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Abstract

Reproductive effort and output in seasonal animals, especially in hibernators is limited by energy but also time constraints since the final part of the active period has to be dedicated to preparation for the hibernation phase. In addition, the juveniles need sufficient time to grow and allocate external and internal energy reserves to survive over winter. Common hamsters have a relatively long breeding season lasting for up to 6 months and some females can even produce three litters per season ranging from one to nine juveniles per litter. The goal of this study was to investigate the effects of food supplements provided during the breeding season on female reproductive output, body condition at the end of the active season and offspring condition before natal dispersal. Free-ranging Common hamsters living on green patches surrounding the buildings of the Kaiser Franz Josef Hospital in Vienna were studied from March 2014 until November 2014. Capture-mark-recapture techniques were applied to gain information about the reproductive status and output of the females as well as to record morphometric parameters of females and their offspring. Focal hamsters were provided with a onetime serving of sunflower seeds during the active season and reproductive performance was compared to that of control females. The results revealed that the provided food did not affect reproductive output, since neither the number of litters nor the total number of juveniles per season differed between supplemented and control females. To compare maternal effort we recorded lactation duration and the time juveniles spent at the natal burrow. Lactation duration was similar between supplemented and control females, however, juveniles of supplemented mothers tended to stay at the natal burrows for longer periods. Body mass and proportion of body fat before immergence into the hibernacula was determined in the focal females. Neither body mass nor body fat proportions differed between supplemented and control hamsters. Based on previous studies, these results indicate that decisions on reproductive effort and timing might depend on the females' emergence date and condition and not on high food availability later in the season, in particular in an area in which food did not seem to be a limiting factor for the hamsters. However, the low sample size – the intended timing for supplementation between the first and second litter was only possible in a few individuals – does not allow general conclusions. Future investigations will focus on supplementations after the reproductive period which might show more direct effects on female condition and/or hibernation patterns.

Introduction

Seasonal animals, especially hibernators, have to deal with both time and energy constraints during the active period (Humphries et al. 2003). The time for reproduction is limited, thus most hibernators produce only one litter per season (Davis 1976, Millesi et al. 1999, Humphries et al. 2003, Turbill et al. 2011). In addition to energetic requirements for reproductive effort, they have to prepare for hibernation in a limited amount of time by accumulating body fat and building up food stores (Humphries et al. 2003).

Our study species, the Common hamster (*Cricetus cricetus*) is a solitary living rodent and typically lives in the steppe and forest steppe with loam, clay-loam, and clay-sand soils they need to build their burrows. The main distribution of these animals stretches from Eastern-Europe to Central-Europe (Eibl-Eibesfeld 1953, Nechay 2000). In Austria the Common hamster is found in the Pannonian parts of the country (Spitzenberger 1998). Due to pest control, hamster trapping because of its fur, as well as intensified agriculture Common hamster populations have declined in the last years and the species is presently listed as “endangered” in most parts of its distribution range (Weinhold 2008, Ulbrich & Kayser 2004, La Haye 2014).

Since the Common hamster is a culture follower and most of its natural habitat was converted to agricultural areas (Nechay 2000) the hamster is also abundant in some urban areas since the city grew around their natural habitat (Feoktistova et al. 2013). Hamsters seem to have adapted well to this new environment as reflected in behavioral and ecological changes like higher population densities which is often connected to smaller individual territories, changes in diet and in foraging behavior as well as habituation to human activities (Luniak 2004). Adaptation to the urban environment with high population densities is also often associated with increased intraspecific aggression but earlier studies at a similar study site showed that apart from increased intrasexual aggression among males during the spring breeding period, conflict rates were relatively low (Siutz 2008). The hamsters showed a bimodal activity pattern with activity outside the burrow between 4 a.m. to 10 a.m. and from 4 p.m. to 10 p.m. depending on seasonal changes in daylight (Kaim et al. 2013). Even though the environmental changes have some impact on the behavior of this species urban populations are still comparable to those in agricultural or dry grass areas (Franceschini and Millesi 2005, Franceschini-Zink & Millesi 2008, Hufnagl et al. 2011a).

The active season of Common hamsters usually starts between March and early May, depending on the location and weather conditions in spring. Males emerge from their hibernacula before females (Eibl-Eibesfeld 1953, Weinhold & Kayser 2006). Shortly after emergence of the females the reproductive period starts which can last until late August, sometimes even until early September (Eibl-Eibesfeld 1953, Grulich 1986). Common hamsters have a promiscuous mating system with frequent changes of mating partners (Weinhold & Kayser 2006). Female Common hamsters have a high reproductive potential and different from most hibernators can have up to three litters per season (Seluga 1996, Franceschini & Millesi 2005) ranging from one to nine juveniles per litter (Eibl-Eibesfeld 1953, Franceschini-Zink & Millesi 2008). One adaptation to high reproductive output in a limited active season is a postpartum estrus leading to an overlap of lactation of the current and gestation of the next litter (Grulich 1986; Franceschini-Zink & Millesi 2008).

Gestation lasts around 20 days and after 3 weeks juveniles emerge from the natal burrow starting to explore their surroundings for the first time (Eibl-Eibesfeld 1953, Weinhold & Kayser 2006). After six to eight weeks they are weaned (Eibl-Eibesfeld 1953). Juveniles can reach sexual maturity at an age of about 2.5 months and thus are able to reproduce in their first year (Niethammer 1982). However this seemed to be the exception as most individuals started to successfully reproduce as yearlings (Franceschini-Zink & Millesi 2008).

Shortly after the end of the reproductive season, which is the most energy demanding time of the year particularly for females (Wade and Schneider 1992), the hamsters have to prepare for hibernation. Hamsters have two strategies to survive overwinter. They can build up body fat reserves as well as hoard food in their burrows (Humphries et al. 2003). These food stores seem to be essential for survival until the following spring (Wassmer and Wollnik 1997). Both of these strategies are used by the hamsters, but recent studies indicate that adult males depend more on body fat reserves and adult females more on food stores inside their burrows during winter leading to females spending less time in torpor than males (Siutz et al. 2012).

Ulbrich and Kayser (2004) assessed that the survival of the females play a crucial role in population dynamics and Boutin (1990) concluded that reproductive output and/or body condition could be increased by providing additional food resources. Although Common hamsters show an opportunistic reproductive strategy, the timing of seasonal activities appeared to highly affect reproductive success (Franceschini et al. 2007). Thus, the provision

of additional food items could positively affect litter and/or offspring number in the current season. In addition, food supply could shorten the time span between first and second litter and thus allow more time for growth and preparation for hibernation in juveniles. Another benefit could be that additional food of high quality could enable the females to compensate the energy expenditure caused by maternal effort resulting in a better condition before the hibernation season and correspondingly higher survival chances compared to females without these resources. Finally, food supply could positively affect juvenile condition before natal dispersal. In this study individual females were provided with sunflower seeds during the reproductive period. Reproductive timing, output as well as female and offspring condition were compared to that of control individuals.

Materials and methods

Study site

The study was conducted at the Kaiser Franz Joseph Hospital in Vienna, Austria, located between the 10th and 12th district. Common Hamsters live on green patches associated within the hospital buildings, mainly consisting of grassland, trees and bushes divided by small streets and buildings. Three focal areas were chosen (in total 2.25ha). Data collection started in late March 2014 and lasted throughout the active season until the end of November 2014.

Live trapping

Live-trapping was carried out three to four times a week, mainly during the early morning hours from 5:30 a.m. until 11 a.m. and occasionally also in the evening hours. All procedures performed on animals were approved by 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).

The animals were captured using tomahawk live traps, baited with peanut butter and placed directly in front of the burrows. Immediately after the animal was trapped the hamster was removed from the trap and put into a cone shaped cotton sack which was fastened with Velcro. This bag enabled the handling of the animals with minimal stress for the hamster. Each investigation lasted five to ten minutes, thereafter the animals were released near their burrows (Franceschini et al. 2007).

To collect morphometric parameters we first weighed the animals and measured head, tibia and foot length with a caliper. Sex was determined at capture and the reproductive status was categorized based on the vaginal opening on a four point scale ranging from completely closed (0) to wide open with bloody mucus (3). In addition, teat size was documented using a scale from almost invisible (0) to very swollen with milk remains (3). These data enabled us to discriminate between pre-mating, gestation, lactation and post reproduction (Franceschini et al. 2007).

Each female was individually marked with a transponder (PIT tag, Data Mars SA) for permanent identification and a red colored symbol painted on their back with hair dye to enable distant recognition. The same procedure was done in juveniles. Depending on the sex of the juvenile the symbols were done with red color for females and black for males. Other recorded parameters were date, time of capture, temperature and location of the burrow as well as weather conditions (Franceschini et al. 2007). With the help of the morphometric parameters head, tibia length, foot length and body mass, body fat proportion could be calculated non-invasively (Siutz et al. 2012).

Depending on the reproductive state, vaginal opening, body mass loss and teat size we could determine parturition in focal females and when the juveniles emerged, litter size and juvenile body mass at emergence could be recorded. In some females we were able to determine the number of litters and total offspring number per season. The teat size was also used to determine the duration of lactation. Since the burrows of the focal females were continuously monitored we could also record the time period the juveniles stayed at the mother's burrow until they dispersed or the mother herself left (Franceschini et al. 2007).

Food supplements

For supplements sunflower seeds were used. Sunflower seeds were chosen because of their high content of polyunsaturated fatty acids which play an important role for reproduction and hibernation (Ruf & Arnold 2008, Abayasekara & Wathes 1999, Wathes et al. 2007). In addition they are easily storable and have also been successfully used in other experiments with captive Common hamsters (Siutz et al. unpublished data).

Each female got a onetime serving of 300g sunflower seeds within the breeding period. The seeds were placed directly in front of the females burrow and, to make sure that only the focal

animal cached the supplements, the animals were continuously observed until all seeds had been cached. The supplements were usually provided in the early morning hours but some females received them in the evening.

Focal females were chosen based on the data from previous captures to ensure that the supplements were placed in front of the right burrow and to determine in which reproductive state the female was at the time of supplementation. Our goal was to supplement the females after they had weaned their first litter but were not pregnant with the second one. However, some juveniles stayed at the burrow for an extended time span and some females overlapped gestation and lactation the accurate timing of food supplementation was very difficult. Due to these difficulties two females could only be supplemented after their reproductive period causing the sample size to vary in our results. Control animals were chosen by matching age as well as body mass. Individuals that left the study site during the active season were excluded from analyses.

Statistics

The statistical analysis was performed using SPSS for Windows (PASW Statistics 18). Student's t-test and Mann-Whitney u-tests were applied depending on data distribution. Data in results is shown as means \pm SD if not stated otherwise.

Results

In the active season of 2014, 30 adult females, 44 adult males and 242 juveniles were captured and marked. The adult female population density was 13.3 individuals per ha. The active season lasted from 26.3.2014 until 24.11.2014.

Reproduction

In 2014 the first adult female could be captured on 1. April and the last females on 21. November 2014. Although we were able to capture and mark 30 adult females during the study period, some of them were captured only a few times, before they left the study site. Reproductive output in the season 2014 could be determined in 22 females ranging from 0 to 3 litters. 19 of these adult females had at least one litter. From those, 7 adult females could be successfully supplied with sunflower seeds, but one female left the study area shortly thereafter.

The first juveniles emerged on 15.5.2014 and the last litter of the season emerged on 25.8.2014. To investigate potential effects of food supplements on reproductive output we first compared the number of litters/season between supplied and control females (Fig. 1, Fig. 2). Half of the females in both groups had 2 litters and only one female in the control group was able to successfully raise a third litter (Fig. 1). The other individuals had only one litter in 2014. No significant differences could be found between the supplied individuals and the control group (Fig. 2, $U = -0.707$, $p = 0.480$).

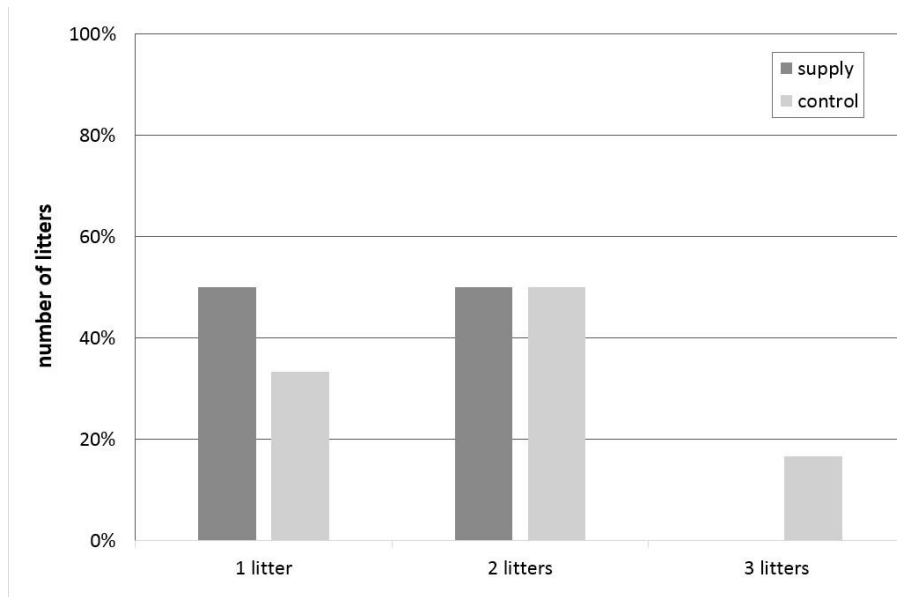


Fig.1: Proportions of supplemented and control females with one, two and three litters per season (n=4/6).

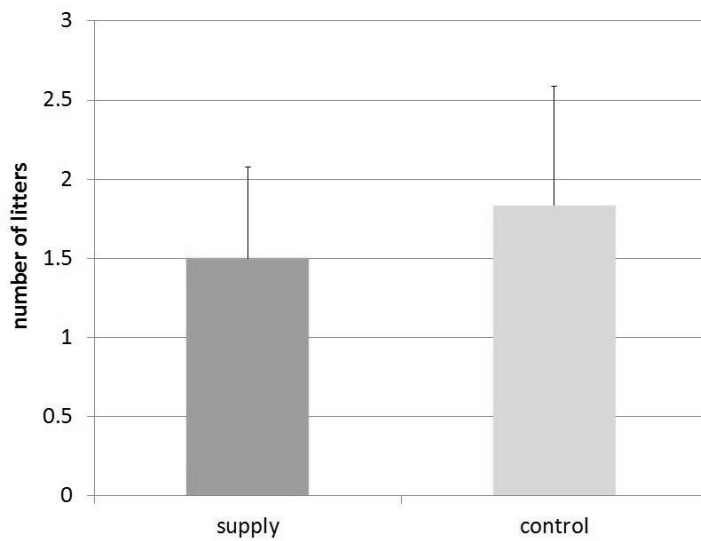


Fig. 2: Number of litters per season (means+SD) of supplemented and control females (n=4/6)

Litter size in first litters per season was slightly higher than in second litters in both groups and the only third litter contained 2 juveniles (Fig. 3). Corresponding to the litters per season, the total number of juveniles did not differ between the two groups ($t = -0.93$, $p = 0.38$) (Fig. 4).

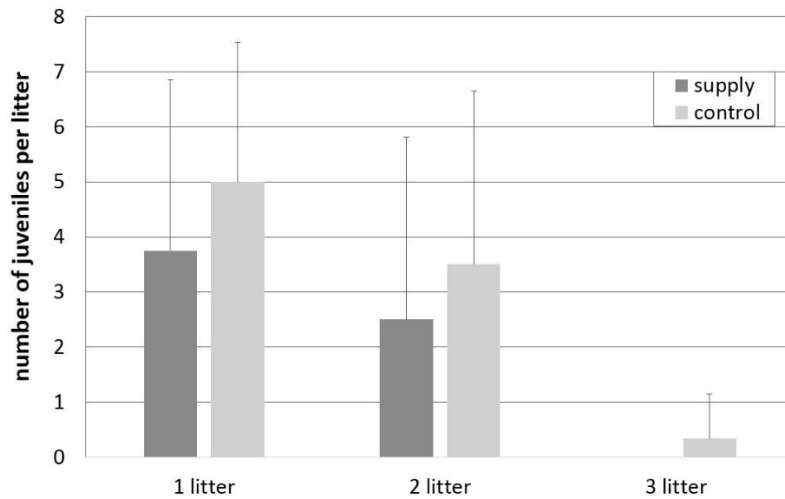


Fig. 3: Number of juveniles per litter in supplemented and control females (n=4/6, means+SD)

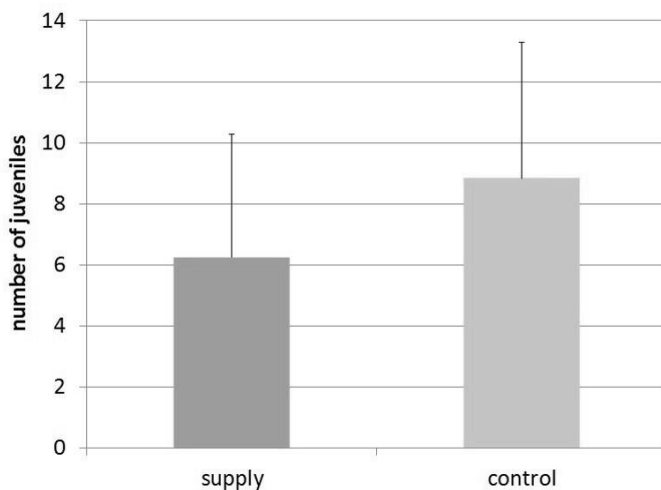


Fig. 4: Total number of juveniles (means+SD) in supplemented and control females (n=4/6)

The time span between a female's first and second litter could only be determined in 6 individuals (2/4), therefore we were unable to test for potential effects of food supplements.

Food supplements might affect maternal effort, thus we compared lactation duration in supplemented and control females. We found no significant differences, both groups lactated their offspring for about 30 days ($t= 0.50$, $p= 0.63$, $n: 4/6$, supplied $32d \pm 6.57$, control $30.25d \pm 4.60$).

To compare body condition shortly before hibernation between supplemented and control females we used the parameters body mass and the proportion of body fat. Body mass before immergence into the hibernaculum did not differ between supplemented and control females

(Fig. 5, $t = -1.58$, $p = 0.16$). The proportion of body fat both in supplied and control individuals ranged between 15% and 25% before immersion into the hibernacula (Fig. 6, $t = -0.76$, $p = 0.47$) and, similar to body mass, did not differ significantly between the two groups.

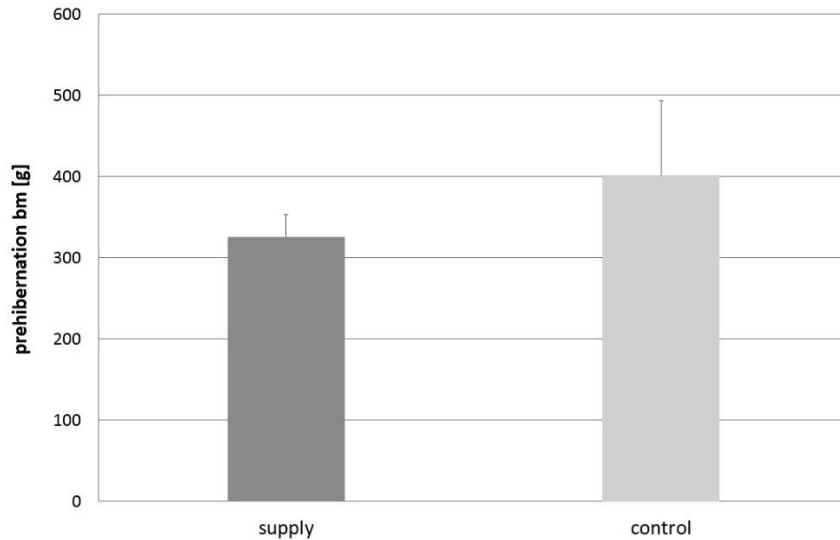


Fig. 5: Body mass of supplemented and control females shortly before the hibernation period (means+SD, $n=4/5$)

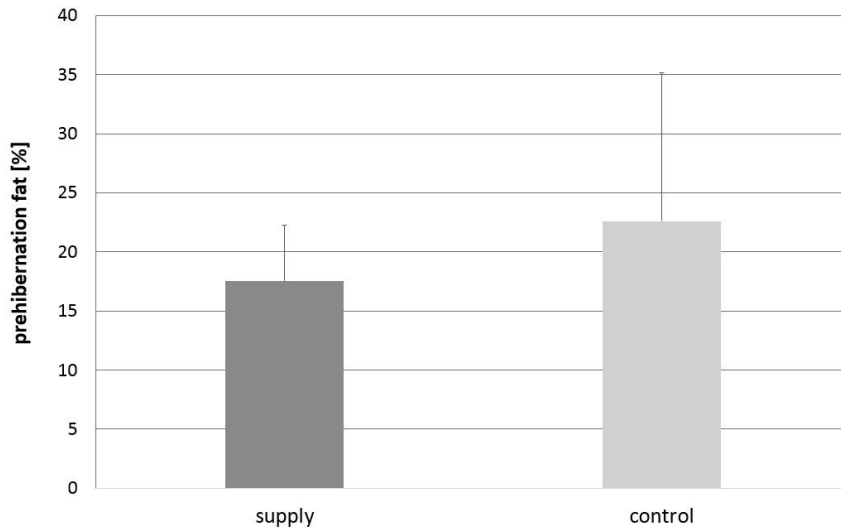


Fig. 6: Proportion of body fat in supplemented and control females shortly before immersion into the hibernacula (means+SD, $n=4/5$).

Immersion into the hibernacula occurred between 4.9.2014 and 21.11.2014. No differences in the termination of above ground activity was found between the two groups ($t = -0.42$, $p = 0.69$, $n = 4/5$, supplied 6.10.2014 \pm 28.05d, control 13.10.2014 \pm 27.62d).

Juveniles

Food supplements could affect the mother's but also the offspring's condition. When we compared body mass of the juveniles at emergence from the natal burrow, no significant differences could be found between the groups ($t= 0.29$, $p= 0.79$, $n: 3/3$, mothers supplied $100.27g \pm 11.93$, control $96.83g \pm 16.59$). Both the juveniles of supplemented and those of control females weighed around 100 g at natal emergence.

Finally we tested the duration the juveniles stayed at the natal burrow before they dispersed. Litters of supplied females tended to stay longer at the natal burrow than those of control females, however the difference was not significant ($t= 2.088$, $p= 0.082$; $n: 4/4$, Fig. 7).

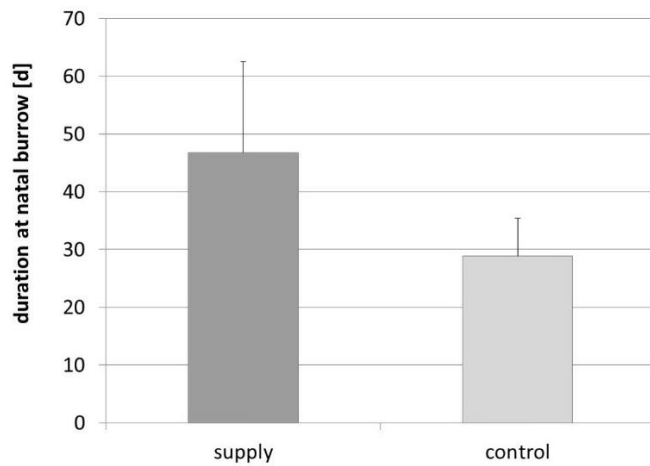


Fig. 7: Total duration juveniles of supplemented and control females stayed at their natal burrows (means+SD).

Discussion

Similar to previous studies, the active season 2014 started in late March because no severe weather conditions delayed the onset (Hufnagl et al. 2011a, Franceschini & Millesi 2005, Franceschini-Zink & Millesi 2008) and lasted until the end of November. The timing of vernal emergence can highly affect reproductive timing and output in Common hamsters, since time for reproduction is limited in hibernators. It has been shown that early emerging females also breed earlier than later ones leading to a higher litter and offspring number in the respective season (Franceschini-Zink & Millesi 2008). Even though the reproductive period is not longer in early emerging individuals compared to ones that started the active season later, the chances of raising a successful postpartum litter are increased. In addition, the postreproductive period has been shown to be prolonged in early females leading to more time to prepare for hibernation as well as better chances to survive overwinter (Franceschini-Zink & Millesi 2008). The early start of the active season and reproduction also enables the juveniles, particularly those of first litters in the season, more time to grow before hibernation. Corresponding to the unexceptional onset of the active season in adult individuals in 2014, first litters started to emerge in late May which is in line with most studies both in urban and other habitats (Franceschini-Zink & Millesi 2008, Franceschini & Millesi 2005, Hufnagl et al. 2011a, Seluga et al. 1996, Eibl-Eibesfeld 1953, Nechay 2000).

During the active season of 2014 we were able to monitor reproductive performance of 22 female hamsters. The reproductive output of the females in 2014 varied among individuals. Most females were able to produce one to two litters, a few individuals were not able to reproduce successfully at all and one female even had three litters. These results corresponded to previous studies in similar habitats (Franceschini and Millesi 2005, Franceschini-Zink & Millesi 2008). Litter size in 2014 varied between 1 and 9 pups per litter, which is also in line with the results of the above mentioned studies. Also the number of reproducing females that stayed in the study area until hibernation was similar to earlier studies at nearby study sites (Franceschini-Zink & Millesi 2008, Siutz 2008). In general reproductive performance in 2014 did not differ from those found in previous studies conducted in close distance of the study site.

Since female Common hamsters have a high reproductive potential and can raise up to three litters per season (Seluga 1996,) we wanted to investigate if additional food resources could

have immediate positive effects on reproductive output. We expected that food supplements could lead to larger second litters, a shorter time span between first and second litter, or even a third litter. Other studies have shown that additional food can increase reproductive success in small mammals (Boutin 1990). In Arctic ground squirrels food supplements led to increased adult body mass, a higher percentage of lactating females, a higher percentage of weaned litters, larger litter sizes and as a consequence, higher population density compared to control areas. This effect could be enhanced if predators had no access to the study grid (Karles et al. 2000). Similar results could be found in Deer mice when food supplements were provided late in winter. Mice with additional food had more offspring, bred earlier, maintained higher body mass during winter and the immigration rate tripled in comparison to control grids (Taitt 1981). Another experiment supplementing vole populations resulted in higher proportions of breeding females, an increase in body growth and larger litter sizes (Cole & Batzli 1978). Similar results were found in other vole populations showing an increase in population density, higher numbers of lactating females and more juveniles entering the supplemented area (Taitt & Krebs 1981). In our study however, supplemented females neither had more litters nor more offspring per season than control females. In most studies investigating the effect of food supplements, grids with and without additional food were compared, (Karels et al. 2000, Flowerdew 1972, Taitt 1981, Taitt & Krebs 1981, Cole & Batzli 1978) whereas in our study food supplementation was carried out on an individual basis, comparing supplemented and control females in the same area. This was done because we aimed to provide food in a specific period, between the first and second litter, which had to be determined individually. With this method we were able to ensure that all females that received the additional food got the exact same amount of food and record the individuals' reproductive performance as well as juvenile development during the first weeks.

Most studies on effects of food supplements on offspring number reported increased numbers of juveniles, although only very few studies measured exact litter sizes (reviewed in Boutin 1990). Even though in most cases supplemented individuals had a larger litter size (Cole & Batzli 1978, Taitt 1981), this was not the case in Yellow-bellied marmots where the additional food did not affect litter size similar to our study (Woods & Armitage 2003). Another long-term study on Snowshoe hares showed that additional winter food resulted in tripled population densities on the supplemented areas in comparison to the control grids. These higher densities however, were mainly contributed to higher immigration rates into the

supplemented areas, since neither the survival of the juveniles nor the breeding success seemed to be affected by extra winter food (Krebs et al. 1986). Since the supplemented individuals in our study were observed to transport the food into their burrows they initially did not have to compete for these resources.

Since the females did not invest in a third litter which, considering the time constraints, might not have been very promising, we analyzed if the females invested more energy in their second litter compared to the control individuals. Extra energy could be invested in more juveniles but also in the offspring's quality. As most females received the food supply between the first and second litter, the latter could benefit via increased maternal effort. It has been shown that providing cows with supplemented fat extracted from soybeans and sunflower seeds increased the milk yield as well as infused the milk with a higher concentration of unsaturated fatty acids (Schingoethe et al. 1996). Since we were not able to measure the amount or quality of the females' milk we compared the duration of the lactation phase between supplemented and control females. Lactation duration did not differ between the two groups but the individual variation was very high in both groups, which has also been shown previously in Common hamsters (Weisinger 2013). Gross (2005) also stated that the extent of parental care is highly variable between species as well as between individuals of the same species, depending on the litter size, the mother's body condition and further mating opportunities. Litter size varied among the focal females and thus could cause longer lactation periods in larger litters. However, in our study, litter size did not seem to affect lactation duration.

Another parameter related to maternal effort is the time span of common burrow use between mother and offspring. The duration of common burrow use can depend on a number of factors like litter size and predation risk (Weisinger 2013) and even though we did not find a significant difference between both groups, juveniles of supplemented females tended to stay longer with their mother at the natal burrow than juveniles of control females. Our data showed that juveniles stayed at the natal burrow even though the female was not lactating anymore, still giving them the advantage of lower predation risk as well as access to the mother's food stores. Thus they can profit from the high-energy food that may be stored in the burrow, which could improve their body condition. In addition, as has been shown previously, extended periods of common burrow use were related to lower cortisol secretion

in the juveniles, indicating reduced stress load (Weissinger 2013). Considering the negative effects of chronic stress on developmental factors, immune competence and survival, delaying natal dispersal could be beneficial for the pups (Keay et al. 2006).

To examine the possibility that the juveniles of supplemented females have profited from the extra food in the natal burrow we compared emergence body mass of juveniles from both groups, since several studies have shown that food supplements can accelerate the growth rates and weight gain of juveniles (Boutin 1990). Juvenile Yellow-bellied marmots which were provided with high protein supplements had higher growth rates and therefore increased body mass gain in comparison to control juveniles (Woods & Armitage 2003). Food supplements given to a vole population also led to higher body growth rates in these animals (Cole & Batzli 1978). The growth rates of juvenile red squirrels was also higher with food supplements than without (McAdam & Boutin 2003). In our study emergence body mass did not differ between juveniles of supplemented and control females, even though juveniles had access into the mother's foods stores and could have been able to feed there from an age of eight days (Eibl-Eibesfeld 1953). Eibl-Eibesfeld (1953) reported that juvenile hamsters can eat leaves and grass at an age of a few days but feeding on seeds is probably a more difficult task. We do not know when they can start. So maybe the sunflower seeds that were given to the mothers are too difficult to eat and digest shortly after birth, explaining why no weight difference could be found between the juveniles of supplemented and control females. Another study conducted at the same study site in the same season showed that older juveniles are able to profit from sunflower seeds at least during the first weeks after supplementation. These juveniles were supplemented after they had left the natal burrow and had found their own burrow. Supplemented juveniles had higher body mass and body fat increase rates than same-aged controls. (Grimm unpub. data). Making it plausible that the juveniles at emergence are still too young to profit from the sunflower seeds. In the above mentioned study the youngest juvenile was 66 days old at supplementation whereas in our study the juveniles that stayed the longest at their natal burrows left after 60 days. So it is possible that the pups of supplemented females stayed longer at their mother's burrow to profit from the sunflower seeds later on in their development.

Even though a high reproductive output can be energetically costly, female Common hamsters with high reproductive output managed to reach a relatively good body condition before

hibernation (Franceschini-Zink & Millesi 2007). Since the reproductive output of supplemented females was not different to that of control females we examined the possibility that the mothers used the extra energy to gain body weight and/or body fat in preparation for hibernation. A number of food supplement experiments have revealed weight gains or increase in growth rates after the animals had received additional food (Boutin 1990). In Arctic ground squirrels supplements led to improved adult body condition (Karles et al. 2000) similar to wood mice in which the additional food increased the weight of both males and females (Flowerdew 1972). Similar results were found in Columbian ground squirrels (Neuhaus 2000), deermice (Taitt 1981) and voles (Cole & Batzli 1978). We could not find any evidence for increased body condition in supplemented females. Thus females did not seem to have invested the additional energy in improving their body condition before immergence, which leaves the possibility that the females stored the sunflower seeds for the winter period. Female Common hamsters do not accumulate as much body fat as males prior to hibernation, they mainly rely on food stores. Males usually fed above ground during the active season whereas females almost exclusively cached food (Siutz et al. 2012). In addition, during winter, males spent more time in torpor than females (Siutz et al. 2012). Thus females have to rely on food caches inside the burrow for several weeks. Unfortunately the low sample size in our study did not allow to compare survival rates of supplemented and control females.

In comparison to previous studies (Hufnagl et al. 2011a), the active season of 2014 had lasted until late autumn. This could be due to the mild climatic conditions until late November. The prolonged season of 2014, could be the reason that all studied females had enough time to prepare for the winter period. Other studies have shown that if food availability is high, supplements are not as effective as if food is more limited (McAdam & Boutin 2003, Karels 2000). The timing of immergence into the hibernacula did not seem to be affected by the food supplements because immergence dates did not differ between the female groups.

The high population density (33 adult hamster/ha) caused some problems with regard to supplementing individual females. Frequently other hamster also were interested in the sunflower seeds and many supplementation attempts had to be stopped. Sometimes the supplements even led to conflicts between the focal female other individuals. After the sunflower seeds were cached we expected that adult females were able to defend their food stores but how long the animals were able to monopolize their resources remains unknown.

However pilfering does not seem very likely since we never observed other hamsters in the burrows of supplemented females and they also did not change their burrows after supplementation.

We supplied all females with 300g of high energy food which is not enough to survive over winter but it should be enough to give these animals an advantage in comparison to control individuals. An experimental study conducted with Common hamsters in a climate chamber showed that the amount of food, which consisted of mixed seeds, that the animals consumed over winter ranged from 353g up to 1700g depending on hibernation durations (Mikovits 2013). Based on these results 300g seemed sufficient for the purpose of our study but if both mothers and juveniles ate the food items, the effects might have been too small to be detected. However, the supplementation of larger food amounts would have been even more difficult because the animals take quite a long time to cache the seeds.

To provide the females with extra food between the first and second litter turned out to be very difficult and caused the low sample size. Some of the females had a postpartum estrus (Grulich 1986; Franceschini-Zink & Millesi 2008) and overlapped lactation of the first litter and pregnancy with the second litter. In addition, the juveniles of some females' first litters stayed for extended periods at the mother's burrows before they dispersed.

In conclusion we found no effects on reproductive output, seasonal timing or prehibernation body condition in the supplemented females. The fact that the offspring of supplemented mothers tended to delay dispersal could indicate that they were attracted by the high quality food.

It might have been more effective to provide the supplements earlier in the season at the onset of reproductive activity. As the timing of the first litter has been shown to be related to reproductive output in the respective season (Franceschini-Zink & Millesi 2008), the provision after weaning of the first litter could have been too late to significantly affect reproductive performance. This could point to limits in opportunistic strategies in these hibernators.

Food supplements shortly before emergence could affect overwinter survival particularly in females but this is presently being investigated. Knowledge on crucial phases for food supplementation could be important for conservation issues, for instance with regard to re-establishing this endangered species in suitable environments.

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Appendix

Zusammenfassung

Tiere, deren Aktivitäten jahreszeitlich stark beschränkt sind, vor allem Winterschläfer, müssen mit ihren Energiereserven sorgfältig haushalten. Durch die Kürze der Saison bleiben für die Reproduktion nur wenige Monate, weil auch die Vorbereitung auf den Winterschlaf einige Zeit in Anspruch nimmt. Zusätzlich ist die Reproduktionszeit limitiert, um den Jungtieren vor dem Winterschlaf genügend Zeit zu bieten sich zu entwickeln und ausreichend Körperfettreserven und Futtermittel aufzubauen. Der Europäische Feldhamster zeichnet sich unter den Winterschläfern durch eine relativ lange Reproduktionsphase aus, die bis zu 6 Monate dauern kann. Während dieser Zeit produzieren manche Weibchen sogar drei Würfe, mit Wurfgrößen von einem bis neun Jungen. Ziel dieser Studie war es, die Wirkung von zusätzlichen Futtermitteln, welche individuell ausgewählten Tieren während der aktiven Saison angeboten wurden, auf den reproduktiven Erfolg, den Körperzustand der Weibchen vor dem Winterschlaf und den der Jungtiere kurz nach dem Auftauchen aus dem mütterlichen Bau zu untersuchen. Diese Studie wurde mit freilebenden Feldhamstern, welche auf dem Gebiet des Kaiser Franz Josef Spitals in Wien vorkommen, durchgeführt. Die Daten wurden von März bis November 2014 mittels der Fang/Wiederfang Methode erhoben. Dadurch konnten sowohl der reproduktive Status der Weibchen als auch morphometrische Parameter der Mütter und Jungtiere erfasst werden. Jedes der Tiere, welche für die Zufütterung ausgewählt wurden, erhielt eine einmalige Portion Sonnenblumenkerne (300g) während der reproduktiven Phase der aktiven Saison. Die Ergebnisse weisen auf keine Einflüsse der zusätzlichen Futtermittel auf den reproduktiven Erfolg hin. Weder die Anzahl der Würfe pro Saison noch die Gesamtzahl der Jungtiere der zugefütterten Weibchen unterschied sich von jenen der Kontrolltiere. Um herauszufinden, wie viel Aufwand die Muttertiere in die Pflege der Jungen investierten, wurden sowohl die Dauer der Laktation als auch die Aufenthaltsdauer der Jungtiere beim mütterlichen Bau zwischen zugefütterten Tieren und der Kontrollgruppe verglichen. In beiden Fällen konnten keine signifikanten Unterschiede gefunden werden, allerdings zeigte sich eine Tendenz, dass Jungtiere von zugefütterten Müttern länger beim mütterlichen Bau blieben als die von Kontrollmüttern. Der körperliche Zustand der Weibchen vor dem Winterschlaf wurde anhand von Körpergewicht und Körperfettanteil verglichen. Die Werte der zugefütterten Weibchen unterschieden sich allerdings nicht signifikant von denen der Kontrollgruppe. Dies

lässt die Möglichkeit offen, dass die Weibchen das zusätzliche Futter für die Steigerung der Überlebenschancen während des Winterschlafs gehortet haben könnten. Andererseits könnten die Jungtiere an den Vorräten mitgefressen haben, ohne deutliche Unterschiede zur Kontrollgruppe aufzuweisen, weil die Auswirkungen zu gering waren. Der geplante Zeitpunkt der Zufütterung zwischen erstem und zweitem Wurf war aufgrund der hohen individuellen Variation in Bezug auf das Geburtsdatum der einzelnen Würfe, die Laktationsdauer und dem Zeitpunkt, zu dem die Jungtiere endgültig den mütterlichen Bau verließen, nur bei einigen wenigen Tieren möglich. Dennoch weisen die Ergebnisse darauf hin, dass die einmalige Futterportion innerhalb der reproduktiven Phase keine nachhaltigen Auswirkungen auf die Weibchen oder ihre Jungen hatte. Das könnte möglicherweise darauf hinweisen, dass die Entscheidung über den reproduktiven Erfolg weiblicher Feldhamster stärker vom Zeitpunkt des ersten Auftauchens der Weibchen im Frühjahr und deren körperlichen Zustand als von der Zufütterung in der späteren Jahreszeit abhängig ist.