness in yearlings. Different factors including access to specific nutritional resources, suitable hibernacula and social interactions do vary with density and may affect developmental processes in young individuals (MILLESI et al. 1999a, MILLESI et al. 2004, NUNES et al. 2002, PULAWA & FLORANT 2000, STRAUSS et al. 2007).

Timing of vernal emergence has been shown to affect individual reproductive performance during the active season. Females that mated earlier had larger litters than later ones, and lactated their offspring for longer periods (MILLESI et al. 1999b, HUBER et al. 2001).

Body condition at vernal emergence may determine reproductive success, and body mass shortly before hibernation can be crucial for overwinter survival, because like other ground squirrels, *S. citellus* do not cache food and rely on their body-fat reserves (MILLESI et al. 1999a).

In this study, we compared body mass of different age and sex classes at high and low densities, both at vernal emergence and at the end of the active season. In juveniles we analyzed body mass at natal emergence and shortly before the onset of hibernation in both density situations.

To gain insight into potential causes and consequences of physical condition, we analyzed local survival in juveniles both for individuals born in the study area and individuals that had immigrated to the study area during the active season.

MATERIAL AND METHODS

The study was conducted in a suburban park area in Langenzersdorf (48° 31' N, 16° 36' E, elevation 164 m), near Vienna in the period 1990–2000. From 1990 to 1995, the research was concentrated on a central 1-ha portion of the site. Animals on adjacent meadows were captured and observed occasionally. From 1996 to 1998, all ground squirrels in a 4-ha area, which included the former central site, were monitored, and in 1998, we enlarged the study site for further 4 ha. Capture-mark-recapture was carried out on 3–5 days per week throughout the active season except in the year 1995, which was excluded from the analysis. Tomahawk live traps baited with peanut butter were used. At capture the squirrels were weighed, sex and reproductive status (descended or abdominal testes in males, teat development indicating gestation and lactation in females) were determined and the individuals were marked with PIT-tags (Datamars Comp., Bedano, Switzerland) for permanent identification, and with fur marks for distant recognition (for details see MILLESI et al 1999a, HOFFMANN et al. 2003).

The individuals were assigned to one of the three age classes: juvenile (<1 year), yearling (1 year, between first and second hibernation), adult (≥2 years). Individuals that could not be classified as yearlings or adults at the initial capture were categorized as reproductive or nonreproductive.

Checklists of active individuals in the population were maintained each year from mid February until early October (MILLESI et al. 1999a). Censusing was carried out by scanning the site several times each day, and supplementing daily scans with all additional sightings not recorded during the scans (PFEIFER 1982). A previous analysis of the checklists showed that by scanning an area of 1ha five times per day, more than 90% of the marked individuals could be identified (MILLESI et al. 1999a).

Survival rates of juvenile individuals were determined and defined either as the percentage of juveniles that survived until their first hibernation (survival during the active season) or the percentage of juveniles that survived from the year of their birth to the next year (inter-year survival). In juvenile ground squirrels we further discriminated between residents (individuals born in the study area) and immigrants (individuals that had dispersed into the study area during the active season).

The first and the last observations were determined for each individual from the checklists. Emergence date was defined as the first day in a year that an individual ground squirrel was observed above ground (MILLESI et al. 1999a). We used the appearance of the last individual of any age or sex class, which had immerged in the study area in the previous year, as a time limitation for the emergence period. Juvenile emergence was the date when a litter was first observed above ground. Immergence date was defined as the last day that an individual ground squirrel was observed above ground, when this date was within the immergence period of the corresponding age and sex class (MILLESI et al. 1999a).

Emergence body mass could be determined in animals that were captured and weighed within 5 days after emergence. Immergence body mass was measured in ground squirrels trapped within five days before immergence into hibernation. We defined the time span from 1990 to 1994 as years with high population density and from 1996 to 2000 as years with low population density. 1995 was excluded from the analyses, because trapping and observations were performed only occasionally.

The years included in the two periods differ in age cohorts because recaptured animals of known age were first available in 1991.

Statistics

Samples of reproductive individuals include initial captures that could not be assigned to any age class, and thus may be larger than the respective sum of yearlings and adults.

As it was not possible to capture all individuals at the onset and offset of the active season, sample sizes for body mass and date of emergence differ from those at immergence. Samples of reproductive, adult and yearling males at immergence were not sufficient to analyze their body mass at hibernation onset.

Dates of onset and offset of the active season were not available for 1990 and 1991. In addition, we increased the study area with decreasing population density. Observation samples may therefore be equal or even larger at low than at high densities.

