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Seasonal constraints and diet composition in Common hamsters (*Cricetus cricetus*) living in an urban environment

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„Am Ziele deiner Wünsche wirst du jedenfalls eines vermissen:
dein Wandern zum Ziel.“

Marie von Ebner-Eschenbach

In diesem Sinne allen, die mich auf diesem Weg - mit seinen Höhen und Tiefen - begleitet und unterstützt haben, ein herzliches Danke!

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Seasonal constraints and reproductive performance in female Common hamsters (*Cricetus cricetus*)

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Abstract

Common hamsters (*Cricetus cricetus*) are hibernators and therefore show a pronounced seasonal breeding behaviour. Previous studies have suggested that an early onset of reproduction after vernal emergence can be crucial for reproductive success in the current year. In Vienna, the winter 2005/06 was the coldest winter since 1987 and snow cover lasted until late March. This enabled us to investigate the effects of harsh winter conditions on seasonal timing and reproductive success in female Common hamsters. We aimed at investigating differences between 2006 and previous years (2003-05) to determine potential environmental effects on seasonal timing, reproductive performance, physical condition before hibernation and overwinter survival rates. Hamsters were live-trapped throughout the active period, weighed, individually marked and reproductive status was recorded. The number of litters per season and litter size were determined in focal individuals. Vernal emergence in 2006 was remarkably delayed and females mated significantly later than in 2003-05. Reproductive output in 2006 was about half of that in the years before. This was particularly pronounced in the size of the females' first litters per season. The number of litters per female was similar in all periods. Almost 90% of the females in 2006 mated shortly after parturition and overlapped lactation of the first and gestation of the second litter. In 2003-05 only about one third of the focal females successfully produced a litter after a postpartum oestrus. The consequences of previous reproductive effort and timing were estimated by measuring prehibernation body mass and overwinter survival rates. In 2006, females entered hibernation with the lowest body mass found in all studied years. This could be due to the shorter postbreeding period compared to previous seasons. However, survival rates in the winter 2006/07 were almost twice as high as in the years before. The reason for this could be the exceptionally warm winter in this year, allowing foraging above ground. In conclusion, the results demonstrate that environmental factors appeared to affect seasonal timing, reproductive output and preparation for hibernation in female Common hamsters.

Introduction

Seasonal breeders, in particular hibernating mammals like Common hamsters (*Cricetus cricetus*) are limited by time and energy constraints. Processes like structural growth, reproduction, moult and preparation for hibernation have to be completed within an active period of 6-7 months (Nechay, 2000; Monecke, 2004; Franceschini-Zink & Millesi, 2008). Previous studies have shown that in Common hamsters the timing of seasonal processes, like reproduction and preparation for hibernation, can be crucial for reproductive success and survival (Franceschini-Zink & Millesi, 2008). Females, which emerged early in spring also breed earlier and therefore managed to produced more litters and more offspring per season (Franceschini-Zink & Millesi, 2008).

Depending on the geographical range, the active season in Common hamsters starts between March and early May (Monecke, 2004; Franceschini & Millesi, 2004; Weinhold & Kayser, 2006; Franceschini et al., 2007; Franceschini-Zink & Millesi, 2008). Female emergence is followed by the onset of the mating phase (Nechay, 2000; Franceschini & Millesi, 2004; Franceschini et al., 2007), lasting for up to 5

months until mid-August (Grulich, 1986; Monecke, 2004; Franceschini-Zink & Millesi, 2008).
Common hamsters have a promiscuous mating system (Weinhold & Kayser, 2006; Franceschini-Zink & Millesi, 2008) and differ to many other hibernators in producing up to three litters per season (Franceschini-Zink & Millesi, 2008). The first litters emerge from the natal burrows at an age of about 3 weeks in mid-May (Franceschini & Millesi, 2004; Weinhold & Kayser, 2006). In our study population high individual variation in the number of litters per season as well as in litter size has been recorded (Franceschini-Zink & Millesi, 2008).
Furthermore, earlier studies have shown that female Common hamsters can have a postpartum oestrus and mate shortly after parturition. This allows simultaneously lactating the first litter while being pregnant with the second one (Vohralik, 1974; Grulich, 1986; Franceschini-Zink & Millesi, 2008). This time-saving adaptation could maximise reproductive output in a limited active period (Grulich, 1986), but might produce considerable demands on the mother's condition (Martínez-Gómez et al., 2004). After the breeding period, hamsters have to prepare for hibernation, including both accumulation of body fat (internal energy reserve) as well as storing food in their burrows (external energy reserve), (Nechay, 2000; Weinhold & Kayser, 2006). Hibernation onset was found to vary among individual females and occurred between early September and late October (Nechay, 2000; Monecke, 2004; Franceschini-Zink & Millesi, 2008). Environmental factors - like snow cover, winter and spring temperatures - are assumed to affect the timing of the active season (Grulich, 1986; Nechay et al., 1977; Weinhold & Kayser, 2006) and thereby may have a significant impact on reproductive output (Bronson, 1985).

In Vienna, the winter 2005/06 was the coldest winter since 1987 and snow cover lasted until late March (Central Institute for Meteorology and Geodynamics, Vienna, Austria, data obtained from online archive downloaded on 3 June 2009, www.zamg.ac.at). This enabled us to investigate the effects of harsh winter conditions on seasonal timing and reproductive success in female Common hamsters. In the previous seasons (2003-05), the winter temperatures did not differ significantly. Female reproductive output, emergence and immergence date in these years were similar. We aimed at investigating differences between 2006 and previous years (2003-05) to determine potential environmental effects on seasonal timing, reproductive performance, physical condition before hibernation and overwinter survival rates of female Common hamsters.

