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Common hamsters (*Cricetus cricetus*)“

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TABLE OF CONTENT

ABSTRACT	1
INTRODUCTION	3
MATERIAL & METHODS	7
STUDY SITE	7
FIELD TECHNIQUES	7
FOOD SUPPLEMENTS	8
BODY FAT PROPORTION	9
STATISTICS	9
RESULTS	10
JUVENILE BODY MASS, BODY FAT PROPORTIONS AND MORPHOMETRIC PARAMETERS	10
JUVENILE FEMALES	11
DISCUSSION	15
REFERENCES	22
APPENDIX	29
ZUSAMMENFASSUNG	29

Abstract

Energy-availability is often limited, especially in seasonal environments when food quality and quantity is changing throughout the year. To ensure overwinter-survival the animals have to build up energy reserves either internally as body fat or externally in the form of food hoards. The Common hamster (*Cricetus cricetus*) – a facultative hibernating rodent – combines both strategies. Moreover, the Common hamster has a prolonged reproductive period (April–August) and shows a high reproductive potential: one female can have up to three litters per season with one to nine pups per litter. The juveniles are weaned when they are ca. 25 days old and leave the natal burrow to find their own one within the next five weeks. Before hibernation onset, juvenile hamsters have to grow, build up food hoards and body fat reserves – a challenge in time and energy management. Hence, the question of the present study was, if food supplements offered to juvenile hamsters shortly after weaning could positively affect their development.

Data-collection lasted from March until November 2014. Each focal juvenile received 200 g sunflower seeds post weaning. The hamsters were live-trapped and capture-mark-recapture techniques were applied to monitor body mass and other morphometric parameters. Based on these the proportion of body fat was calculated by using a validated non-invasive method. Two weeks after supplementation body mass increase rates were higher in supplemented juveniles than in unsupplemented ones, but later in season no differences were found. Body mass, body fat, body fat increase rates, and structural growth rates did not differ between supplied and control animals. However, in supplemented female juveniles body mass and body fat increase rates were higher than in control animals of same age and sex during the first two weeks after supplementation. Later in season these differences disappeared. The low sample size in juvenile males did not allow a separate analysis for males.

The results indicate that the juveniles consumed the supplied food shortly after provision (at least partly) as reflected in higher body mass and body fat increase rates. As structural growth rates did not differ between supplemented and control individuals, the provided food appeared to be mainly accumulated in body fat. This is not surprising as sunflower seeds contain high amount of polyunsaturated fatty acids. Considering the high population density at our study site and personal observations, we assume that at least in some cases

the food stores of our focal animals were pilfered by conspecifics which could explain the short-term supplementation effect.

Determining the optimal seasonal timing for food supplementation in free-ranging Common hamsters is a challenging task and basic knowledge, like presented in the current study, is urgently needed to successfully implement management plans to protect this endangered species.

Introduction

The evolution of life histories and the role of trade-offs for the development of different traits has been frequently discussed (e.g. reviewed by Stearns 1976). According to Stearns (1989) trade-offs exist both at the genotypic and phenotypic level. The latter includes physiological and developmental mechanisms involved in reproduction, growth, maintenance, energy storage and survival (Stearns 1989).

Considering energy limitation, the optimal balance of energy supply for these functions is of crucial importance (Stearns 1989, Noordwijk & de Jong 1986, Speakman 2008). Moreover, the potential for energy allocation can vary especially in seasonal environments as food quality and quantity change throughout the year. In consequence, the animals have to cope with food shortage during winter combined with increased thermoregulatory costs which require specific adaptations (Humphries et al. 2003a, Ruf et al. 2012). In order to survive winter energy reserves have to build up by the animals – a challenge that is often more severe for juveniles than for older individuals (Nunes & Holekamp 1996, Lenihan & van Vuren 1996, Neuhaus 2000, Pluch et al. 2013).

Energy reserves can be built up either internally as body fat or externally in the form of food hoards (Humphries et al. 2003b, Siutz et al. 2012, Day & Bartness 2003, Buck & Barnes 1999). The Common hamster (*Cricetus cricetus*), a ground-dwelling rodent species, combines both strategies and accumulates body fat as well as stores food in its burrow in preparation for hibernation (Nechay 2000, Weinhold & Kayser 2006). In contrast to many other hibernators, the Common hamster has a prolonged reproductive period lasting from April to August and shows a high reproductive potential: Females can have up to three litters per season with one to nine pups per litter (Petzsch 1937, Grulich 1986, Franceschini & Millesi 2005). Moreover, a postpartum oestrus has been documented in several cases, implying that a female can be pregnant while still lactating the current litter (Grulich 1986, Franceschini-Zink & Millesi 2008). The gestation period can vary from 17 to 37 days (Weinhold & Kayser 2006). After another 25 days in the natal burrow, the juveniles start to be active aboveground and are weaned shortly thereafter (Eibl-Eibesfeldt 1953).

However, in a more recent study done by Weissinger (2013) a high variation in the juveniles' natal emergence from 10 up to 33 days has been reported. Despite this high variation in age, body mass at natal emergence was similar among juveniles leading to the conclusion that a

sufficient body mass has to be reached before the juveniles leave the breeding burrow for the first time (Weissinger 2013).

It is well documented, that the juveniles stay at the natal burrow for up to 40 days, whereas the mother is often leaving the burrow when the juveniles are 30 days old (Weinhold & Kayser 2006, Seluga et al. 1996, Kayser & Stubbe 2003). However, Weissinger (2013) could show that the phase of common burrow use was highly variable and ranged from 10 to 36 days, but surprisingly was not correlated to lactation duration. Furthermore, the larger the litter size was the longer the females stayed with their pups after natal emergence (Weissinger 2013). With an age of 60 days most juveniles had settled at their own burrow: ca. 45 % build the burrow by them-selves, while the majority takes over an abandoned burrow (Seluga et al. 1996). The latter makes sense, as these burrows can be seen as an indicator for a high-quality habitat other hamsters colonized before. Moreover, the juveniles save time and energy which they otherwise had to invest for building a new burrow (Seluga et al. 1996).

Time and energy management are essential for the juveniles' survival: they have to grow and prepare for hibernation, including finding a suitable hibernaculum, building up food hoards and gaining body fat (Seluga et al. 1996, Weinhold & Kayser 2006, Siutz & Millesi 2012). However, the later a hamster is born in year the fewer time is left to accomplish these tasks. Hence, early-born juveniles have an advantage compared to late-born ones. This is supported by many studies, reporting reduced survival chances for late-born juveniles (Seluga et al. 1996, Weinhold & Kayser 2006, Kirn 2004, Siutz & Millesi 2012).

Considering the proportional distribution of age groups in a Common hamster population it becomes obvious why the survival of the juveniles is of crucial importance for the populations' viability: At emergence in spring only one third of the population consists of adult animals (hibernate at least two years) and two third makes the "yearlings", which means the juveniles from the previous year (Weinhold & Kayser 2006). Consequently, a low reproductive output and juvenile survival in one year highly affects the reproductive output in the following season. Thus reducing mortality rates of juvenile hamsters might be a promising approach to counteract the species' markedly decline that started in the second half of the 20th century and already resulting in a highly endangered status in several Western European countries (Weinhold 2008, Meinig et al. 2014, La Haye et al. 2014).

Many authors relate the Common hamsters' decline to modern monocultural farming in combination with habitat loss and fragmentation (Nechay 2000, Kayser & Stubbe 2003, Weinhold & Kayser 2006, Weinhold 2008, La Hayne et al. 2014). One of the main problems is the high mortality rate (50 % to 61.5 %) of the hamsters during winter often due to starvation (Kayser et al. 2003, Wendt 1991). Today's intensive agriculture includes immediate ploughing after an exhaustive harvest with highly efficient machines. Hence, in these areas the hamsters often are chanceless to collect enough storable food items in preparation for hibernation (Kayser et al. 2003, Ulbrich & Kayser 2004, Weinhold 2008). Consequently, one possible method to increase survival rates in Common hamster populations is to improve food availability. The positive effect of less intensive harvest and late harvesting has already been documented in a number of studies (Kayser & Stubbe 2003, La Haye et al. 2014, Ulbrich & Kayser 2004). However, to investigate potential effects of food availability via individual food supplementation might be an efficient experimental approach.

Several studies have investigated effects of supplementing food to different kind of animals. In reptiles food supplementation to lizards (Licht 1974, Guyer 1988, Olsson & Shine 1997) and snakes (Taylor et al. 2005, Wasko & Sasa 2012) led to an increase of body mass but mainly to an improved reproductive output. A positive effect on reproduction could also be found when supporting birds with extra-food (Schoech et al. 2004, Aparicio & Bonal 2002). However, probably most studies about food limitation and the effects of food supplementation were carried out in small mammal species, especially rodents.

Boutin (1990) reviewed 55 cases in which rodents received extra-food under field conditions. Only three of the reviewed studies failed to measure a response by rodents to a food supplementation at all (Boutin 1990). However, in 43 % of the cited studies by Boutin (1990) positive effects on reproductive parameters (litter size, length of the reproductive period, breeding intensity) could be documented after food supply. Furthermore, in 9 % the authors measured an increase of the juveniles' body weight and in 31 % the extra-food was positively related to juvenile survival. Moreover, changes in population dynamics after food supplementation were also reported. For example, Doonan & Slade (1995) found that a population of Cotton rats was two times higher after a one-year food supplementation in comparison to the control population. Byrom et al. 2000 even reported a fourfold increase of populations' density in Arctic ground squirrels as a result after a five-year study.

All in all the outcomes of the cited studies could be promising strategies with regard to maintaining Common hamster populations. As Common hamsters' reproductive strategies are clearly opportunistic, sufficient juvenile survival rates are essential to prevent the extinction of populations (Weinhold & Kayser 2006). Hence, in this study juvenile hamsters were chosen to investigate the effects of food supplementation. The following question was addressed in this study:

Do food supplements given to juvenile Common hamsters shortly after weaning affect juvenile development?

To document juvenile development we measured body mass, the proportion of body fat and morphometric parameters for monitoring structural growth. We expected that the extra-food would positively affect juvenile development, reflected in increased body mass, proportion of body fat and growth rates in supplemented compared to control individuals.

Material & Methods

Study site

The data was collected in a 2.25 ha sized area located in the south of Vienna, Austria (48°10'30" N, 16°20'56" E). A population of Common hamsters (*Cricetus cricetus*) inhabits a park-like terrain consisting primarily of plain grassland, some bushes and trees. The area is associated with a hospital complex bounded by chain-link fences and walls. To allow dispersal from and to other populations, the walls are equipped with tubes on ground level. The hamsters in the area are habituated to human activity, neither the presence of humans nor the hospital traffic provoked escape reactions (Grimm, personal observations).

The data collection started in March 2014 and lasted until the end of the hamsters' active season in November 2014. In general, hamsters are active above ground during the early morning and in the evening (Schmelzer & Millesi 2003, Schmelzer 2005). As the study site was associated with a highly frequented hospital complex life-trapping was primarily conducted in the morning from 5:30 a.m. to 11:00 a.m. four times per week. We tried to capture each focal animal once per week which was not always successful.

Field techniques

The hamsters were captured using Tomahawk live-traps baited with peanut butter. The traps were covered with a piece of cloth to calm the animals after being captured and to protect them against the sun. Within a short period of time (maximum of ten minutes) the hamster was released into a dark colored cone shaped cotton sack. As Velcro® fasteners were sewn in at the side of the sack it was possible to investigate the animals' abdominal region without anesthesia (Franceschini et al. 2007).

The following parameters were documented at each capture event: date, time, ambient temperature, weather conditions, location of the trap, sex, age, body mass, structural data (head-, tibia- and foot-length), as well as reproductive status. For determining the reproductive status in males, testes width was measured (Franceschini et al. 2007). In females, teat and vulva development were categorized on a four point scale. Thus teat size was classified from nearly invisible (0), visible and pale (1), heightened and red (2) to swollen with milk rests (3). Whereas vulva development was scaled from completely closed (0), small opened (1), widely opened (2) to wide opened with bloody mucus (3) (Franceschini et al.

2007). For calculating the juveniles' birth date it was necessary to document gestation (increase in body mass combined with teat swelling) and parturition/ lactation onset (rapid body mass loss paralleled with swollen teats sometimes with milk remains) in the focal females (Franceschini et al. 2007). By monitoring these parameters juvenile natal emergence could be expected about three weeks after parturition (Eibl-Eibesfeldt 1953, Kayser & Stubbe 2003). The breeding burrows of lactating females were then frequently checked and juveniles were captured as soon as possible after first emergence from the natal burrow. Thereby, emerging juveniles could be allocated to a particular mother and were individually marked. Furthermore, weaning was determined based on decreasing teat size and juveniles feeding above ground (Franceschini et al. 2007).

For individual identification the hamsters' fur was marked with unique symbols by using a commercial hair dye. Males were marked with black and females with red symbols. All juveniles received their mothers' symbol plus extra dots in a defined scheme: on the lower legs and lateral behind the front legs. The symbols represented the order the juveniles of one litter were captured for the first time. These optical marks were helpful for long distance observations. Moreover subcutaneously injected transponders (PIT-tag, Data Mars Company) were used to permanently mark the hamsters. The City of Vienna (MA22, 2546/08, 1216/09, 2484/10), and the Ethical Committee for Animal Welfare (GZ BMWF-66.006/0020-II/3b/2012) approved all procedures performed on the animals.

After the investigation which lasted for about five to ten minutes the hamsters were immediately released in front of their burrows, whereas small juveniles were put directly into the mother-burrow to guarantee a direct orientation in well-known surroundings.

Food supplements

In this study early-born juvenile hamsters (day of birth between late-April and mid-June) were provided with high-energy food supplements in the form of unpeeled sunflower seeds. Sunflower seeds were chosen as they contain polyunsaturated fatty acids (23.1 g per 100 g, USDA National Nutrient Database) which are known to have a positive impact on hibernation (Ruf & Arnold 2008). Feeding experiments in the laboratory (Wendt 1991, Mikovits 2013) showed that the amount of food for winter survival varied depending on individual hibernation patterns but could be estimated with 1 to 1.5 kg per individual. Furthermore, a previous study by Siutz (unpub. data) about food supplements in free-living hamsters

revealed that the amount of supplied food must be chosen carefully: if offered too much, the animals stopped caching the extra-food.

Based on this information, each focal juvenile that had been weaned and had already found its own burrow received 200 g of seeds in a single serving. The extra-food was placed directly in front of the animals' burrow. The hamsters were continuously observed by using binoculars from long distance (ca. 20 m) until all seeds had been cached. Thus it was possible to ensure that only the focal animal received the supplements.

The data of supplied and non-supplied juveniles of the same sex and age were compared weekly after treatment and at prehibernation. *Prehibernation* was the period before the juveniles immersed into their hibernacula, lasting from October until November. The juveniles' last capture during this period was then recorded as "at prehibernation".

We did not compare data from litter-siblings, because an insufficient number of litter-siblings were successfully tracked throughout the active season. As our study site was surrounded by equally suitable areas a lot of juveniles dispersed after weaning. Thus, only a few juveniles could be supplied and monitored until emergence into the hibernacula. However, none of them were litter-siblings.

Body fat proportion

The proportion of body fat was calculated based on morphometric parameters (body mass, head-, tibia- and foot-length) using a validated multiple regression model (Siutz et al. 2012). This non-invasive method easily allowed computing the proportion of body fat in free-living hamsters.

Statistics

The statistical analyses were done using Microsoft Excel 2007 and in SPSS for Windows (PASW Statistics 18). First data distribution was tested for normality by using Shapiro-Wilk tests. In case of normally distributed data Student's *t*-tests were performed; otherwise, Mann-Whitney *U*-tests were applied. Significance values were received from two-tailed statistics. When $p < 0.05$ group-differences were assumed statistically significant. All tested samples were independent as the focal animals were no litter-siblings and the hamsters were treated differently (supplied or non-supplied animals).

Results

In the season 2014, the first hamster was captured on 26th March, the last one on 24th November. In total, 301 hamsters were marked in the study area: 74 adults (43 males and 31 females) and 227 juveniles (126 males and 101 females). This represents a density of approximately 134 individuals per ha. Adult density in the study area was 33 hamsters per ha.

Eight juvenile early-born hamsters (2 males, 6 females, born between late-April and mid-June) were provided with extra-food. All juveniles originated from females' first litters in the season of 2014. Developmental parameters of supplied animals were compared to those of non-supplied control animals in weekly intervals. The control group consisted of juveniles of the same age and sex. The sample size differed between the intervals and data was tested statistically after one, two, three, four, six and nine weeks from the supply-day, as well as at prehibernation.

Juvenile body mass, body fat proportions and morphometric parameters

The **body mass increase** rate per day differed significantly between supplied and control animals in the second week after treatment. Supplied animals had a higher body mass increase rate compared to the control group (Tab. 1). After one, three, four, six and nine week(s) from the supply-day, there were no significant differences in the body mass changes between the groups (Tab. 1).

Body fat increase rates showed no significant differences between supplied and control animals in any of the analyzed weeks (Tab. 1).

Morphometric parameters (head-, tibia- and foot-length) did not differ significantly between both groups in any of the sampling intervals (Tab. 2).

Tab. 1: Body mass and body fat increase rates (per day) in supplied and control juvenile Common hamsters after one, two, three, four, six and nine weeks from the supply-day (mean \pm SD).

Week(s) after supply	Body mass (g/d)		Body fat (%/d)	
	Supplied	Control	Supplied	Control
1 (n = 6/6)	1.40 \pm 1.15	0.18 \pm 2.16	0.07 \pm 0.40	-0.24 \pm 0.54
	$t = 1.22$; $P = 0.25$		$t = 1.12$; $P = 0.29$	
2 (n = 4/4)	0.58 \pm 0.61	-0.75 \pm 0.68	-0.05 \pm 0.24	-0.31 \pm 0.16
	$t = 2.93$; $P = 0.03$		$t = 1.86$; $P = 0.11$	
3 (n = 6/6)	0.54 \pm 0.78	1.26 \pm 0.57	-0.05 \pm 0.18	0.13 \pm 0.24
	$t = -1.82$; $P = 0.10$		$t = -1.52$; $P = 0.16$	
4 (n = 3/3)	0.44 \pm 0.15	0.46 \pm 0.89	-0.01 \pm 0.06	-0.03 \pm 0.18
	$t = -0.04$; $P = 0.97$		$t = 0.15$; $P = 0.89$	
6 (n = 4/4)	0.73 \pm 0.60	1.18 \pm 0.52	0.05 \pm 0.14	0.08 \pm 0.21
	$t = -1.13$; $P = 0.30$		$t = -0.29$; $P = 0.78$	
9 (n = 3/3)	1.13 \pm 0.51	1.51 \pm 0.55	0.12 \pm 0.09	0.10 \pm 0.08
	$t = -0.88$; $P = 0.43$		$t = 0.36$; $P = 0.74$	

Tab. 2: Head-, tibia- and foot-length increase rates (mm/d) in supplied and control juvenile Common hamsters after one, two, three, four, six and nine weeks from the supply-day (mean \pm SD).

Week(s) after supply	Head (mm/d)		Tibia (mm/d)		Foot (mm/d)	
	Supplied	Control	Supplied	Control	Supplied	Control
1 (n = 6/6)	0.09 \pm 0.08	0.11 \pm 0.12	0.04 \pm 0.05	0.16 \pm 0.18	0.01 \pm 0.02	0.01 \pm 0.01
	$t = -0.36$; $P = 0.73$		$Z = -1.86$; $P = 0.07$		$Z = -0.19$; $P = 0.85$	
2 (n = 4/4)	0.06 \pm 0.05	0.06 \pm 0.04	0.05 \pm 0.04	0.03 \pm 0.04	0.01 \pm 0.01	0.01 \pm 0.01
	$t = 0.21$; $P = 0.84$		$Z = -0.58$; $P = 0.56$		$Z = -0.66$; $P = 0.51$	
3 (n = 6/6)	0.07 \pm 0.05	0.05 \pm 0.07	0.06 \pm 0.04	0.05 \pm 0.04	0.02 \pm 0.02	0.01 \pm 0.01
	$t = 0.56$; $P = 0.59$		$t = 0.36$; $P = 0.73$		$Z = -1.36$; $P = 0.17$	
4 (n = 3/3)	0.04 \pm 0.03	0.03 \pm 0.05	0.01 \pm 0.07	0.06 \pm 0.07	0.01 \pm 0.00	0.00 \pm 0.00
	$t = 0.19$; $P = 0.86$		$t = -1.13$; $P = 0.38$		$t = 1.47$; $P = 0.21$	
6 (n = 4/4)	0.04 \pm 0.02	0.06 \pm 0.07	0.03 \pm 0.02	0.06 \pm 0.07	0.01 \pm 0.00	0.01 \pm 0.01
	$t = -0.73$; $P = 0.52$		$t = -0.81$; $P = 0.47$		$Z = -0.87$; $P = 0.38$	
9 (n = 3/3)	0.03 \pm 0.01	0.07 \pm 0.06	0.02 \pm 0.01	0.08 \pm 0.01	0.01 \pm 0.00	0.01 \pm 0.01
	$t = -1.19$; $P = 0.30$		$Z = -1.96$; $P = 0.10$		$t = 0.03$; $P = 0.98$	

Juvenile females

Due to the low sample size in juvenile males the analyses was further restricted to female juveniles. Juvenile females with and without additional food were compared one, two, three and six weeks after the food supply and at prehibernation.

In the first week after supply, **body mass increase** rates of supplied females tended to be higher than that of control ones (Fig. 1). Two weeks after supply, juvenile females which

received extra-food had significantly higher body mass increase rates than control females (Fig. 1).

The body mass increase rates three weeks (supplied: $0.71 \text{ g/d} \pm 0.74$, control: $1.29 \text{ g/d} \pm 0.63$; $Z = -1.15$, $P = 0.25$, $n = 5/5$) and six weeks (supplied: $0.52 \text{ g/d} \pm 0.52$, control: $0.96 \text{ g/d} \pm 0.36$; $t = -1.20$, $P = 0.30$, $n = 3/3$) after supplementation did not differ significantly between the female groups.

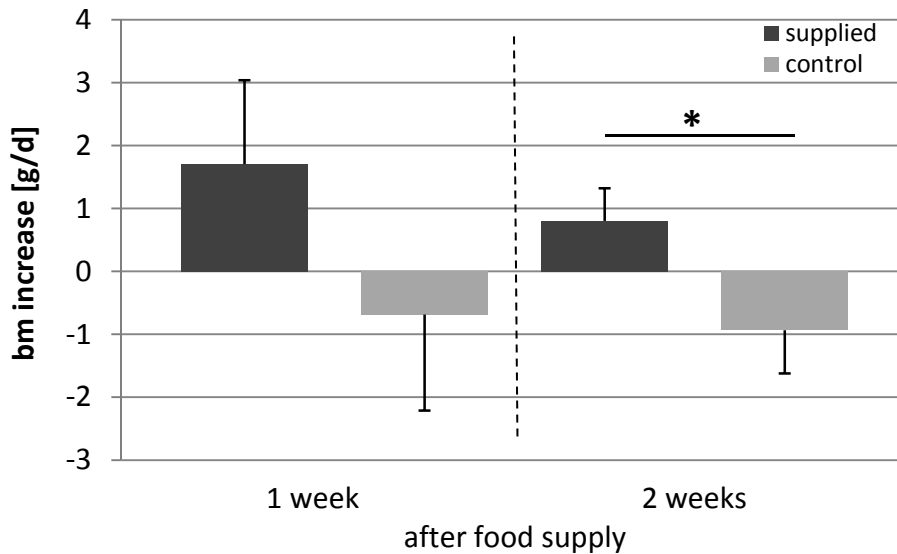


Fig. 1: Body mass (bm) increase per day (mean \pm SD) in supplied and non-supplied (control) female juvenile Common hamsters after one and two weeks from the supply-day ($t_1 = 2.36$, $P_1 = 0.06$, $n_1 = 6/6$; $t_2 = 3.50$, $P_2 = 0.03$, $n_2 = 3/3$).

Compared to the control animals, the **body fat increase** rates of supplied females were significantly higher in the first week after supply (Fig. 2). There was also a trend after two weeks showing lower body fat increase rates in control females (Fig. 2).

Three weeks (supplied: $0.00 \text{ %/d} \pm 0.13$, control: $0.17 \text{ %/d} \pm 0.18$; $t = -1.69$, $P = 0.13$, $n = 5/5$) and six weeks (supplied: $0.02 \text{ %/d} \pm 0.15$, control: $0.09 \text{ %/d} \pm 0.25$; $t = -0.46$, $P = 0.67$, $n = 3/3$) after the supply-day the body fat increase rate differed not significantly between the two female groups.

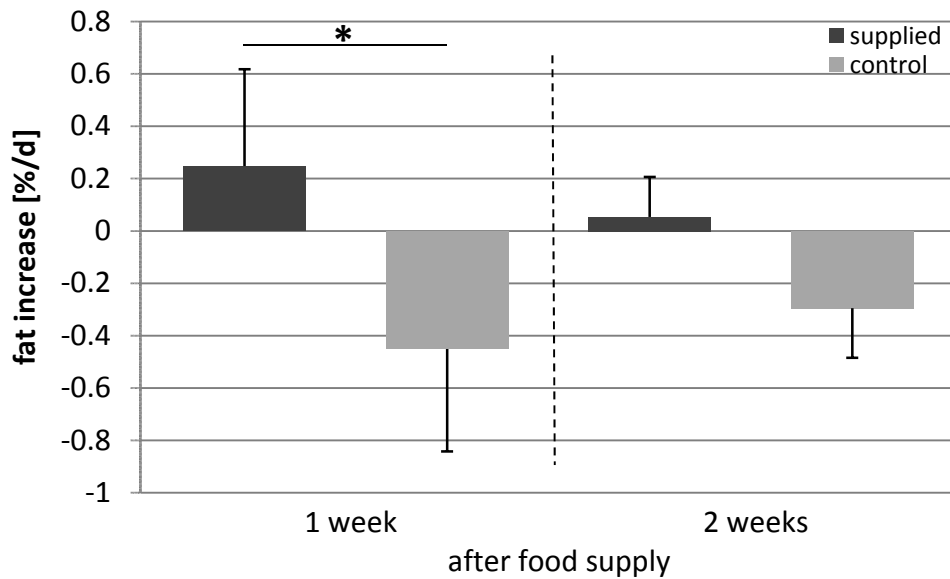


Fig. 2: Body fat increase per day (mean \pm SD) in supplied and non-supplied (control) female juvenile common hamsters after one and two weeks from the supply-day ($t_1 = 2.60$, $P_1 = 0.04$, $n_1 = 6/6$; $t_2 = 2.49$, $P_2 = 0.07$, $n_2 = 3/3$).

Morphometric parameters did not differ significantly between supplied and non-supplied female juveniles in any of the analyzed weeks. In both groups the increase rates in head-, tibia- and foot-length were almost equal.

At the end of the active season (**prehibernation**) neither body mass increase (Fig. 3) nor body fat increase rates (supplied: $0.01\% \pm 0.12$; control: $0.15\% \pm 0.121$; $t = -1.90$, $P = 0.09$, $n = 5/5$) differed significantly between the two groups.

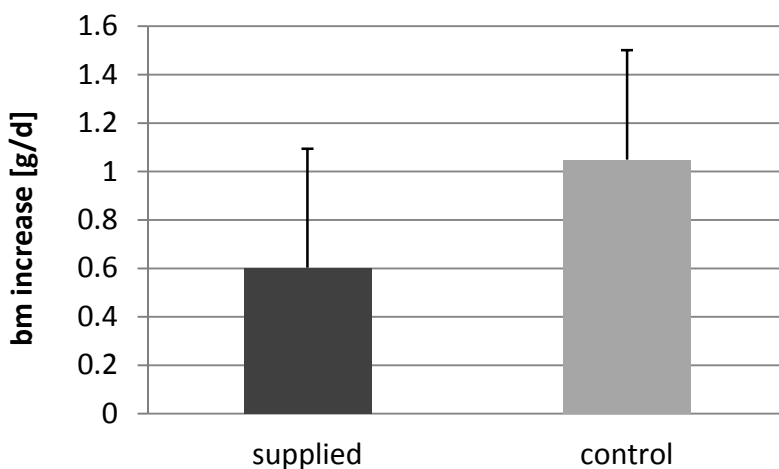


Fig. 3: Body mass (bm) increase rates (mean + SD) in supplied and control female juvenile Common hamsters from the supply-day until prehibernation ($t = -1.49$, $P = 0.17$, $n = 5/5$).

Furthermore, at prehibernation the total body mass and body fat content were not significantly different between the supplemented and unsupplemented female juveniles (Fig. 4a, b).

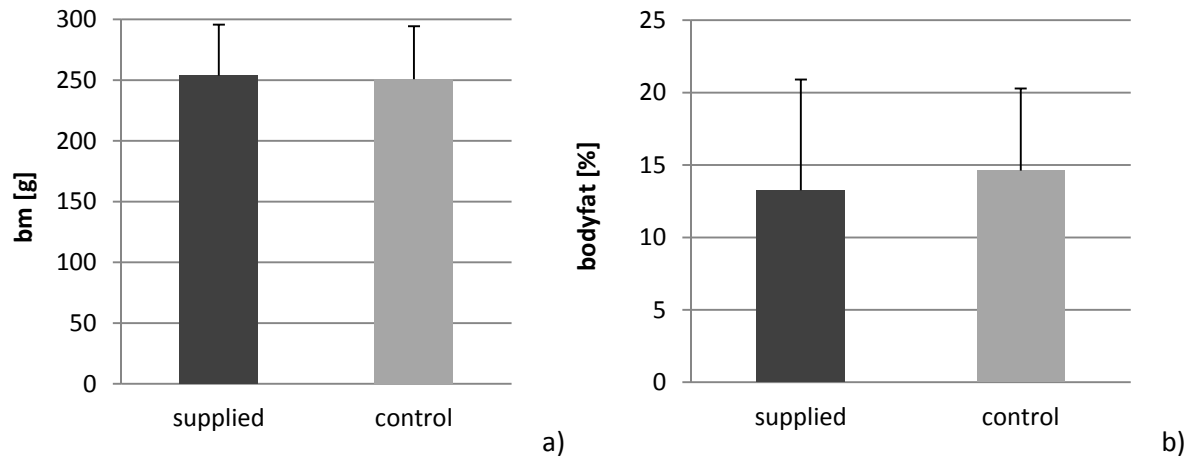


Fig. 4: a) Body mass (bm) and b) body fat content (bf) (mean + SD) in supplied and control female juvenile Common hamsters at prehibernation ($t_{bm} = 0.11$, $P_{bm} = 0.91$; $t_{bf} = -0.32$, $P_{bf} = 0.76$; $n = 5/5$).

There were no significant differences in the **immersion dates** of female juveniles; both supplied and non-supplied females terminated above ground activity at the same time of year (supplied: 22nd Oct. \pm 16 d; control: 20th Oct. \pm 14 d; $t = 0.23$, $P = 0.82$, $n = 5/10$).

Discussion

At our study site the first hamsters emerged in late March/ early April. Shortly thereafter the mating period started. Most females had one or two litters with six to eight juveniles. Franceschini-Zink & Millesi (2008) monitored a Common hamster population in Vienna over a 3-year period (2003–06) at a study site in close distance to the one of the present study. The data from 2003–05 were consistent: The hamsters emerged around April and the females had one or two litters with one to nine juveniles per litter (Franceschini-Zink & Millesi 2008). Only a few individuals were able to raise a third litter in one season. However, the winter 2005/06 was exceptionally harsh which appeared to affect reproductive timing and output (Hufnagel et al. 2011a). In 2006 the females emerged and mated about two weeks later than in the previous years. Reproductive output was about 50 % lower in 2006 compared to the seasons 2003–05 (Hufnagel et al. 2011a). These results clearly demonstrated the potential influences of environmental factors on the Common hamsters' seasonal timing and reproductive success. As the timing of vernal emergence and reproductive output of our focal individuals in 2014 were similar to those of 2003–05, strong climatic effects as identified in 2006 can be excluded.

We investigated if food supplements provided shortly after weaning affected structural growth and body mass/ body fat accumulation in juvenile Common hamsters.

In fact two weeks after treatment the supplemented animals showed higher body mass increase rates than unsupplemented ones. Interestingly, in juvenile female hamsters we documented differences in body mass increase rates up to two weeks after the food supplementation, but later in season these differences disappeared. Unfortunately, the low sample size in males did not allow separate analyses for male juveniles.

Other authors also reported accelerated body mass gain in juvenile rodents after a food supplementation. For example, McAdam & Boutin (2003) documented higher body mass increase rates in juvenile Red squirrels after food supplementation. Similar results are described by Woods & Armitage (2003) when they provided juvenile marmots with extra food. However, an increase in body mass can be reflected in a gain in body fat and/or in structural growth. Effects of food supplementation on structural growth are rarely described in previous studies: Growth rates were based on body mass changes without measuring

morphometric parameters (reviewed in Boutin 1990). Based on a recently developed and validated non-invasive method we were able to calculate the proportion of body fat using morphometric parameters in free-living hamsters (Siutz et al. 2012). This enabled us to investigate juvenile development in more detail and to distinguish between structural growth and the accumulation of body fat.

Differences in structural growth could not be detected in our study. Head-, tibia- and foot-length growth rates were similar in supplemented and unsupplemented juvenile hamsters. In addition the changes in the proportion of body fat did not differ significantly between the two groups. However, when we analyzed juvenile females separately, we found that body fat increase rates one week after the supplementation were significantly higher in supplemented females than in control individuals. In the second week there was a trend pointing in the same direction: Supplemented females increased body fat while others on average showed a slight decline. These outcomes appeared to be directly linked to the juvenile females' body mass increase rates. Hence, this indicated that higher body mass increase rates in female juveniles reflected body fat accumulation while structural growth rates remained constant.

An explanation for this outcome can probably be found in the nutritional composition of the supplemented food. Sunflower seeds consist to a high amount of fat (51.5 g per 100 g, USDA National Nutrient Database). The body mass increase in the supplemented hamsters indicated that they consumed the extra-food directly (at least partly) and the high-fat diet resulted in higher body fat content potentially serving as important internal energy reserves. Several studies investigated if and how various nutritional compositions in the diet might affect growth rates, reproductive success and survival in different species. In Prairie voles (Cole & Batzli 1978), California voles (Batzli 1986) and Florida scrub-jays (Schoech et al. 2004) a protein-rich diet was reported to be positively related to reproductive success. Moreover, Woods & Armitage (2003) showed that juvenile Yellow-bellied marmots were more likely to survive hibernation when provided with a low-protein diet. Interestingly, another study showed that proteins seem to affect juvenile development: Strauss et al. (2007) found faster structural growth in male juvenile European ground squirrels when provided with a high-protein diet.

However, not only quantity but also quality of dietary fat appeared to play an important role. Especially polyunsaturated fatty acids (PUFAs), which can be found in high amounts in

sunflower seeds (23.1 g per 100 g, USDA National Nutrient Database), seem to be related to enhanced hibernation patterns (e.g. Geiser & Kenagy 1987, Frank 1992, Geiser et al. 1994, Harlow & Frank 2001, Humphries et al. 2003b, Munro et al. 2005). Diets with high levels of PUFAs positively influenced hibernation patterns in several rodent hibernators, like e.g. in Yellow-pine chipmunks (Geiser 1990, Geiser & Kenagy 1987, Geiser et al. 1994), in Golden-mantled ground squirrels (Frank 1992), and Black/ White-tailed prairie dogs (Harlow & Frank 2001). Moreover, it has been shown, that experimental manipulations of dietary lipids altered the lipid composition of body fat (Fawcett & Lyman 1954), tissues and cell membranes in hibernating rodents (Geiser 1990). Nevertheless, the exact mechanism by which PUFAs affect torpor still remains unclear (Munro & Thomas 2004, Ruf & Arnold 2008).

The most surprising outcome of our study is that the positive effects of food supplementation only lasted for a short time period. Already three weeks after supplementation no significant differences between supplemented and control juveniles could be detected. Also later in season and prior to hibernation no differences between the two groups were found. These results raise the question why the effect of the high-fat supplementation only lasted for about two weeks?

One possible explanation is that the supplemented juveniles were not able to monopolize the provided food resources. The population density at our study site with 33 adult hamsters/ ha can be classified as very high (Niethammer 1982, Grulich 1986, Nechay 2000). For agricultural areas an average density of 2.8 to 3.6 hamsters/ ha has been reported (Weidling & Stubbe 1997, Weinhold 1998), while the density of hamsters at our study site was nearly ten times higher. According to Feoktistova et al. (2013) the Common hamster profits from synurbism because in urban habitats the animals have access to food resources existing due to human settlements (e.g. garbage, human stores, vegetable-beds and fruit-trees) and, the animals are less exposed to predators due to human presence. However, in urban environments, areas like gardens, cemeteries, parks, and grassland patches suitable for Common hamsters are rare and limited in size (Feoktistova et al. 2013). In combination with limited dispersal corridors caused by highly frequented roads and buildings acting like dangerous or insurmountable barriers, Common hamster densities can reach high levels in urban habitats. Consequently, increased competition for resources (e.g. home range/ burrows, food and mating partner) occurs, intensifying during summer when the population

reaches its highest level and the weaned juvenile hamsters are searching for suitable burrows and food sources (Weinhold & Kayser 2006).

As we provided the juveniles during the summer months at the populations' highest density level, it is likely that the juvenile hamsters might not have been able to defend the provided food against conspecifics in the long run. Indeed, we occasionally observed other hamsters at burrows of their conspecifics. Furthermore, especially juvenile hamsters frequently were trapped at different burrows. At two events we were able to observe adult hamsters trying to collect the supplements that a juvenile had recently been provided with. These episodes indicate that the supplemented juveniles probably could not monopolize the additional food resources for longer than two weeks. In particular against adult hamsters juveniles are unable to defend their resources. Sometimes the smaller opening of the juveniles' burrow prevents adults from entering burrows of juveniles (Niethammer 1982, Weinhold & Kayser 2006). However, juvenile hamsters mainly take over an abandoned adults' burrow, which have a larger opening and therefore can be easily entered by older individuals (Seluga et al. 1996). Thus it seemed highly possible that especially adult hamsters were able to pilfer the supplemented food from the juveniles.

Another factor that could affect the success of food supplementation is the timing in the respective season. Many studies conducted supplementary feeding shortly before a food-limited time in year (mainly winter). For example, Banks & Dickman (2000) supplied small rodents with extra food prior to winter and during winter resulting in an increase in population density, body mass and reproduction rate. Taitt (1981) reported that late-winter addition of food positively affected a population of deermice, as reflected in the population density, sexual maturity and reproductive output. In obligate hibernators like marmots (Woods & Armitage 2003) and ground squirrels (Bennett 1999) food supplementations resulted in a higher body mass prior to hibernation. Furthermore, Bennett (1999) documented that the supplemented ground squirrels were more likely to survive winter; in marmots this was not the case (Woods & Armitage 2003).

However, Common hamsters are facultative hibernators (Wassmer & Wollnik 1997) and do not depend solely on internal body fat reserves during hibernation, but also rely on food hoards which they build up during the active season (Buck & Barnes 1999, Humphries et al. 2003a, Day & Bartness 2003, Siutz et al. 2012). Over-winter mortality is

relatively high both in adult and juvenile individuals with 50 % (Kayser et al. 2003) to 61.5 % (Wendt 1991) often due to starvation (Weinhold & Kayser 2006, Kayser et al. 2003). Thus caching a sufficient amount of storable food items for the winter period seem to be essential for survival, but can be limited due to time constraints.

Especially the juveniles are confronted with time constraints during their first active season: they have to grow, find a burrow, store food and build up body fat reserves (Seluga et al. 1996, Weinhold & Kayser 2006, Siutz & Millesi 2012). However, chances are not equal for all juveniles. As Common hamsters have the potential to reproduce several times during the active season offspring can be born early and late in season (Grulich 1986, Franceschini-Zink & Millesi 2008). Late-born hamsters have less time to prepare for hibernation often resulting in a poorer body condition before hibernation onset in comparison to early-born ones (Pluch et al. 2013). Moreover, higher energetic demands in late-born juveniles are assumed to be related to higher stress levels determined in these animals, possibly due to intensified food caching associated with prolonged exposure to predators or humans (Siutz & Millesi 2012). The combination of these factors most probably affected the juveniles' mortality rate which is 30 % higher for late born hamsters than for early born ones (Siutz & Millesi 2012). Furthermore, the advantage in time management of early-born juveniles can be possibly reflected in the animals' direct fitness: Even though successful reproductive activity of juvenile hamsters has to be classified as exceptional (Weinhold & Kayser 2006, Weinhold 2008), they are able to reproduce in their first season (Niethammer 1982). Early-born males in good body condition could try to get access to mating partners late in the season, which also is possible for early-born females (Vohralik 1974, Grulich 1986, Nechay 2000). In Vienna, Franceschini (unpub. data) observed two early-born females producing offspring in their first year.

Hence, the timing of food supplementation might be crucial for the effects on the individuals: supplements given early in the season could lead to an increase in body condition whereas supplements provided shortly before hibernation are more likely be used as food stores in the burrows. Both strategies could enhance overwinter-survival of the animals. However, supplements given early in season might additionally include the possibility for early-born juveniles to reproduce in their first year.

We supplied early-born juvenile hamsters early in the season, and our outcomes indicate that the animals invest the extra-energy directly in body condition. We found no evidence

for reproductive activity of the supplemented juveniles. Moreover, shortly before hibernation no differences in body mass and -fat were recorded between the supplemented and control hamsters. In the following season (spring 2015) we recaptured three of the eight supplied juveniles (37.5 %) and four of the eleven control animals (36.4 %). Body mass changes during hibernation did not differ between the two groups, and the analysis of the juveniles' emergence body mass revealed similar results.

Based on these outcomes we cannot infer that the survival of the juveniles was positively influenced by our given food supplements. Previous studies on Common hamsters living in urban habitats in Vienna showed that food resources are available for the hamsters nearly all over the active season (Hufnagel et al. 2011b, Ketzner 2012). Hence, probably all hamsters were able to collect well storable and high nutritive food items (e.g. berries, seeds, and rhizomes) in preparation for hibernation. This might explain why no differences in overwinter-survival rates were detectable.

Furthermore, the amount of supplied food should be considered. We supplied the juveniles with 200 g of sunflower-seeds. This extra-food appears as a small amount in comparison to the food consumption during hibernation (Górecki & Grygielska 1975, Wendt 1991, Nechay 2000). Wendt (1991) estimated a minimum amount of 1–1.5 kg of crops per individual for successful overwinter-survival in the wild. Mikovits (2013) investigated the amount of food juvenile hamsters consuming during hibernation in the climate-chamber, and found a large individual variation in food consumption ranging from ca. 350–1700 g per juvenile hamster. However, we wanted to investigate how an “extra” portion of high-quality food affects the juvenile development during the active season and therefore supplied the hamsters shortly after weaning early in season. Moreover, supplying higher amounts of food includes a higher risk of pilfering by other hamsters while the focal juvenile is caching the food. In this case, individual supplementation as conducted in our study can no longer be guaranteed.

Considering all aspects discussed above, we assume that some juveniles consumed the supplements during the first days after treatment (at least partly), as reflected in the higher body mass/body fat increase rates in the first two weeks after food-supplementation. Moreover, extra-energy seemed to be invested rather in body fat than in morphometric growth, which possibly can be explained by the nutritive composition of sunflower seeds. As

the conditional advantage of supplied juveniles had disappeared during the third week after the treatment, we suppose that the supplied food was either totally consumed or that the remaining were pilfered by conspecifics. Considering the timing and extent of supplementation, the alternative explanation that the extra-food was stored for hibernation appeared unlikely.

Overall, the current study can be viewed as valuable with regard to determining the optimal seasonal timing of food supplements in particular in juvenile hamsters. The results of our study indicated that food supplementation positively affected juvenile hamsters early in season but only for a short time period. Food supplements given later in season might have a longer lasting effect which is currently investigated in a further study.

As basic knowledge of the hamsters' behavior as well as physiology is urgently needed when developing action plans for the species' conservation in the future, studies like the present one are required. The alarming decline of the Common hamster in the last decades underlines the necessity of stabilizing the species' current populations (Nechay 2000, Meinig et al. 2014, Weinhold 2013). Common hamster populations are faced to various problems which are highly related to the environment (urban or agricultural) the animals are living in (Luniak 2004, Feoktistova et al. 2013, Monecke 2013): In urban habitats the hamsters often have to deal with high intraspecific (Luniak 2004) and interspecific competition (other rodents like rats, Franceschini-Zink & Millesi 2003) as well as with high human impact (Feoktistova et al. 2013), whereas in agricultural circumstances the timing and method of harvesting is crucial for the growth and stability of hamster populations (La Haye et al. 2014, Ulbrich & Kayser 2004).

Previous studies already showed that food availability is limiting Common hamster populations' survival (Ulbrich & Kayser 2004, La Haye et al. 2014, Weinhold 2013). Food supplementation treatments could be a promising approach, but to which extent and at what time of year maximal success can be achieved is still unclear and should be addressed in future studies.

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Appendix

Zusammenfassung

Energieverfügbarkeit in Form von Nahrung ist besonders in Ökosystemen mit Jahreszeitenwechsel starken saisonalen quantitativen und qualitativen Schwankungen unterlegen. Um das Überleben auch unter diesen Bedingungen zu sichern, müssen Energiereserven entweder in Form von Körperfett gespeichert oder extern in Futterspeichern angelegt werden. Der Feldhamster (*Cricetus cricetus*) ist ein fakultativer Winterschläfer (Hibernator) und kombiniert beide Strategien. Darüber hinaus hebt er sich von anderen Winterschläfern durch eine lange Fortpflanzungsperiode von bis zu sechs Monaten ab, sowie durch ein hohes saisonales Fortpflanzungspotenzial (pro Weibchen bis zu drei Würfe mit 1–9 Jungtieren). Mit einem Alter von etwa 25 Tagen sind die Jungen entwöhnt und haben innerhalb der nächsten fünf Wochen zumeist ihren eigenen Bau bezogen. Die Jungtiere müssen nun Vorräte für den Winter sammeln, Körperfettreserven anlegen, aber auch Energie in Wachstum investieren – eine sowohl zeitliche als auch energetische Herausforderung für die Junghamster. Da im Besonderen die Energieverfügbarkeit ein limitierender Faktor darstellt, wurde die vorliegende Studie auf der Basis von Zufütterungsexperimenten durchgeführt. Ziel dieser Studie war, zu untersuchen, ob die Entwicklung juveniler Feldhamster durch zusätzliches, ausschließlich den Jungtieren angebotenes Futter, positiv beeinflusst werden kann.

Die Studie wurde in Wien an einer freilebenden Hamsterpopulation durchgeführt (März – November 2014). Mit Hilfe der Fang/Wiederfang Methode wurden u.a. die morphometrischen Parameter der Tiere erfasst, sowie im Anschluss der Körperfettanteil der Tiere mittels eines validierten Computer-Models errechnet. Sobald die Junghamster ihren eigenen Bau bezogen hatten, wurden ihnen einmalig 200 g ungeschälte Sonnenblumenkerne angeboten. Es zeigte sich, dass die zugefütterten Tiere in der zweiten Woche nach der Futterzugabe einen höheren Gewichtszuwachs aufwiesen als die Kontroll-Tiere. Dieser Unterschied bestand in den darauf folgenden Messungen nicht mehr. In allen anderen untersuchten Parametern (Gewicht, Körperfettanteil, Körperfettzuwachs und Körperlängenmaße) konnten keine Unterschiede festgestellt werden. Eine geschlechtsspezifische Auswertung war aufgrund der geringen Stichprobengröße der Männchen nur bei den weiblichen Jungtieren möglich. In den ersten beiden Wochen nach der Futterzugabe, konnte

bei den zugefütterten Weibchen ein höherer Gewichtszuwachs, sowie ein höherer Körperfettzuwachs festgestellt werden. Später in der Saison bestanden diese Unterschiede nicht mehr.

Die Ergebnisse zeigen, dass die Tiere das fettreiche Futter nach der Zugabe zum Teil gefressen haben müssen. Dies spiegelt sich sowohl in den höheren Gewichts-, als auch Körperfettzuwachsraten wider. Da der Effekt aber nur kurzzeitig anhielt, ist es wahrscheinlich, dass die Junghamster nicht in der Lage waren, das hochwertige Futter langfristig gegenüber Artgenossen zu verteidigen, vor allem unter Berücksichtigung der nachweislich hohen Dichte im Gebiet. Eine andere Erklärung wäre, dass die Tiere das gut lagerbare Futter bereits für den Winter in ihren Futterspeichern angelegt und nur einen Teil davon direkt konsumiert haben. Gegen diese Annahme sprechen, der saisonal frühe Zeitpunkt des Zufütterns, sowie die eher geringe Futtermenge, die den Tieren angeboten wurde. Zur Bestimmung des optimalen Zeitpunkts für Zufütterungsmaßnahmen werden noch weitere Studien nötig sein, trotzdem konnte die vorliegende Arbeit dazu einen wichtigen Beitrag leisten.