We conducted statistical analyses with SPSS 15.01 for Windows statistical package (SPSS Inc. 2006). Data distributions were analyzed for normality by Shapiro-Wilk tests. Normally distributed samples were compared with t-tests, others with Mann-Whitney U-tests. Statistical significance was set at $p<0.05$.

RESULTS

Males

Among reproductive males, yearlings emerged from hibernation with a lower body mass than older males, both at high and at low population density (high density: $t=-5.81$, $p<0.001$, n=4

Table 1. Onset and offset of the active season in European ground squirrels (median, n, range) at high and low densities
Tab. 1 Začátek a konec sezónní aktivity sysla obecného při vysoké a nízké populační hustotě (medián, n, rozpětí). emergence date – datum ukončení hibernace, immergence date – datum začátku hibernace

	emergence date		immergence date	
	high	low	high	low
males				
reproductive	7 March (41) 15 Febr. – 26 March	13 March (36) 26 Febr. – 30 March	2 Sept. (17) 17 August – 6 Sept.	26 August (11) 17 July – 22 Sept.
adult	4 March (34) 15 Febr. – 25 March	13 March (14) 28 Febr. – 30 March	4 Sept. (14) 17 August – 6 Sept.	25 August (4) 29 July – 10 Sept.
yearling	31 March (30) 11 March – 15 April	13 March (22) 26 Febr. – 28 March	19 Sept. (7) 2–28 Sept.	26 August (7) 17 July – 22 Sept.
rep. yearling	22 March (6) 11–26 March	13 March (22) 26 Febr. – 28 March	10 Sept. (2) 2–18 Sept.	26 August (7) 17 July – 22 Sept.
nonrep. yearling	1 April (24) 24 March – 15 April	– (0)	21 Sept. (4) 13 Sept. – 28 Sept.	– (0)
juvenile			20 Sept. (16) 7 Sept. – 1 Oct.	29 Sept. (12) 21 August – 9 Oct.
females				
reproductive	1 April (82) 18 March – 15 April	5 April (109) 24 March – 28 April	16 August (32) 22 July – 3 Sept.	18 August (50) 11 July – 10 Sept.
adult	5 April (47) 18 March – 13 April	5 April (65) 26 March – 28 April	14 August (22) 25 July – 24 August	18 August (33) 11 July – 6 Sept.
yearling	1 April (34) 24 March – 15 April	5 April (33) 24 March – 21 April	22 August (9) 22 July – 3 Sept.	20 August (11) 27 July – 10 Sept.
juvenile			19 Sept. (23) 3 Sept. – 5 Oct.	6 Sept. (31) 7 Aug. – 29 Sept.
juveniles (m & f)	8 June (213) 26 May – 26 June	8 June (428) 31 May – 3 July		

yearlings/19 adults; low density: $t=-3.40$, $p=0.011$, n=6 yearlings/3 adults). At high density, reproductive yearling males started the active season later than older males ($U<30$, $p=0.006$; Table 1). However, emergence date did not differ significantly between the two age classes at low density (Table 1a). Emergence body mass of reproductive males was slightly, but not significantly higher at high than at low density ($t=1.65$, $p=0.112$; Fig. 1). In reproductive yearlings an opposite tendency was found, body mass at emergence was marginally higher at low density ($t=-1.99$, $p=0.082$; Fig. 1). In the high-density period, reproductive males emerged earlier than in that with low density ($U=479$, $p=0.008$; Table 1a). Yearling males (including nonreproductive individuals) were lighter at high compared to low density ($t=-5.29$, $p<0.001$, n=22/6) and emerged later in the season ($U=70$, $p=0.016$, n=22/6; Table 1a). Reproductive yearling males were heavier at emergence ($t=-2.35$, $p=0.029$, n=4/19), and started above ground activity earlier than nonreproductive yearlings ($U=9.5$, $p=0.001$), whereas the timing of the hibernation onset was similar (U=1.5, p=0.244; Table 1b). These comparisons could only be made for the high-density years because data on nonreproductive yearling males were not available for low densities. Emergence dates of reproductively active yearling males did not differ significantly between high and low density (U>45, p=0.256; Table 1a).

Concerning male immergence dates, no significant differences were found in the particular male categories between the two periods (U=15.0–120.5, each p>0.130).