Material and Methods

Study area
This study is part of a long-term project on a population of Common hamsters in an urban habitat. The study site was located in southern Vienna, Austria, and included 1.56ha. The Common hamsters (*Cricetus cricetus*) live in green patches associated with apartment complexes and are used to the presence of humans, which facilitated behavioural observations.

Study period
Data were collected throughout the active season in 2003-06 (from late March to late October) and from vernal emergence until late June 2007. This analysis was based

on the extreme climatic situation in the season 2006, which clearly differed from that in the three previous years. The winter 2005/06 was very long and harsh in Vienna, with exceptionally low temperatures (the mean temperature in January 2006 was about 2°C lower than the long-term average) and snow cover until late March (Central Institute for Meteorology and Geodynamics, Vienna, Austria, data obtained from online archive downloaded on 3 June 2009, www.zamg.ac.at).
As no significant inter-year differences between 2003, 2004 and 2005 were found in seasonal timing as well as in reproductive output - defined as the number of litters (Kruskal-Wallis-test, p=0.496, n=18), litter size (Kruskal-Wallis-test, p=0.694, n=17) and offspring number per season (Kruskal-Wallis-test, p=0.995, n=18) - data from these three seasons were pooled (Franceschini-Zink & Millesi, 2008) and compared to 2006.

Capture techniques
Live-trapping was done three times per week during the morning hours. The hamsters were captured with Tomahawk live-traps baited with peanut butter. From the traps, the hamsters were immediately released into black cone-shaped cotton sacks, which enabled us to handle the animals without the use of anaesthesia. The hamsters were weighed (±1g) and reproductive status of females was determined on the basis of teat and vulval development (Franceschini et al., 2007): Size and pigmentation of teats were defined in three classes from small (1) to maximal swollen with milk rests (3). Vulval development was categorised from completely closed (0), small opening (1), wide opening (2) to wide opening with bloody mucus (3) indicating parturition. For individual identification the animals were fur-marked with a commercial hair colour in different symbols and a transponder (PIT-tag type Data Mars) was injected subcutaneously at first capture. Capture techniques and frequency did not differ between the studied years.

Litter size was defined as the number of juveniles emerging from a female's breeding burrow. Only pups which could be definitely assigned to a female were used for analysis. As the juveniles began to disperse shortly after they had emerged (Franceschini-Zink & Millesi, 2008), litter emergence coincided with the onset of weaning. Accordingly, the breeding period was defined as the time span between an individual female's first conception and the emergence of her last litter. Thereafter, the postbreeding period began and lasted until the females had immerged into hibernation.

Moreover, some hamsters had a postpartum oestrus, mated shortly after parturition and consequently overlapped lactation and gestation (Vohralik, 1974; Grulich, 1986; Franceschini-Zink & Millesi, 2008). Signs of a postpartum oestrus were increasing body mass during lactation, a rapid body mass loss at the expected time, continuous lactation after the second parturition and a second litter emerging about 3 weeks thereafter (Franceschini-Zink & Millesi, 2008).

Female Common hamsters reduced above-ground activity and started to immerge between early September and late October in previous years (Monecke, 2004; Franceschini-Zink & Millesi, 2008). Therefore, we checked for immergence into hibernation by frequently observing the females' burrows and recapture attempts within this time span. The duration of the active season was defined as the time period between vernal emergence and immergence into hibernation. Immergence body mass was defined as body mass within one week before immergence.

Overwinter survival rates were calculated on the basis of recaptures in the following spring. Females that had immerged in the study area but could not be recaptured in the subsequent year were assumed to have died during winter.

Statistics
Statistical analysis was done with SPSS 13.0 and 15.0 for Windows. Data distributions were tested for normality using Shapiro-Wilk-tests. Normally distributed samples were tested with t-tests. Otherwise, non parametric tests were applied, Wilcoxon-tests for related samples and Mann-Whitney U-tests for independent samples. Correlation statistics were done with Pearson correlations in case of normally distributed data; otherwise Spearman rank correlations were used. Significance values were obtained from two-tailed statistics. If not stated otherwise means with standard deviation are shown in parentheses. Sample sizes differ in the data sets because reliable information about all variables could not be obtained from all focal females.

Results

In 2006, vernal emergence in female Common hamsters was clearly delayed compared to 2003-05 (Tab.1). The individuals started above ground activity about two weeks later in 2006 than in the years before (Tab.1). Nevertheless, female body mass at emergence did not differ significantly between the two periods (2003-05: 237g ± 32, n=27; 2006: 253g ± 54, n=17; t-test, p=0.207).

According to the delayed emergence in 2006, females also reproduced later. Gestation started about two weeks later in 2006 than in the seasons before (Tab.1). The individual latency between emergence date and the onset of reproduction was about one month and did not differ significantly between the two periods (2003-05: 31d ± 22, n=13; 2006: 30d ± 19, n=10; U-test, p=0.852).

Although in 2006 the first juveniles emerged from their natal burrows about 10 days later than in the previous years, natal emergence of the first litter/female/season did not differ significantly between the two periods (Tab.1).

Tab.1: Emergence date, first conception, first and second litter emergence date of individual female Common hamsters in the two periods (2003-05 and 2006), means ± SD, (n).

	2003-2005	2006	p
Emergence date	10.4. ± 15d (27)	22.4. ± 10d (17)	0.003
First conception	5.5. ± 24d (23)	22.5. ± 20d (11)	0.055
First litter emergence	19.6. ± 24d (25)	29.6. ± 21d (12)	0.241
Second litter emergence	5.8. ± 28d (17)	31.7. ± 19d (7)	0.617

To investigate potential time-saving strategies of individual females in 2006, we compared the proportion of females overlapping gestation and lactation after a postpartum oestrus between the two periods. In 2006, most females (86%) successfully weaned a postpartum litter compared to only one third of the females (27%) in 2003-05. Hence, natal emergence dates of females' second litters in 2006 did not differ from previous seasons (Tab.1).

The number of litters per female did not differ between the two periods (Tab.2) and was positively correlated with offspring number per season (2003-05: r_s=0.624, p=0.006, n=18; 2006: r_p=0.760, p=0.007, n=11). However, litter size was significantly lower in 2006 compared to the years before (Tab.2). Consequently, female reproductive output was significantly lower in 2006 than in 2003-05 (Tab.2).

Tab.2: Reproductive output of female Common hamsters in 2003-05 and 2006: Number of litters/female, mean litter size and number of pups/female. Means ± SD, (n).

	2003-2005	2006	p
Number of litters	1.7 ± 0.7 (19)	1.7 ± 1.1 (11)	0.848
Litter size	4.3 ± 2.1 (17)	2.5 ± 2.1 (14)	0.023
Offspring number	6.9 ± 3.9 (18)	3.7 ± 2.2 (14)	0.009

In 2003-05 a female's first litter per season was significantly larger than the second one (p=0.01, Fig.1). When we compared sizes of first and second litters in 2006 we found the opposite result: A female's second litter was larger than her first one (p=0.05, Fig.1). Accordingly, females' first litters had significantly fewer pups in 2006 than in previous seasons (p=0.01, Fig.1). However, in 2006, first-litter juveniles were heavier than those in 2003-05 (2003-05: 97g ± 23, n=27; 2006: 151g ± 32, n=10; t-test, p=0.000).

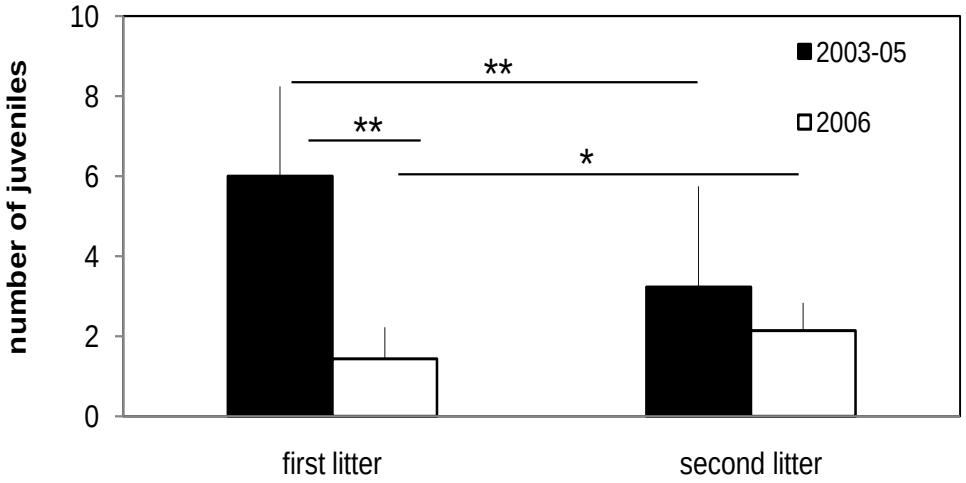

Fig.1: Litter size of individual females' first and second litters in 2003-05 and 2006 (n=13/7), mean ± SD.

The hamsters started to hibernate in late September in all studied years (Tab.3). Due to the delayed onset of above-ground activity in 2006, the hamsters were active for a shorter period than in 2003-05 (Tab.3).

To investigate this in more detail we compared the duration of both the breeding and the postbreeding phase between the two periods. We found no difference in the breeding phase but the postbreeding phase was significantly shorter in 2006 (Tab.3).

Tab.3: Hibernation onset (date), duration (d) of the active period, the breeding and postbreeding period in female Common hamsters during 2003-05 and 2006, means ± SD, (n).

	2003-2005	2006	p
Female immergence	30.9. ± 14d (14)	25.9. ± 19d (8)	0.258
Active season	172 ± 20 (9)	146 ± 25 (7)	0.036
Breeding period	93 ± 27 (16)	94 ± 27 (6)	0.896
Postbreeding period	58 ± 25 (13)	31 ± 17 (6)	0.033

Female body mass at immergence was used as an indicator for body condition shortly before hibernation. Prehibernation body mass did not differ significantly between the seasons but tended to be lower in 2006 than in the previous years (2003-05: 347g ± 26, n=15; 2006: 282g ± 64, n=7; t-test, p=0.087).

When we compared overwinter survival between the two periods, we found higher survival rates in the winter 2006/07 than in earlier years (2003-05: mean: 32%, range: 25% - 43%; 2006: 63%). About two thirds of the females marked in 2006 could be recaptured in the following spring.

Discussion

Environmental effects like climatic changes are known to affect reproduction and survival in many small mammal species (Sinclair et al., 1993; Merritt et al., 2001; Aars & Ims, 2002). Harsh conditions during winter and low food availability can cause high mortality rates and critical physical condition in spring leading to low reproductive success in the following season. Hibernators try to avoid these unfavourable conditions by lowing metabolic costs during torpidity and/or using food stores during euthermic phases in the hibernaculum (Niethammer, 1982; Wendt, 1991; Nechay, 2000; Humphries et al., 2003a; Monecke, 2004; Weinhold & Kayser, 2006). Nevertheless, the limited active season leads to pronounced temporal and energetic constraints that are affected by unfavourable weather conditions. Our results indicate that low ambient temperatures combined with an extended snow cover in spring delayed emergence from hibernation in Common hamsters. Similar observations were made in other populations (Nechay et al., 1977; Grulich, 1986; Kayser & Stubbe, 2003; Weinhold & Kayser, 2006) as well as in other hibernating small mammals like ground squirrels (*Spermophilus lateralis*, Mrosovsky, 1990; *Spermophilus columbianus*, Murie & Harris, 1982). Ambient temperatures during winter are known to affect hibernating patterns (Pévet et al., 1989; Barnes & Ritter, 1993). However, spring temperatures seem to play a major role to stimulate vernal emergence (Mrosovsky, 1990; Murie & Harris, 1982). Moreover, snow falls during spring have been shown to delay emergence in Columbian ground squirrels (Murie & Harris, 1982).

Delayed emergence lead to delayed reproduction in female hamsters. Females mated about one month after emergence in all years studied. This is in line with other studies suggesting that ovarian activity was stimulated after three weeks of exposure to increasing day length (Monecke, 2004). Similar observations were made in male hamsters in the studied population. Although males reactivated the reproductive system in the hibernaculum (Wendt, 1989), testes growth was completed above

ground (Adlassnig, 2005; Lebl & Millesi, 2008). Consequently, in both sexes, gonadal activation has to be completed postemergence.
Natal emergence of the first litters in 2006 was only slightly delayed, indicating that the juveniles in 2006 needed a shorter postnatal period until they started above ground activity.
The exceptional climatic conditions in 2006 appeared to affect reproductive output in Common hamsters. The number of pups born in this season was only half of that in the previous years. This was mainly due to unusually small litter sizes early in the season. The common pattern in all years studied was that a female's first litter per season was larger than her later ones. Franceschini-Zink & Millesi (2008) supposed this to be an adaptive reproductive strategy because juveniles born early in the season have more time to grow and hence better chances for survival. Besides, early born pups can reach puberty in the year of birth and reproduce before their first hibernation period (Petzsch, 1937; Niethammer, 1982; Franceschini-Zink & Millesi, 2008). Maternal effort may decrease with season due to increasing energetic constraints. This could cause less maternal investment in second or even third litters, particularly when the availability of high quality food decreases, resulting in smaller litter sizes (Tauscher, 2006).
On the other hand, juveniles of smaller litters have faster growth and higher survival rates than those of larger ones due to higher maternal investment per pup (Petzsch, 1943; Festa-Bianchet & King, 1991; Tauscher, 2006). This is supported by our results in that juveniles of a female´s first litter in 2006 were significantly heavier than those in 2003-05. Hence, females in 2006 had fewer but larger pups early in the season. We assume that in a delayed season, offspring quality may be more important than quantity.

An effective time-saving strategy to compensate the seasonal delay appeared to be the production of a postpartum litter, overlapping gestation and lactation. In 2006, a higher proportion of females successfully reared a postpartum litter compared to the years before. This might have been facilitated by the lower energetic demands for weaning fewer pups in the first litter (Kenagy, 1990; Festa-Bianchet & King, 1991). Correspondingly, in previous years, high maternal investment early in the season may have caused the loss of postpartum litters in 4 of 8 focal females (Franceschini-Zink & Millesi, 2008). The overlap of lactating the first while being pregnant with the second litter enabled the mothers to significantly catch up time in 2006. Natal emergence dates of second litters were similar in all years.

Females terminated reproduction in late August 2006, slightly, but not significantly, delayed compared to 2003-05. Surprisingly, females in 2006 had a shorter postbreeding period and consequently a shorter active season. During the postbreeding period, females have to build up body fat reserves and food stores to survive over winter (Wassmer, 2004; Weinhold & Kayser, 2006; Franceschini-Zink & Millesi, 2008). Common hamsters can use both strategies, allowing a more flexible preparation for hibernation and a less strict annual schedule compared to non-caching hibernators (Millesi et al., 2004). This is supported by a high individual variation in the length of the postbreeding period in all studied seasons. During 2003-05, females with low or no reproductive output started hibernation earlier than more successful individuals (Franceschini-Zink & Millesi, 2008). Accordingly, low reproductive effort and output in 2006 may enable the females to complete preparation for hibernation in a shorter time span. Food storing may be more pronounced in 2006 because females entered hibernation with the lowest body mass

measured in all studied years. This could indicate that in 2006 females could build up less body fat due to the seasonal delays. Consequently, they had to use the less limited strategy of food hoarding to a greater extend (Humphries et al., 2003a & b).

Food stores appear to be essential during euthermic phases, occurring between immergence and the onset of hibernation (first torpor bouts), between the last torpor bouts and vernal emergence as well as during arousals between the torpor bouts (Petzsch, 1937; Barnes et al., 1986; Wassmer & Wollnik, 1997; Wassmer, 2004; Franceschini-Zink & Millesi and Hufnagl & Millesi, unpubl. data).

Survival rates in the winter 2006/07 were about twice as high as in earlier years. In our opinion this was again due to winter conditions. In contrast to the winter 2005/06, the following one was very mild, particularly in the eastern part of Austria where the mean temperature in January was about 5°C higher than the long-term average (Central Institute for Meteorology and Geodynamics, Vienna, Austria, data obtained from online archive downloaded on 3 June 2009, www.zamg.ac.at). This could on one hand, have lead to lower energetic costs during extended euthermic phases. Secondly, hamsters could have been active above ground during winter (Nechay, 2000; Wassmer, 2004; Weinhold & Kayser, 2006) and collected food in the numerous snow-free days (Grulich, 1986; Wendt, 1989 and 1991). This is supported by the observation that during the winter 2006/07 some females managed to maintain their body mass from immergence in autumn until vernal emergence and a few even gained weight during the winter.

Thus, it appears that low reproductive output caused by harsh weather conditions in one winter was compensated by favourable climatic conditions the following, resulting in similar population densities in our study area in spring 2006 and 2007.

In conclusion, the results demonstrate that environmental factors appeared to affect seasonal timing, reproductive output and prehibernation body mass in female Common hamsters.

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Diet composition of Common hamsters (*Cricetus cricetus*) living in an urban environment

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Abstract

This study investigates the diet composition of Common hamsters (*Cricetus cricetus*) living in an urban area in southern Vienna, Austria. The hamsters were live-trapped throughout the active period of 2006 and from March to June 2007. At capture, the animals were weighed, individually marked and reproductive status determined. Diet composition was recorded by analysing cheek pouch contents that were expelled by the hamsters in the traps. We investigated seasonal and annual variations in diet composition, differences between sex and age classes and between the breeding and postbreeding period. Most of the samples contained fresh, green parts ("leaves") of the predominant plant species growing in the study area: grass, dandelion and clover. Seasonal and annual changes in food preferences were found to reflect the varying availability of different plant components like seeds and berries. Juvenile hamsters collected more berries and fewer rhizomes than older individuals. However, we found no evidence that adult hamsters changed their food preferences in the breeding versus postbreeding period. This indicates that higher energetic demands during critical periods like reproduction are met by increased food intake, without pronounced changes in food preferences. In general, the results demonstrate that Common hamsters are able to cope with the anthropogenically shaped food abundance typically found in urban habitats.

Introduction

For animals living in seasonal environments, food availability and quality vary throughout the year. Herbivorous species depend on the annual cycle of plant development, which is often affected by yearly changes in temperature and rainfall. In addition, the need for caloric input and specific nutrients like proteins or polyunsaturated fatty acids usually varies with sex, age and reproductive state of an individual (Kenagy, 1987; Kenagy et al., 1989a; Strauss et al., 2007). For instance, lactating females have particularly high energetic constraints (Kenagy, 1987; Franceschini, 2001). Consequently, according to the optimal foraging theory, animals should adjust their foraging behaviour to seasonal changes in abundance and quality (energetic value) of food items as well as to the energetic needs for growth, reproduction or other seasonal processes (Mac Arthur & Pianka, 1966).

The harsh winter months with low food availability and increased thermoregulatory costs are most critical for survival. Like several other mammals, Common hamsters (*Cricetus cricetus*) hibernate to avoid cold ambient temperatures and food shortages (Humphries et al., 2003a; Monecke, 2004). During hibernation, the animals typically stay in their burrows and express torpor bouts characterised by reduced metabolism and body temperature (Nechay, 2000; Wassmer, 2004; Weinhold & Kayser, 2006).

In contrast to many other hibernators, Common hamsters do not solely depend on their body fat reserves to survive over winter. Preparation for hibernation is characterised by both accumulation of body fat (internal energy reserve) as well as storing food in the burrow (external energy reserve). Starting in late summer, the animals transport considerable amounts of food into their burrows (Wendt, 1989; Nechay, 2000), using their morphologically specialized, extensible cheek (buccal) pouches (Vander Wall, 1990; Wassmer, 2004). These food items are stored for later ingestion, especially during winter (Nechay, 2000; Weinhold & Kayser, 2006).

Undoubtedly, hoarded food permits animals to manage food availability in space and time - independent of seasonal changes in abundance - and adds a complex dimension to foraging decisions (Gerber et al., 2004). On the other hand, caching behaviour is associated with increased energetic costs due to locomotor activity and can delay the onset of hibernation (McLean & Towns, 1981), thereby extending the active season and the risk of predation (Gillis et al., 2005; Franceschini-Zink & Millesi, 2008).
In Common hamsters, the active season starts in March/April (Monecke, 2004; Franceschini & Millesi, 2004; Weinhold & Kayser, 2006; Franceschini et al., 2007; Franceschini-Zink & Millesi, 2008), and breeding starts shortly thereafter (Nechay, 2000; Franceschini & Millesi, 2004; Franceschini et al., 2007).
Common hamsters differ from many other hibernating mammals in having a 4-month mating season and a high reproductive potential, with females having up to three litters per season (Franceschini-Zink & Millesi, 2008; Hufnagl & Millesi, unpubl. data). High reproductive effort, however, may lead to low body mass in females late in the season and to less time to prepare for hibernation. Earlier studies have shown that females with an extended postbreeding period before entering hibernation had a lower overwinter mass loss than those that started hibernation earlier (Franceschini-Zink & Millesi, 2008). Accordingly, the time period between the termination of reproduction and immergence into hibernation may be crucial for overwinter survival and individual condition in the subsequent spring.

The typical habitats for Common hamsters are agricultural landscapes, where they feed on crops (Nechay, 2000; Weinhold & Kayser, 2006). These food items are highly abundant and storable for long periods. However, modern agricultural technologies - like prompt and careful harvesting, manuring, reduction of perennial cultures and plant diversity - as well as herbicides and rodenticides in combination with excessive trapping have lead to decreasing numbers in this species (Nechay, 2000; Spitzenberger, 2001; Monecke, 2004; Neumann & Jansman, 2004; Weinhold & Kayser, 2006). As a result, Common hamster populations have rapidly declined, particularly in the western range of their distribution area (Mitchell-Jones et al., 1999; Monecke, 2004; Neumann & Jansman, 2004). Hence, in Western Europe their population status is “threatened” and they are protected by the EU Habitats and Species Directive (Mitchell-Jones et al., 1999). Several populations are found in urban habitats like industrial sites, cemeteries, parks, gardens (Mitchell-Jones et al., 1999; Spitzenberger, 2001; Weinhold & Kayser, 2006) or green areas of apartment complexes - like our study site in Vienna. In these locations the vegetation is artificially arranged and quite uniform. Hamsters living in these urban environments are confronted with high human impact: habitat as well as population fragmentation can easily occur due to anthropogenic barriers (streets, buildings, etc.; Franceschini & Millesi, 2001).

In this study we investigate the diet composition of Common hamsters in an urban habitat by analysing cheek pouch contents expelled during live-trapping. In addition, we examine seasonal changes as well as differences between sex and age classes and individuals during the breeding and postbreeding periods. We expected seasonal changes in the availability of plant components, like buds and berries, to be reflected in the samples. We also expected selective food choice to occur mainly during critical periods like reproduction and preparation for hibernation.

Material and Methods

Study area
The study was carried out in an urban area (1.56ha) in southern Vienna, Austria. The Common hamsters (*Cricetus cricetus*) inhabit a park area associated with apartment complexes and are used to the presence of humans, without being fed by them. Regularly mowed grassland accounted for approximately 74% of the study site and mainly consisted of grass (*Poaceae*), clover (*Trifolium* sp.) and dandelion (*Taraxacum* sp.). The remaining 0.4ha were characterised by goldenrain- (*Laburnum anagyroides*), cherry- (*Prunus avium*) and spindle trees (*Euonymus europaea*) as well as lavender (*Lavandula angustifolia*), lilac (*Syringa vulgaris*), wild rose (*Rosa* sp.), privet (*Ligustrum vulgare*) and snowball (*Viburnum opulus*) bushes.

Capture techniques
Live-trapping was carried out three times per week, mainly during the morning hours. The animals were captured with Tomahawk live-traps baited with peanut butter and covered with a cloth. From the traps, the hamsters were immediately released into black cone-shaped cotton sacks equipped with Velcro fasteners, which enabled us to handle them without the use of anaesthesia.
Reproductive status was determined at capture based on testis width in males and on vulval and teat development in females (Franceschini et al., 2007). Gestation was characterised by an increase in body mass paralleled with teat swelling. Parturition and, accordingly, the onset of lactation were identified by a rapid body mass loss at the expected date. Moreover, lactation could be clearly determined by intensely swollen teats, sometimes with milk rests. At weaning, teat size decreased and juveniles started to feed above ground (Franceschini et al., 2007).
The hamsters were fur-marked using a commercial hair dye, allowing individual recognition at distance; a transponder (PIT-tag, Data Mars Company) was injected subcutaneously for permanent identification. After investigation the individuals were immediately released at the place of capture. We compared two age groups: hamsters born in the current season (juveniles) and individuals after at least one hibernation period (adults). Live-trapping was conducted during the active season of the animals in 2006 (March to October). In addition, trapping was performed from March to June 2007, but less frequently than in 2006. We compared the corresponding periods of both years to investigate annual differences, but restricted the further analysis to the 2006 season.

Reproductive phases
In adult females, we defined the individual breeding and postbreeding phase based on the natal emergence of the pups as well as individual teat and vulval development (Franceschini et al., 2007). The breeding phase started at the individual onset of gestation and lasted until the weaning of a female's last litter. The postbreeding period started thereafter and lasted until immergence into hibernation.
Based on the calculated birth dates of the last litters in 2006 (late July to early August), we assumed that the mating period in adult males did not exceed early August. The mating period was followed by the postmating phase, characterised by testis regression in males and lasting until hibernation onset. This classification was supported by behavioural data: we never observed sexual interactions during the defined postbreeding period.

Diet analysis

We were able to collect individual cheek pouch contents at capture because the animals frequently expelled them in the traps. Components of different plant species were identified using field guides (Stichmann & Stichmann-Marny, 1999; Rothmaler, 2000; Vitek et al., 2004; Kusel, 2006) and by comparing them with plant specimens gathered during the active season in the study area.

To examine seasonal changes in food composition, means over two months (April and May, June and July, August and September) were calculated for adult hamsters. This classification paralleled seasonal changes in reproductive events: During April, the hamsters emerged from hibernation and the breeding period started shortly thereafter. Accordingly, mating as well as first gestation and lactation phases in individual females occurred until May. In June and July, first litters emerged from the natal burrows and some of the females produced a second litter (Franceschini & Millesi, 2004; Hufnagl & Millesi, unpubl. data). August and September included the postmating period, characterised by testis regression in males (Lebl, 2005) and weaning of the last litter in females (Franceschini & Millesi, 2004; Hufnagl & Millesi, unpubl. data). In both sexes, these months are used to prepare for hibernation (Wendt, 1989; Nechay, 2000; Franceschini-Zink & Millesi, 2008).

As the first litter emerged from the natal burrow in early June, cheek pouch contents of juvenile hamsters were collected solely thereafter. This enabled collected food samples of adult and juvenile hamsters to be compared from litter emergence until the adults had started to hibernate.

Statistics

Statistical analysis was done using SPSS 15.0 for Windows. Non-parametric tests were applied in all cases. Kruskal-Wallis-tests (significance levels were Bonferroni corrected) and Mann-Whitney U-tests were applied for group comparisons. Significance values were obtained from two-tailed statistics. Differences were considered statistically significant if $p<0.05$. Unless stated otherwise, means with standard deviations are shown in parentheses.

All animal manipulations were approved by the Federal Ministry of Agriculture, Forestry, Environment and Water Management, the City of Vienna and the Ethical Committee for Animal Welfare (GZ 68.210/12-BrGT/2003 and MA22-2605/02) and are in accordance with their guidelines.

Results

To examine annual changes in diet composition, we compared samples of 2007 to those collected in the equivalent time period in 2006 (Fig.1). In 2007, 20 cheek pouch samples were collected between the onset of the active season (12.4.) and late June (22.6.). In 2006, the samples of adult and juvenile hamsters contained significantly more leaves (2006: 83.5% ± 26.7, n=28; 2007: 56.6% ± 43.0, n=20; U-test, p=0.026) and significantly less berries than in 2007 (2006: 3.6% ± 18.8, n=28; 2007: 20.7% ± 34.3, n=20; U-test, p=0.006). Due to these annual differences we restricted the further analysis to 2006.

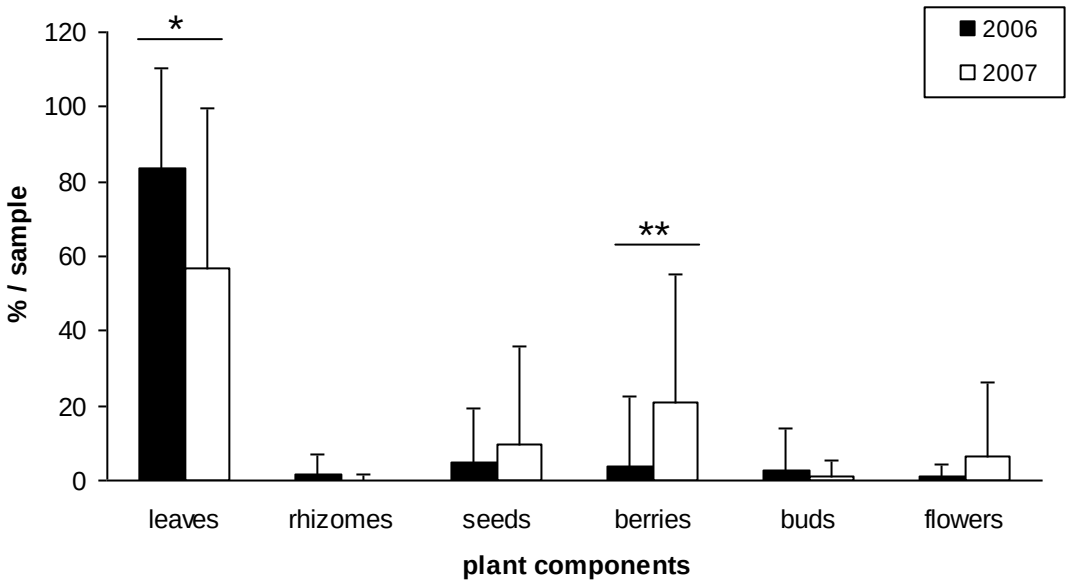

Fig.1: Plant components in cheek pouches of adult and juvenile Common hamsters in 2006 and 2007 (n=28/20), means ± SD.

In 2006, we collected 56 samples of cheek pouch contents. Forty samples were taken from 11 adult females and 16 samples from 9 adult males. On average, 3 samples (range 1-8) were obtained from each individual.

Adult hamsters here mainly fed on fresh, green parts of plants ("leaves") including grass, dandelion and clover (Tab.1). None of the three plants dominated in the samples. Other food items like rhizomes, seeds, berries, buds or flowers were much less frequently taken (Tab.1). Rhizomes and seeds mainly belonged to the grass family *Poaceae*. Dandelion buds were found in twice as many samples as clover.

Tab.1: Percentage of samples containing components from different plant species in adult Common hamsters (n=56) and percentage representation. Solely genus listed if species-level determinations not possible or more than one species of a genus occurred. In grass, all species pooled as family *Poaceae*.

plant components	percentage	plant species/genus		percentage
leaves	66.3	grass dandelion clover	*Poaceae* *Taraxacum* sp. *Trifolium* sp.	41.0 32.5 26.5
rhizomes	12.1	grass clover	*Poaceae* *Trifolium* sp.	88.9 11.1
seeds	9.6	grass maple elm	*Poaceae* *Acer* sp. *Ulmus* sp.	50.0 25.0 25.0
berries	4.8	snowball bush spindle tree cherry tree plum tree	*Viburnum opulus* *Euonymus europaea* *Prunus avium* *Prunus domestica*	25.0 25.0 25.0 25.0
buds	3.6	dandelion clover	*Taraxacum* sp. *Trifolium* sp.	66.7 33.3
flowers	3.6	clover maple	*Trifolium* sp. *Acer* sp.	50.0 50.0

The proportion of leaves/sample was about 80% and did not differ significantly between the three defined periods (Kruskal-Wallis-test, p=0.95, Fig.2). The amount of cached buds was significantly higher in spring (April-May) than in the later periods (Kruskal-Wallis-test, Bonferroni corrected, p=0.013). Although not significant, we found some variation in the other plant components (Fig.2). Berries and rhizomes were only present in samples collected after May, whereas seeds were lacking in samples collected later than July.

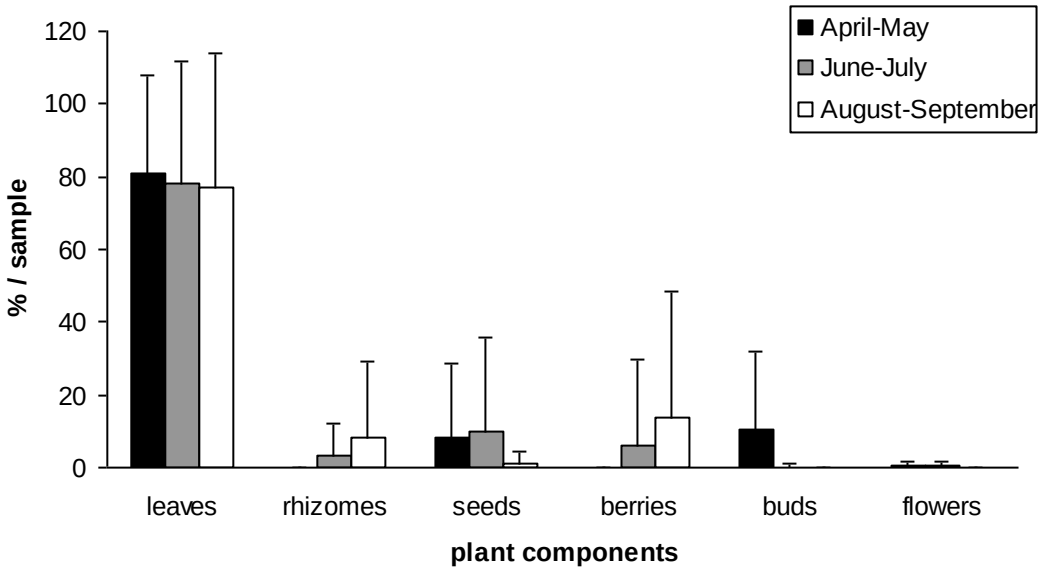

Fig.2: Plant components in cheek pouches of adult Common hamsters (n=7/34/14), means ± SD.

Juvenile hamsters cached significantly more berries than older individuals during the same time period. Moreover, significantly more rhizomes were found in adult compared to juvenile samples (Tab.2).

Tab.2: Percentage of plant components in samples of adult and juvenile hamsters (n=48/43), means ± SD.

	leaves	rhizomes	seeds	berries	buds	flowers
adults	77.7 ± 34.4	4.8 ± 13.3	7.2 ± 22.4	8.1 ± 27.2	0.1 ± 0.6	0.2 ± 1.3
juveniles	70.9 ± 43.0	0.3 ± 1.6	3.4 ± 12.6	23.1 ± 39.8	0.0	2.4 ± 13.5
p	0.893	0.020	0.588	0.016	0.344	0.876

We found sex differences in the cached plant components in that samples of adult males contained significantly more rhizomes than those of adult females (males: 4.3% ± 7.8, n=16; females: 4.0% ± 14.0, n=40; U-test, p=0.032).
We found no significant evidence that adult hamsters changed their food preferences in the breeding versus postbreeeding period (Tab.3). However, during the breeding period, adult males tended to carry less leaves in their pouches than thereafter. Furthermore, in males, seeds were present only in samples collected during the breeding and berries exclusively during the postbreeeding period (Tab.3).

Tab.3: Percentage of plant components in samples of adult male and female hamsters during the breeding and postbreeding periods (males: n=9/7; females: n=27/5), means ± SD.

sex	period	plant components					
		leaves	rhizomes	seeds	berries	buds	flowers
♂	breeding	79.6 ± 31.2	6.5 ± 9.6	11.2 ± 33.1	0.0	0.0	1.0 ± 3.1
	postbreed.	85.5 ± 34.4	1.6 ± 3.5	0.0	12.9 ± 34.2	0.0	0.0
	p	0.091	0.408	0.470	0.681	1.000	0.758
♀	breeding	81.2 ± 30.9	3.0 ± 10.6	8.6 ± 23.1	3.7 ± 19.2	0.7 ± 3.1	0.0
	postbreed.	63.3 ± 45.8	14.1 ± 31.5	2.7 ± 6.0	20.0 ± 44.7	0.0	0.0
	p	0.389	0.650	0.960	0.579	0.801	0.920

We were unable to perform intra-individual comparisons between the breeding and postbreeding period due to the low sample size in both sexes. In females we compared the percentage of each plant component in the samples between the gestation and lactation period and found no significant differences (U-test, $p>0.5$ in all cases, n=12/15). We were able to perform intra-individual comparisons in five individuals for each plant component and found no significant differences between gestation and lactation (Wilcoxon-tests, $p>0.3$ in all cases, n=5).

Discussion

Although Common hamster populations typically inhabit agricultural areas (Nechay, 2000; Spitzenberger, 2001), they apparently cope well with the limited space and plant diversity in urban habitats. On the other hand, the grass area at the study site was frequently mowed and irrigated, enhancing plant growth and quality (Charbonneau, 2008). This seemed to provide sufficient food resources for the hamsters because they fed primarily on the green parts of three plant species - grass, dandelion and clover - throughout the active season. Another reason for this could be that these plants grew all over at the study site in high densities and were therefore easy to obtain close to the burrows, minimizing the risk of predation (Lima & Dill, 1990). Similarly, the diet composition of European ground squirrels (*Spermophilus citellus*, Pieta, 1997) in a suburban park area and of male arctic ground squirrels (*Spermophilus paryii*, Gillis et al., 2005) has been shown to be dominated by only a few but highly abundant plant species.

The comparison between 2006 and 2007 indicated annual changes in diet composition. More leaves but fewer berries were found in 2006. This may be due to the different climatic constraints in these two years. The winter 2005/06 was very long and harsh, with exceptionally low temperatures and snow cover until late March. In contrast, the following winter period was very mild, particularly in the eastern part of Austria, where the mean temperature in January was about 5°C higher than the long-term average (Central Institute for Meteorology and Geodynamics, Vienna, Austria, data obtained from online archive downloaded on 3 June 2009, www.zamg.ac.at). In plants, this may cause an earlier onset of berry development, leading to an increased availability in the early summer of 2007 compared to the previous year.

In contrast to leaves, the availability and consequently the utilization of the other food items found in the samples was seasonally much more limited. Most plants develop

buds in spring. Accordingly, these nutrient-rich plant components were available only briefly. This is reflected in the hamster diet in that buds were almost exclusively found in samples collected during April and May. Moreover, frequent mowing led to a further temporal restriction of buds and flowering plant parts.
Although not significant, the seasonal variation in the availability of some plant parts was to a certain extent reflected in the samples. The amount of berries gathered increased with season, indicating that this food item was mainly cached from late summer until hibernation onset in 2006.
However, the proportion of berries varied highly between the samples. If samples contained berries, these food items were present in high numbers and mostly exclusively. Thus, we assume that hamsters selectively cached berries from bushes and trees, but that they formed only a minor part of their daily diet. Selecting specific items to hoard may be related to ease of harvesting of the different plant species (Gillis et al., 2005). Berries like cherries or plums took longer and were harder to approach and collect, hence less frequently cached. Accordingly, hamsters may have to decide between food items with a longer search and handling time and those close to their burrow but less nutritive and less storable. Berries are well storable and available in the prehibernating period. This makes them appropriate items to store for the winter.
For seeds, a similar assumption was made. Gathering berries and seeds can probably be interpreted as a very selective caching behaviour. