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„Developmental patterns and body fat content of
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Abstract

The Common hamster (*Cricetus cricetus*) is a facultative hibernator having up to three litters per year. Juveniles born late in the season have less time to grow and prepare for the winter than early-born ones. We investigated a free-ranging population in an urban environment in Vienna, Austria. Body mass, proportion of body fat, head, tibia and hind foot length at natal emergence, four weeks post-emergence and shortly before immergence into the hibernacula were compared between juveniles of first and second litters in the respective season. In addition we tested for differences in growth rates during the first four weeks post emergence and potential effects of sex and litter size. Capture-mark-recapture techniques were used. Body fat content was calculated using a multiple regression model integrating morphometric parameters. At natal emergence second litter offspring was larger and heavier than that of first litters. Litter size did not account for these differences. During the first week after natal emergence first litter pups gained body mass faster and during the first two weeks also their head and tibia grew faster than in second litter pups. Four weeks after natal emergence, however, second litter juveniles were still larger and heavier than first litter ones. Body fat content four weeks post-emergence did not differ between first and second litters but decreased with litter size. Shortly before immergence, first litter juveniles, which had more time to grow and accumulate body fat, exceeded second litters ones in all measured parameters. In all litters investigated, we found no sex difference at natal emergence but males were heavier and larger than females four weeks thereafter demonstrating that the commonly known sexual dimorphism in this species developed during this period. Considering the time constraints late born juvenile hamsters face, the conditional advance at natal emergence is assumed to be adaptive, increasing the chances for these individuals to survive overwinter despite the limited time to prepare for the hibernation period.

Introduction

Hibernation is an adaptation to periodically low ambient temperature and consequential seasonal energy shortage (Humphries et al., 2003). To survive the winter period hibernators need sufficient energy reserves especially to enable the energetically costly arousals out of torpor (Nedergaard et al., 1990). In addition, some species, like the Common hamster, spend extended periods at normal body temperatures in their burrows or even above ground (Wassmer, 2004). The two main tactics to allocate energy reserves are building up adipose tissue and hoarding food caches (Day and Bartness, 2003; Humphries et al., 2003; Nedergaard et al., 1990), whereupon Common hamsters use both alternatives (Millesi et al., 2004) with different emphasis in males and females (Siutz et al., 2012). In general, hibernators are seasonal breeders with a temporally limited reproductive period, requiring adaptations in reproductive timing and energy allocation for the winter (Millesi et al., 2004; Nelson et al., 1990) not only to enable the adults' overwinter survival, but also that of the offspring. Vernal emergence in Common hamsters occurs from early March to May (Franceschini-Zink and Millesi, 2008) and first copulations have been observed one month later (Hufnagl et al., 2011). After a gestation time of 17-21 days (Kirn, 2004; Vohralik, 1974) and about three weeks in the natal burrow, juveniles emerge and are weaned shortly thereafter (Niethammer, 1982; Seluga et al., 1996). While most obligate hibernators reproduce only once per season (Millesi et al., 2004), Common hamsters can have up to three litters per year (Endres, 2004; Franceschini and Millesi, 2005; Seluga et al., 1996) with an average litter size of 4.1 ± 2.1 (mean \pm SD) (Franceschini-Zink and Millesi, 2008) and a range of 1-12 pups per litter (Endres, 2004; Franceschini-Zink and Millesi, 2008; Vohralik, 1974). The total number of weaned offspring was higher in females which emerged early in spring and increased with the number of litters per season (Franceschini-Zink and Millesi, 2008). Although juvenile Common hamsters immerse into their hibernaculum later in the season than adults (Endres, 2004; Franceschini and Millesi, 2005; Niethammer, 1982), they face rigid time constraints. They have to grow, find an appropriate burrow by taking over an abandoned one or building a new burrow (Seluga et al., 1996) and prepare for hibernation by gaining body fat and hoarding food. To accomplish these tasks it is beneficial to have as much time as possible, however time spans decrease with birth date. A females' second litter, born later in the year, has less time than her first litter. In addition maternal investment might decrease with season due to limited energy reserves of the females. The aim of our study was to investigate differences in body mass, body fat content and structural body size at natal

emergence, development during the early post emergence period and condition shortly before immergence into their hibernacula in juveniles of females' first and second litters per season. In previous studies Franceschini-Zink and Millesi (2008) showed that litter sizes of first litters in a season were larger than those of second litters and Kirn (2004) indicated a negative influence of being born later in the season on the juveniles body mass in autumn (lab experiment). Based on these results we hypothesized second litters to contain fewer offspring but, assuming similar maternal investment in first and second litters, higher body mass and/or body fat of second litter juveniles at natal emergence. Due to the longer active period, we expected first litter juveniles to be in better condition at the end of the season. We generally expected a negative effect of larger litter sizes on body mass, fat or size like it has been shown in numerous small mammal species (Guerra and Nunes, 2001; Huber et al., 2001; Kaufman and Kaufman, 1987; Neuhaus, 2000).

Methods

Study site and period

The study site was an urban area in Vienna (Austria, +48° 10' N, +16° 22' 31" E) of approximately 2.7 ha. A population of free-ranging Common hamsters inhabited green areas between and encircling buildings. The site consisted mainly of frequently mowed grass crossed by concrete pathways and mesh wire fences, which seemed hardly to limit the hamsters' movements (Pluch, personal observation). Furthermore there were hedges, bushes and trees. The study was carried out from March 29th until October 5th. Due to the bimodal daily activity pattern of the Common hamster (Eibl-Eibesfeldt, 1953; Schmelzer and Millesi, 2008; Wendt, 1989) the capture-recapture techniques were performed five days per week from sunrise to the end of the morning activity period (roughly between 10.30 – 12 am) and approximately twice per week from about 4 pm until sunset.

Field and lab techniques

Adult and juvenile Common hamsters were captured using peanut-butter baited Tomahawk live traps, which were checked every 20 minutes at the latest. To avoid anaesthesia the individuals were led into conical cotton sacks, laterally fitted with Velcro® strips and prepared with different openings to allow measurements of

particular body parts. During the 5-10 minutes lasting investigation the morphometric parameters body mass (± 1 g), head, tibia and hind foot lengths (± 0.1 mm each) were recorded. Sex, reproductive status (testicle width, vagina opening, teats status) and age (adult, juvenile) were determined and date, time and trapping location (4x4 m grid) listed. Individual recognition was enabled by implanting subcutaneous transponders (PIT tag, Data Mars) and visual recognition by applying commercial hair dye in different patterns at the dorsal region. Thereafter the animals were released in front of their burrows (Franceschini et al., 2007) or next to a hideout close to the capture location and were recaptured once per week. All animal manipulations were approved by the Austrian Ministry for Science and Research, Ethical Committee for Animal Welfare (BMWF-66.006/0007-II/10b/2009) and the City of Vienna (MA22-1216/2009).

In our study litter size was defined as the number of juveniles that emerged from a breeding burrow. Litter number was defined as females first, second or third litter of the season. Based on monitoring of the adult females' reproductive status, parturition was identified by sudden loss of body mass and increased teat size, and juvenile natal emergence expected 17-20 days thereafter (Eibl-Eibesfeldt, 1953; Endres, 2004; Vohralik, 1974) Natal emergence dates of all juveniles in one litter was set by the first emerged juvenile of the same litter. Out of 128 recorded juveniles only those, of which natal emergence date, litter size and litter number (offspring of first or second litter) was doubtlessly known, were used for analyses. Thus littermates ($n=47$) of seven different litters (4 first, 3 second litters) were included in statistical models, while due to death (Kayser et al., 2003; Vohralik, 1974) or dispersal (Seluga et al., 1996; Wolff, 2007) during the season or missing data the sample compositions and sample sizes differ between the phases. To increase sample size at testing for sex differences at natal emergence, all known litters were analysed, including those of which litter number was unknown. Pups of third litters (2 litters, 6 individuals) were excluded due to missing data points.

As first conducted in Common hamsters and described by Siutz et al. (Siutz et al., 2012) body fat content was non-invasively calculated by a multiple regression model using the parameters body mass, head, tibia and foot length. The model was developed and validated by measuring recently died (within 12 hours) individuals and by lipid extraction using Soxhlet apparatus and petroleum ether as solvent. Body fat analyses were not performed at natal emergence, because the model is to date not valid for juveniles below a certain body mass.

Date and phase definitions

Natal emergence was defined as day of natal emergence + 2 days. Four weeks post emergence was defined as day 28 ± 2 after the day of natal emergence. The post emergence phase was defined as the first four weeks after natal emergence, subdivided in first-14-days-interval (natal emergence until day 14 ± 2 post emergence) and second-14-days-interval (post emergence day 14 ± 2 until day 28 ± 2). Due to insufficient data of females, only males were included in analyses of the post emergence phase.

Prehibernation data was recorded at last capture within the last week before the juveniles' immergence into their hibernacula (Siutz et al., 2012) between September 1st and October 1st.

Statistics

Statistical analysis was performed in R 2.15.3 (Mazerolle, 2011; Team R - Development Core, 2008) Linear models were computed, testing for normal distribution of model residuals by Shapiro-Wilk tests and for homoscedasticity using Levene-tests. If model residuals were not normally distributed, the response variables were log-transformed. The full models included sex, litter size and litter number (first, second) and their two-way interactions as predictor variables. Model simplification was based on the Akaike information criterion (AIC) (Akaike, 1973) corrected for small sample sizes (AICc) (Hurvich and Tsai, 1991). The respective minimum adequate models are shown in the text. Due to dropping out of every interaction during the model simplification processes Type II ANOVAs from the models were performed. Because of unbalanced data at natal emergence concerning males and females predictor variable sex was excluded from models at natal emergence. Instead we calculated the mean values of males and females of all mixed-sex litters and performed paired *t*-tests, and a Wilcoxon signed-rank test from one not normally distributed sample, to look for sex differences within litters at natal emergence. Computed models with the means of the different litters as response variable only included litter number as predictor variable. Performed single correlations were Pearson's correlation tests, and to test for sex ratio bias Exact binomial tests for goodness of fit were conducted. To test for differences in the prehibernation immergence date between first and second litter offspring a Mann–Whitney *U* test, and to test for length of the active above-the-ground season between those two groups, a student's *t*-test was performed. Significance levels were set at $p = 0.05$ if not stated otherwise. Results are shown as means \pm SD.

Results

Forty-seven individuals of seven different litters (four first, three second litters) were used in our study. Litter sizes at natal emergence were 4, 7, 8, 12 and 4, 5, 7 juveniles for first (L1) and second litters (L2) respectively. First litters emerged from May 25th to June 23rd and second litters from July 28th to August 2nd. A linear model showed no differences between litter sizes of first and second litters ($p = 0.3$, $F_{1,5} = 1.34$, $n = 7$).

Females' body mass before gestation onset had no influence on their litters' size, mass or the average juveniles body mass at natal emergence (Pearson's correlation: $p = 0.54$, $p = 0.72$, $p = 0.36$, $n = 6$ respectively).

There was no biased sex ratio in first or second litters or in all litter pooled (Exact binomial tests for goodness of fit: $p = 0.36$, $n = 31$; $p = 0.40$, $n = 16$; $p = 0.28$, $n = 47$ respectively).

Immergence into hibernacula occurred from September 1st until October 1st with no significant difference between first and second litter individuals (Mann–Whitney U test: $p = 0.058$, $n(L1/L2) = 7/8$), but a tendency of a subsequent immergence of second litter juveniles. The duration of the active season in first litter offspring was significantly different (student's t -test: $t = 13.22$, $p < 0.001$, $n(L1/L2) = 7/8$) and more than two and a half times longer (112 ± 12 days) than that of second litter juveniles (43 ± 8 days).

Natal emergence

At natal emergence mean body mass ($p = 0.18$), head ($p = 0.31$), tibia ($p = 0.17$) and foot length ($p = 0.04$) did not differ significantly between males and females within litters ($n = 5$ respectively, Bonferroni corrected significance levels at $p = 0.0125$).

Juveniles of second litters had larger head, tibia and foot lengths and were heavier than those of first litters (Table 1, Fig. 1). Litter size had no significant influence on the measured parameters.

Table 1

ANOVA (type II tests) tables from AICc based minimum adequate models concerning body mass, head, tibia and foot length at natal emergence

Response variable	n	F-statistic (model)	R ²	p-value (model)	predictor variable	df
Body mass	32	F _{1,30} = 80.02	0.72	< 0.001***	litter number	1
Head length	32	F _{1,30} = 87.29	0.74	< 0.001***	litter number	1
Tibia length	31	F _{1,29} = 79.46	0.72	< 0.001***	litter number	1
Foot length	29	F _{1,28} = 70.09	0.70	< 0.001***	litter number	1

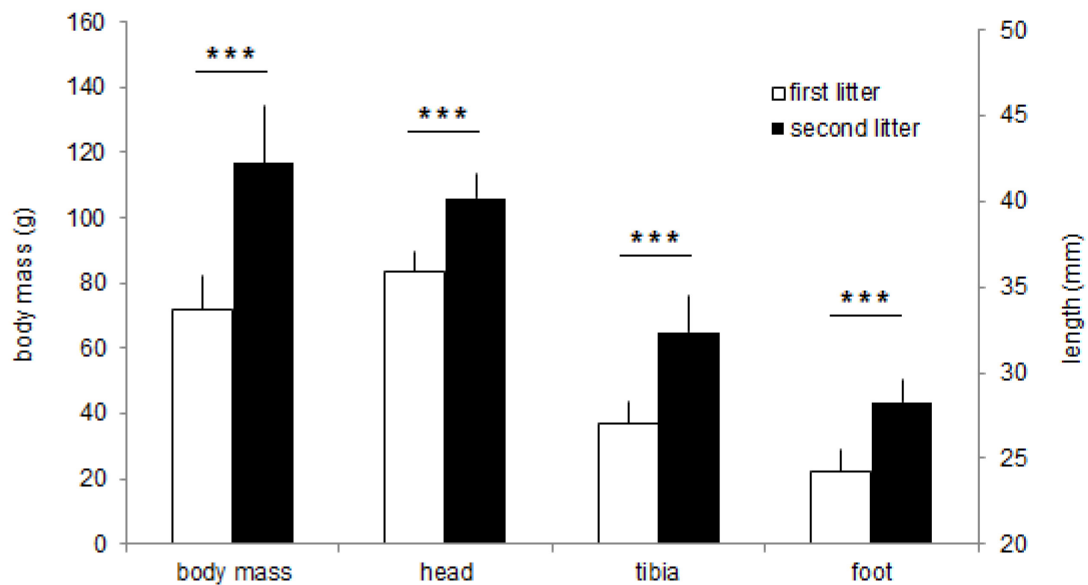


Fig. 1. Morphometric parameters (means ± SD) of first (L1) and second litter (L2) juveniles at natal emergence (sample sizes: L1-body mass and head = 19, L1-tibia = 18, L1-foot = 17, L2-each = 13). ***p < 0.001

To test for potential litter effects we performed linear models with mean values of the different litters as response variable (Fig. 2) and litter number as single predictor variable (Table 2). The results were similar to that of analyses with individuals as response variable (Table 1). The mean values of first litters were significantly lower than those of second litters in all morphometric parameters.

Table 2

ANOVA (type II tests) tables from models concerning body mass, head, tibia and foot length at natal emergence with means of the litters as response variable

Response variable	n	F-statistic (model)	R ²	p-value (model)	predictor variable	df
Body mass	7	F _{1,5} = 16.05	0.72	< 0.010*	litter number	1
Head length	7	F _{1,5} = 21.33	0.77	< 0.006**	litter number	1
Tibia length	7	F _{1,5} = 20.49	0.76	< 0.006**	litter number	1
Foot length	7	F _{1,5} = 22.43	0.78	< 0.005**	litter number	1

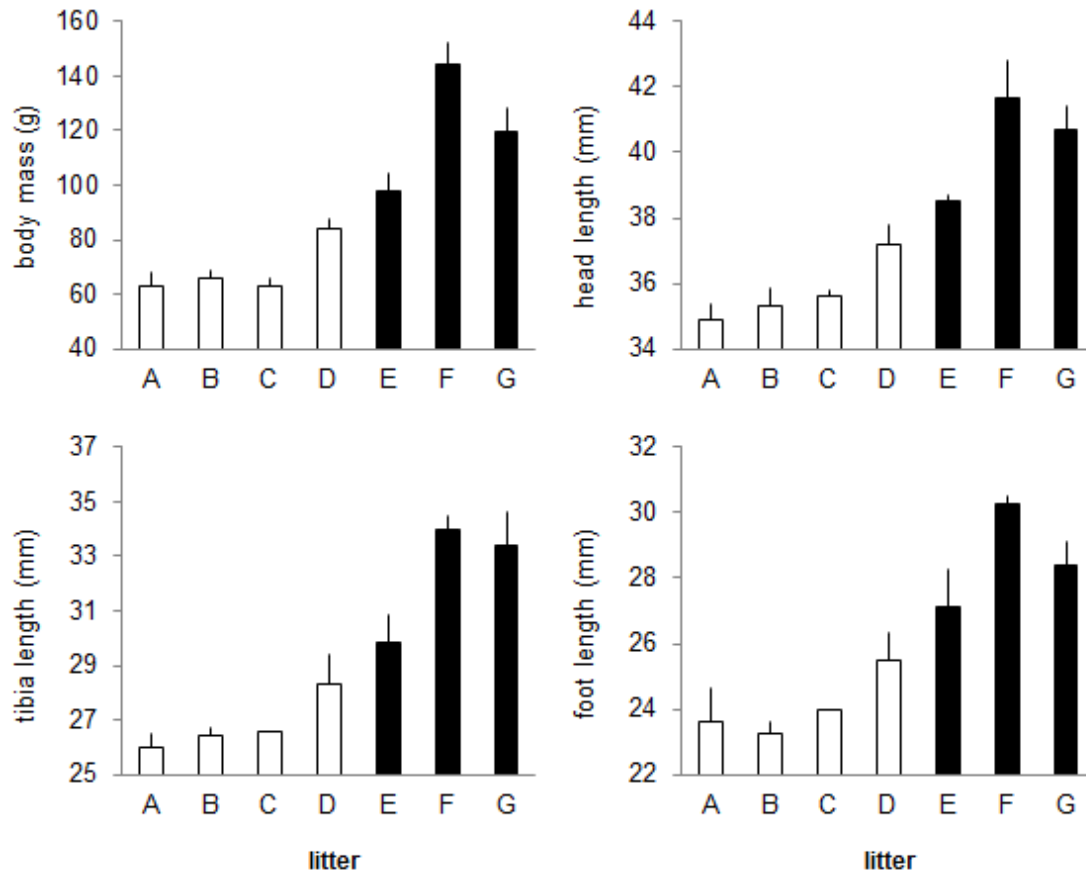


Fig. 2. Morphometric parameters (means \pm SD) of first (white bars) and second litters (black bars) at natal emergence

Four weeks post-emergence

Four weeks after natal emergence second litter juveniles were still larger in all parameters and heavier than first litter ones. Males had a higher body mass and larger tibia and foot length than females after corrected for litter number in the linear model (Table 3). Head length was not influenced by sex. All means \pm SD are shown in Table 5. Body fat content was only depending on litter size and higher in pups of smaller litters (Fig. 4).

Table 4

ANOVA (type II tests) tables from AICc based minimum adequate models concerning body mass, body fat content, head, tibia and foot length four weeks post natal emergence

Response variable	n	F-statistic (model)	R ²	p-value (model)	Predictor variable(s)	df	F-value (predictor)	p-value (predictor)
Body mass	19	$F_{2,16} = 29.73$	0.76	< 0.001***	litter number	1	59.36	< 0.001***
					sex	1	5.61	0.031*
Head length	18	$F_{1,16} = 25.37$	0.59	< 0.001***	litter number	1	25.37	< 0.001***
Tibia length	14	$F_{2,11} = 19.76$	0.74	< 0.001***	litter number	1	34.21	< 0.001***
					sex	1	13.95	0.003**
Foot length	11	$F_{2,8} = 11.56$	0.68	0.004**	sex	1	14.73	0.005**
					litter number	1	13.34	0.006**
Body fat	17	$F_{1,15} = 25.54$	0.61	< 0.001***	litter size	1	25.54	< 0.001***

Table 5

Means \pm SD of morphometric parameters four weeks after natal emergence based on litter number or sex

	Body mass (g)	Head (mm)	Tibia (mm)	Foot (mm)
Litter 1	127 \pm 16	42.3 \pm 0.9	37.9 \pm 2.2	31.1 \pm 1.4
Litter 2	175 \pm 17	44.4 \pm 0.9	36.4 \pm 2.2	28.9 \pm 0.9
Males	158 \pm 36	44.0 \pm 2.1	35.6 \pm 1.9	29.4 \pm 1.4
Females	153 \pm 25	43.9 \pm 1.7	39.0 \pm 1.4	31.3 \pm 2.0

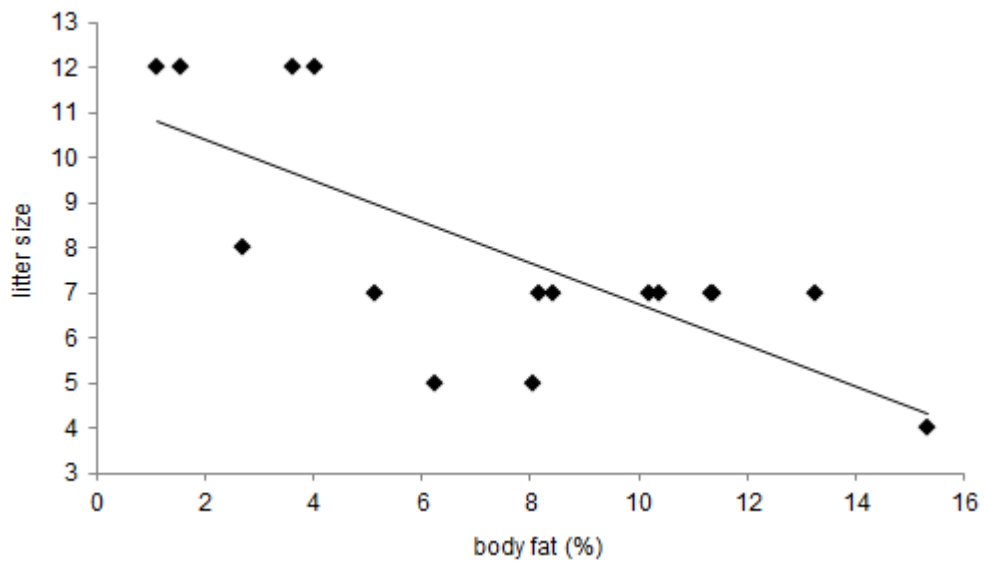


Fig. 4. Relationship of juveniles' litter size and body fat content four weeks post natal emergence ($r = -0.77$; statistical analysis see Table 3)

Post emergence phase

During the first-14-days-interval first litter males grew faster in head and tibia than second litter ones (Table 2, Fig. 2). This was no longer the case during the second-14-days-interval. There were no significant results concerning body mass in either of the two 14-days-intervals. However, during the first week post emergence first litter males (3.58 ± 0.85 g/day) gained weight faster (linear model: $p = 0.009$, $F_{1,11} = 10.17$, $R^2 = 0.43$, $n = 13$) than second litter ones (2.58 ± 0.6 g/day).

Table 3

ANOVA (type II tests) tables from AICc based minimum adequate models concerning gain of body mass and head, tibia and foot growth per day during the first and second 14-days-interval post emergence

Intervall	Response variable	n	F-statistic (model)	R ²	p-value (model)	Predictor variable	df
First 14 days	Body mass	11	$F_{1,9} = 3.43$	0.20	0.097	litter number	1
	Head	10	$F_{1,8} = 25.71$	0.73	< 0.001***	litter number	1
	Tibia	11	$F_{1,9} = 37.28$	0.78	< 0.001***	litter number	1
Second 14 days	Body mass	8	$F_{1,6} = 3.18$	0.24	0.125	litter size	1
	Head length	9	—	—	—	none	—
	Tibia length	8	—	—	—	none	—

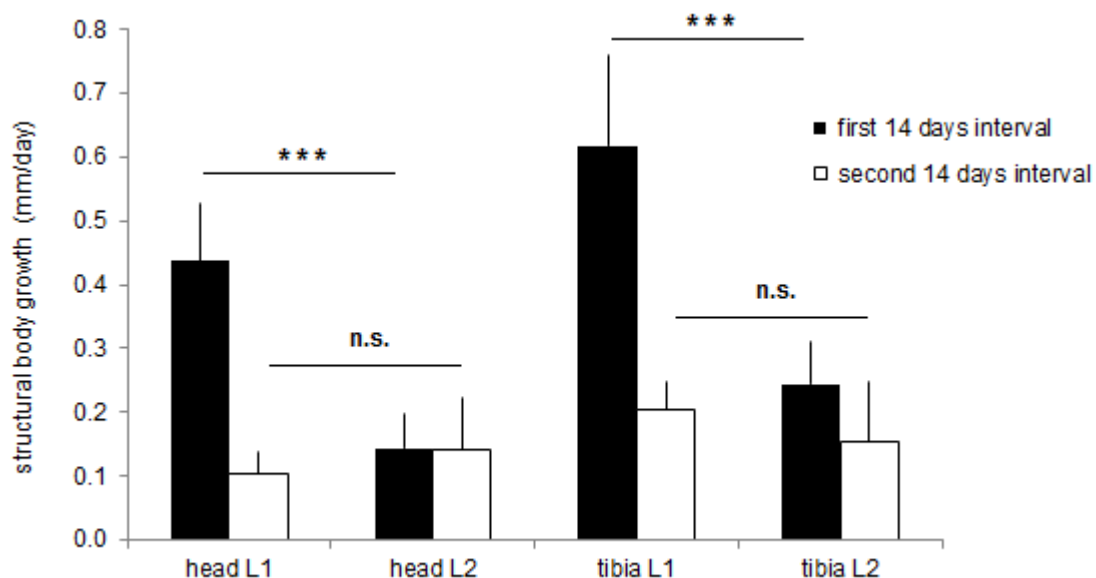


Fig. 3. Growth rates of head and tibia per day of first (L1) and second litter (L2) males in course of the first and second-14-days-intervals post emergence (sample sizes: L1-body mass and tibia = 8, L1-head = 7, L2-each = 3)

Prehibernation

Shortly before immergence into their hibernacula first litter juveniles had higher body mass, body fat and larger heads and tibiae than second litter juveniles (Table 5, Fig. 5, Fig. 6). Foot length was no longer influenced by litter number. Males were heavier than females and had larger tibiae and feet (Table 5, Fig. 7). Head length did not differ between sexes.

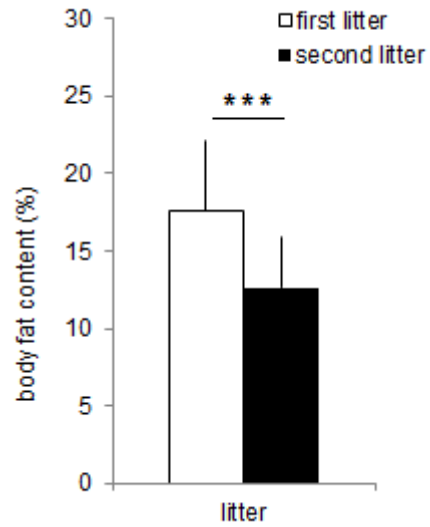


Fig. 5. Body fat content of first and second litter juveniles shortly before immergence

Table 6

ANOVA (type II tests) tables from AICc based minimum adequate models concerning body mass, body fat content, head, tibia and foot length proximate to immergence into hibernaculum

Response variable	n	F-statistic (model)	R ²	p-value (model)	Predictor variable(s)	df	F-value (predictor)	p-value (predictor)
Body mass	15	$F_{2,12} = 19.03$	0.72	< 0.001***	sex	1	23.41	< 0.001***
					litter number	1	11.25	0.006**
Head length	15	$F_{1,13} = 20.69$	0.58	< 0.001***	litter number	1		
Tibia length	15	$F_{2,12} = 21.76$	0.75	< 0.001***	sex	1	28.7	< 0.001***
					litter number	1	11.07	0.006**
Foot length	11	$F_{1,9} = 25.91$	0.71	0.004**	sex	1		
Body fat	15	$F_{3,11} = 26.45$	0.85	< 0.001***	sex	1	21.14	< 0.001***
					litter number	1	12.62	0.005**
					litter size	1	7.94	0.017*

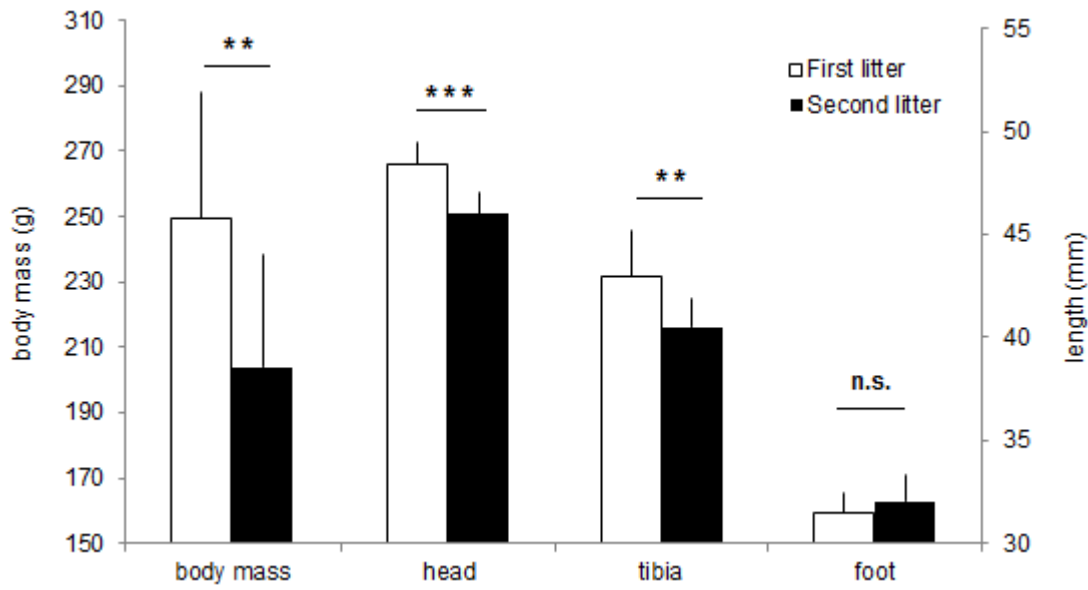


Fig. 6. Morphometric parameters (means \pm SD) of first (L1) and second litter (L2) juveniles at prehibernation phase (sample sizes: L1-body mass, head and tibia = 7, L2-body mass, head and tibia = 8, L1-foot = 6, L2-foot = 5). n.s. = not significant, ** $p < 0.01$, *** $p < 0.001$

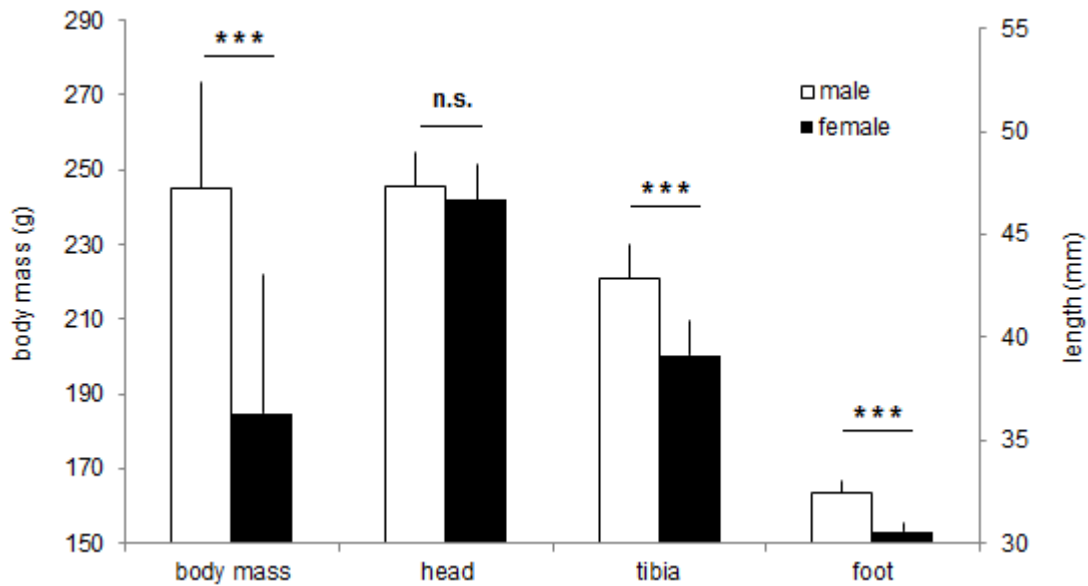


Fig. 7. Morphometric parameters (means \pm SD) of males and females at prehibernation phase (sample sizes: males-body mass, head and tibia = 10, females-body mass, head and tibia = 5, males-foot = 7, females-foot = 4). n.s. = not significant, *** $p < 0.001$

Discussion

Common hamsters usually have up to three litters per season (Endres, 2004; Franceschini-Zink and Millesi, 2008; Weinhold and Kayser, 2000). Earlier studies in Vienna showed, that most females raised two litters per season, few females only one, and three litter were observed rather exceptionally (Franceschini-Zink and Millesi, 2008; Franceschini and Millesi, 2005). These results corresponded to those in our study period, in that only two females had third litters, but due to low sample size we had to exclude them from analyses.

We found no significant differences in litter size between females' first and second litters. This is in contrast to other studies at similar study sites in Vienna, showing that usually first litters contained significantly more offspring than second ones (Franceschini-Zink and Millesi, 2008). However, in a year with delayed vernal emergence due to harsh weather conditions, the opposite situation was found (Hufnagl et al., 2011). Females reproduced later in the season, had lower overall reproductive output and second litters had more offspring than first ones.

The range of 4 – 12 pups per litter in our study was similar to findings in Vienna (Franceschini-Zink and Millesi, 2008; Franceschini and Millesi, 2005) and other studies (Endres, 2004; Vohralik, 1974). In our study the first litters emerged between May 25th and June 23rd and second litter juveniles emerged during a period of six days after July 28th. Juveniles' emergence dates were similar in earlier years in Vienna. Based on these previous observations, reproductive timing and output in our study period can be described as unexceptional for Common hamsters in Vienna.

The most intriguing result of our study was that second litter pups were larger and heavier than first litter ones at natal emergence and this difference persisted at least until four weeks thereafter.

Considering the time constraints late born juvenile hamsters face, this conditional advance is assumed to be adaptive, increasing the chances for these individuals to survive overwinter despite having less time to prepare for the hibernation period. In the Uinta ground squirrel (*Urocitellus armatus*), Rieger (1996) showed that offspring born later in the season was heavier at weaning and that body mass at weaning was positively correlated with body mass shortly before hibernation. Similar findings have been described in Edible dormice (*Glis glis*) (Pilastro et al., 1994). A higher body mass at hibernation onset led to an increased winter survival rate in Uinta ground squirrels

(Rieger, 1996) and Edible dormice (Pilastro et al., 1994) as well as in Yellow-bellied marmots (*Marmota flaviventris*) (Armitage et al., 1976).

Large litter size is known to negatively affect body mass or postnatal growth rate in species of Cricetidae like the Townsend's vole (*Peromyscus polionotus*) (Kaufman and Kaufman, 1987) and Syrian hamster (*Mesocricetus auratus*) (Guerra and Nunes, 2001) or other hibernating rodents like the European (*Spermophilus citellus*) (Huber et al., 2001) and Columbian ground-squirrel (*Urocitellus columbianus*) (Neuhaus, 2000), however in our study we found no effects of litter size on body mass or size.

We also found no differences between first and second litters pups' age at natal emergence. Therefore an age effect can be excluded.

In course of the season females' ability to invest in reproduction may decrease due to increasing energetic constraints. In contrast to that our results indicate higher maternal investment per pup in second litters because these juveniles had higher body mass and larger size than those of first litters at the same age.

Another explanation could be differences in the quality or quantity of food hoards in the natal burrow. Females carry food into the burrow throughout the active season and usually feed underground (Siutz et al., 2012). Considering the fact that juvenile Common hamsters can start to feed on solid food stored in the burrow at the age of 6 days (Eibl-Eibesfeldt, 1953), seasonal changes in available food sources (Hufnagl, 2009) may affect postnatal growth rates. As we have no information on food hoards we cannot exclude such an effect; however it seems unlikely that food quality had increased from May to July in the study area.

We therefore presume that the better condition of second litter pups during the first weeks post-emergence was caused by higher maternal investment in later born offspring compared to earlier ones.

As our first measurements were taken at natal emergence, we cannot answer the question if the differences between first and second litters already existed in utero, at birth, or developed during the pre-emergence period in the breeding burrow.

We decided to pool the individual values of first and second litters respectively, after having performed a linear model with the mean values of the litters as response variable. Based on this result we can exclude that the differences were due to litter effects.

Unfortunately, we were not able to calculate the pups' body fat content at natal emergence, because the morphometric method is so far not validated for this age class. Four weeks after natal emergence, however, body fat content was found to be affected by litter size in that body fat decreased with litter size. This effect was found both in first and second litter pups. Although the pups were already weaned at this time, the strong litter size effect suggests that this relationship was determined during lactation.

Our suggestion to integrate both results, larger and heavier pups in second litters and higher body fat content in litters containing fewer pups, is higher maternal investment in second litter pups via more frequent lactation, and secondly, the higher body fat in smaller litters could have been generated by the mothers' milk fat content. In mammals it is known that the milk fat content increases with decreasing pressure in the mammary gland lumina (Daly et al., 1993; Pflumm and Pflumm-Eisbrenner, 1989). A smaller litter, meaning fewer pups, may have suckled more slowly, thereby prolonging the duration of lactation per suckling event, and increasing the fat content of the milk, which could have caused a higher body fat content in pups of smaller litters.

Four weeks after natal emergence second litter juveniles were still heavier and larger than first litter ones. During these first four weeks following natal emergence first and second litter males (we had insufficient data of females) differed in growth rates. During the first week after natal emergence first litter males gained body mass faster than second litter ones. During the first 14 days after natal emergence first litter males had higher growth rates in head and tibia than second litter ones. Although Common hamster juveniles are weaned at or shortly after natal emergence, the lactation duration after natal emergence differed between the litters in our study period. In European ground squirrels it has been shown (Huber et al., 2001) that lactation duration increased with litter size. In our study juveniles were lactated until up to a week post emergence, however, we found no evidence for a longer lactation period in first litters. An alternative explanation could be seasonal differences in food quality, but this was not investigated in our study.

Shortly before immergence into their hibernacula first litter juveniles were heavier, fatter and larger in head and tibia than second litter ones. This was not surprising considering that they had two and a half times more time to grow and prepare for the winter. The conditional advance during the first weeks did not enable the later born pups to

compensate the temporal deficits but still could increase their chances to survive over winter.

At natal emergence we found no sexual dimorphism, which corresponds, except for the hind foot, to the results of Vohralík (Vohralík, 1975). This result indicates similar maternal investment in male and female offspring. Four weeks after natal emergence males were heavier and larger in tibia and foot than females. These findings support the commonly known sexual dimorphism (Niethammer, 1982; Weinhold and Kayser, 2000) appearing at the age of 3 - 7 weeks. Shortly before hibernation males were heavier and larger than females, but like four weeks post emergence, there were no differences in head length. In addition to the known sex differences in body mass and size, we have previously shown sexual dimorphism in body fat content before hibernation in adult and juvenile Common hamsters (Siutz et al., 2012).

Although we did not include third litters in our study, our small data set indicates, that third litter juveniles are similar in size and weight to first litter juveniles at natal emergence. Due to natal dispersal and relatively high juvenile mortality rates in this species, data allowing to compare overwinter survival rates between early and late born offspring are lacking. Nonetheless our findings could have an impact on the management plans to protect this endangered species (Eppink and Wätzold, 2007; La Haye et al., 2010; Weinhold, 2008).

Zusammenfassung

Der Feldhamster gilt als fakultativer Winterschläfer, mit einer Reproduktionsrate von bis zu drei Würfen pro Saison. Je später die Jungtiere im Jahr geboren werden, desto größer sind die zeitlichen Engpässe für Wachstum und die Vorbereitung auf den Winter. Das Ziel dieser Studie war Körpergewicht, Körperfettgehalt, Kopf-, Tibia- und Fußlänge bei Jungtieren aus ersten und zweiten Würfen der Saison beim ersten Auftauchen aus dem Bau, vier Wochen danach und kurz vor Beginn der Winterschlafperiode zu vergleichen. Mögliche Einflüsse von Geschlecht oder Wurfgröße wurden dabei überprüft. Die Untersuchungen wurden an einer wildlebenden Feldhamsterpopulation im urbanen Lebensraum von Wien, Österreich, durchgeführt. Fang-Wiederfang-Techniken wurden angewandt um Geschlecht und Alter, sowie die morphometrischen Parameter zu erheben. Der Körperfettanteil wurde mittels eines Multiple-Regression-Modells errechnet, welches sich auf die gemessenen morphometrischen Parameter stützte. Zum Zeitpunkt des ersten Auftauchens aus dem Bau waren Jungtiere aus zweiten Würfen deutlich schwerer und größer als Jungtiere aus ersten Würfen. Obwohl die Jungtiere aus ersten Würfen während den ersten beiden Wochen nach dem Auftauchen höhere Wachstumsraten zeigten, konnten sie den Vorsprung der Jungen aus zweiten Würfen auch bis vier Wochen nach dem Auftauchen nicht einholen. Der Körperfettgehalt vier Wochen nach dem Auftauchen aus dem Wurfbau stand in Beziehung zur Wurfgröße, indem Jungtiere aus kleineren Würfen einen höheren Körperfettgehalt aufwiesen als jene aus größeren. Kurz vor ihrem Rückzug in den Winterschlaf-Bau waren die Jungen aus ersten Würfen, nach einer zweieinhalb mal so langen Saison, größer, schwerer und fetter als Jungtiere aus zweiten Würfen. Geschlechtsunterschiede in Größe und Gewicht konnten erstmals vier Wochen nach dem erstmaligen Verlassen des Wurfbaus festgestellt werden, womit gezeigt werden konnte, dass sich der Geschlechtsdimorphismus beim Feldhamster in dieser Zeit entwickelt und nicht bereits bei der Geburt oder zur Zeit der Entwöhnung vorliegt. Der bessere konditionelle Zustand später geborener Jungtiere beim Auftauchen ermöglichte ihnen zwar nicht den Zeitvorteil früher geborener Jungen auszugleichen, könnte aber dennoch die Auswirkungen des zeitlichen Defizits verringern und damit ihre Überlebenschancen für den ersten Winter erhöhen.

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