F e m a l e s

Reproductive female European ground squirrels were significantly lighter at emergence in the high- compared to the low-density years (t=–2.92, p=0.004; Fig. 1). Whereas emergence body

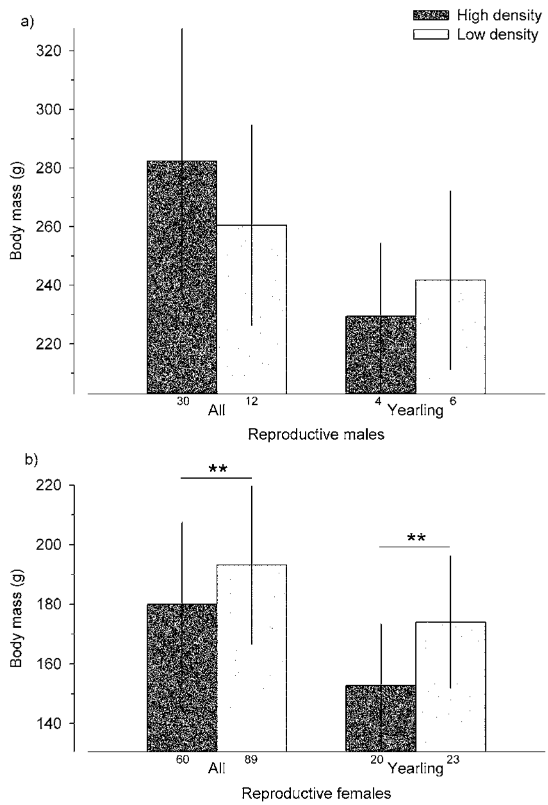

Fig. 1. Body mass of European ground squirrels captured within 5 days after emergence from hibernation (means, SD). a) Reproductive males, b) reproductive females, both adult and yearling individuals are included in the category "all", (*p<0.05, **p<0.01).
Obr. 1. Hmotnost syslů odchycených v průběhu pěti dnů po ukončení hibernace (průměr, SD). a) Rozmnožující se samci, b) rozmnožující se samice, v kategorii "all" jsou zahrnuti dospělí i jednoletí jedinci, v kategorii "yearling" pouze jednoletí (*p<0.05, **p<0.01).

Table 2. Survival of juvenile European ground squirrels. a) Percentages of juveniles that survived until their first hibernation (total numbers of juveniles observed, including juveniles of unknown sex, are given in parentheses). E.g., 23.1% out of 277 juveniles survived until hibernation at high densities. b) Percentages of residents (juveniles born in the focal area) and potential immigrants (males >145g, females >139g at initial capture, cf. Hoffmann et al. 2004) representing survivors (total numbers of juveniles surviving to the following year are given in parentheses). E.g., 41.2% out of 51 inter-year survivors were residents, 58.9% were potential immigrants

Tab. 2. Přežívání mláďat sysla obecného. a) Podíl mláďat, která přežila do své první hibernace (v závorce celkový počet pozorovaných mláďat, včetně mláďat neurčeného pohlaví), např. 23,1% z 277 mláďat přežilo do začátku hibernace při vysoké populační hustotě. b) Podíl mláďat narozených na sledované ploše (rezidenti – Res) a potenciálních imigrantů (– Imm, samci vážící při zahájení odchytu >145g, samice >139g, cf. Hoffmann et al. 2004) reprezentujících přeživší jedince (v závorce celkový počet mláďat, která přežila do následujícího roku). Např. 41,2% z 51 přeživších mláďat byli rezidenti, 58,9% byli potenciální imigranti

density (a)	high 1992–1994	low 1996–1998
total	23.1 (277)	14.2 (323)
males	20.7 (135)	14.0 (143)
females	25.4 (142)	24.3 (107)

(b)		high			low	
	res	imm	n	res	imm	n
total	41.2	58.9	(51)	89.3	11.1	(28)
males	57.1	42.9	(21)	66.7	33.3	(9)
females	30.0	70.0	(30)	100.0	—	(19)

mass of adult females did not differ significantly between the two periods (t=–0.46, p>0.600, n=45/30), yearlings were heavier at low population density (t=–3.23, p=0.002, n=23/20). Vernal emergence date in reproductive females in the high-density period preceded that at low density (U=3068.5, p<0.001; Table 1). This was also true for each of the two age groups when treated separately (adults: U=1143.5, p=0.023; yearlings: U=389.5, p=0.038; Table 1a).

The timing of female immergence into hibernation did not differ significantly between the two density situations (all: U=707.5, p=0.381; yearlings: U=45, p=0.739; Table 1b). Adult females, however, immerged marginally earlier at high densities (U=266.5, p<0.100; Table 1b).

Although at low densities, immergence dates tended to be relatively early in males and relatively late in females, there was no sex difference in hibernation onset of reproductive individuals (U=221.5, p=0.324; Table 1b), whereas female immergence occurred significantly earlier than in males at high densities (t<–6.92, p<0.001).

Juveniles

We found no significant difference in juvenile body mass at natal emergence between the two periods (t>–0.04, p=0.974, n=23/20). However, litters emerged later at low compared to high density (U>40850, p=0.032, Table 1). Natal emergence date and body mass did not differ between the sexes in either of the two periods (p>0.140 in all cases).

Shortly before hibernation, juvenile males were significantly heavier than females in both periods (high density: t=3.06, p=0.005, n=17 in each sex; low density: t=3.19, p=0.009, n=5 males/8 females; Fig. 2). At low density, both male and female juveniles were heavier at immergence than at high density (males: t=–2.83, p=0.011; females: t=–2.94, p=0.007). In males, immergence date did not differ between the two periods (U=72.5, p=0.276), but juvenile females started hibernation later at high density (U=165.5, p=0.001; Table 1b).

We further determined survival rates in juvenile ground squirrels both during the active season and from one year to the next (Table 2a, b). Survival during the active season was higher at high compared to low density. This was mainly due to higher losses in juvenile males (Table 2a). When we compared inter-year survival in juveniles born in the study area (residents) with those that had immigrated during summer, we found that at low density, almost 90% of the survivors had been residents, whereas at high density similar percentages of residents and immigrants had survived (Table 2b). In female juveniles, only one third of the survivors were residents at high density. At low density, however, all juvenile females that had survived over winter were born in the study area (Table 2b).

DISCUSSION

Emergence body mass and the timing of the active period are important prerequisites for subsequent reproductive performance in many hibernators like the European ground squirrel (Dark et al. 1992, Holmes 1988, Schwagmeyer & Brown 1983). A good physical condition in spring can be beneficial for mature males in being successful in intrasexual competition during the

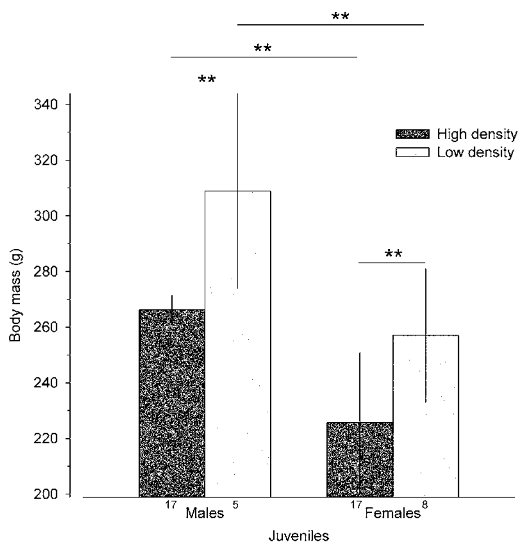

Fig. 2. Body mass of juvenile European ground squirrels captured within 5 days before immergence into hibernation (means, SD, **p<0.01).
Obr. 2. Hmotnost mláďat sysla obecného odchycených v průběhu pěti dnů před zahájením hibernace (průměr, SD, **p<0.01).

mating period. Accordingly, during high-density periods, small males like mature yearlings were never observed to acquire a mate (MILLESI et al. 1998). As shown earlier, males were unable to reach adult body mass after their first hibernation, independent of population density (MILLESI et al. 1999a). The onset of sexual maturity, however, differed with population density. At high density, most yearling males were immature, whereas at low density all yearlings emerged with scrotal testes (HOFFMANN et al. 2003, MILLESI et al. 2004). Hence, the reproductive males in the high-density period were mainly adults, whereas at low density, the proportion of mature yearlings was higher. This could be the reason why reproductive males were slightly heavier in the former period. This potential age effect could also explain the timing of emergence. The testes are developed in the hibernaculum and are activated during the last weeks of hibernation (BARNES 1986, CONCANNON et al. 1989, DARROW et al. 1987, STRAUSS et al. 2008). This process may be initiated later in young males compared to older ones. Reproductive males emerge before the females to be ready for the mating phase, which is energetically the most demanding period for the males (MICHENER 1984, MILLESI et al. 1998). Nonreproductive yearlings delay gonadal activation and can therefore hibernate for longer periods.

Interestingly, reproductive yearling males tended to be heavier at low compared to high density at vernal emergence. As overwinter mass loss appeared to be quite constant throughout the study period (MILLESI et al. 1999a), body condition at the end of the previous season may determine that in the following spring. This is in line with the finding that juvenile males at low density were heavier than those in the high-density period. One reason for the obviously better condition of juveniles at low density could be increased maternal effort. However, body mass at natal emergence did not differ between the two periods, indicating similar growth patterns during the first weeks of life. On the other hand, litter size has been shown to increase with lower density (HOFFMANN et al. 2003). Juveniles from large litters are usually lighter at natal emergence and are lactated longer to compensate for this deficit (HUBER et al. 2001). Considering the larger litter size at low density, there might be evidence for a developmental advance in the low-density pups already during the lactation period. Increased maternal effort delays the onset of fattening and therewith hibernation in dams (HUBER et al. 1999). This could explain why adult females immerged marginally later at low than at high density. More detailed analyses of individual litters and their mothers are needed to confirm this assumption.

Later in the season, shortly before hibernation, body mass of the offspring born during high- and low-density years clearly differed. Faster growth rates at low density could be due to better access to resources like specific food items (FLORANT 1998, FORGER et al. 1986, STRAUSS et al 2007) and/or lower social stress because of rare contact with conspecifics, especially older males (cf. MICHENER 1983, MILLESI et al. 2004). An experimental study in an outdoor enclosure showed that juvenile male European ground squirrels which grew up in the presence of older males had slower growth rates than those kept with females and other juveniles (STRAUSS et al. unpublished data). In addition, most juvenile individuals that survived over winter at low density were born in the study area and hence had not dispersed. In contrast, at high density about a half of the yearlings had immigrated to the area in the previous year. As dispersal is energetically costly, it is not surprising that body mass in these individuals before as well as after hibernation was lower (HOLEKAMP 1984). Another potential explanation is related to predation. High individual densities may attract predators but the individual risk of being killed is lower in a dense colony than in more widely distributed individuals (DEHN 1990). In addition, alarm calls and vigilance may be more efficient at high densities (DEHN 1990). This is supported by the fact that juvenile losses during the active season were higher at low density. Hence, increased predation pressure at low density may lead to increased mortality, particularly in juveniles, and by that selecting the fittest individuals to survive. This may result in a high proportion of reproductive yearlings in the low-density situation.

Similar effects seem to be relevant in females. Individuals were heavier at low compared to high density before and after their first hibernation. This could positively affect reproductive output as indicated by larger litters in this period (Hoffmann et al. 2003). Earlier emergence dates at high density, particularly in yearling females, could point to an earlier termination of hibernation in individuals with low body fat reserves.

In conclusion, our results indicate complex age- and sex-specific effects of population density on several life-history traits.

SOUHRN

V této studii jsme porovnávali načasování období aktivity a tělesnou hmotnost sysla obecného v letech s nízkou a vysokou populační hustotou. Sledování bylo prováděno v kolonii sysla obecného v příměstském parku Langenzersdorf poblíž Vídně v období 1990–2000. Pomocí odchytu do živochytných pastí a vizuálního sčítání bylo zjišťováno datum ukončení hibernace v jarním období, datum zahájení hibernace a tělesná hmotnost u obou pohlaví a v různých věkových kategoriích. Mezi rozmnožujícími se samci vykazovali nižší hmotnost jednoletí jedinci než starší samci. Jejich hmotnost při opuštění nory na konci hibernace však byla o něco nižší při vysoké populační hustotě než při nízké hustotě populace. Když bylo toto hodnocení provedeno pro všechny samce včetně těch, kteří se v daném roce nerozmnožovali, vykazovali jednoletí samci po ukončení hibernace signifikantně vyšší hmotnost při nízké populační hustotě. Podobně jako samci, také jednoleté samice byly na konci hibernace v období nízké populační hustoty signifikantně lehčí. Rozmnožující se samice ukončovaly hibernaci dříve v období vysoké populační hustoty. Datum začátku hibernace se však u obou pohlaví při různé populační hustotě nelišilo.

Hmotnost mláďat při prvním opuštění mateřské nory byla podobná při vysoké i nízké hustotě populace, na začátku hibernace však mláďata obou pohlaví dosahovala vyšší hmotnosti při nízké hustotě. Podíl mláďat, která úspěšně přežila hibernaci, byl nižší při nižší populační hustotě, přičemž většina z nich se v předešlém roce narodila na sledované ploše. Naopak v období vysoké populační hustoty tvořila více než polovinu odchycených jedinců mláďata, která sem imigrovala v předešlé sezóně z okolí. Nižší tělesná hmotnost krátce před zahájením hibernace v období s vysokou populační hustotou může být důsledek energetických výdajů při disperzi. Lepší přístup ke zdrojům a nižší sociální stres v období nízké populační hustoty by zase mohl vést k rychlejšímu přírůstku hmotnosti, a to především u mláďat. Výsledkem pak může být vyšší podíl rozmnožujících se jednoletých zvířat v období nízké hustoty populace.

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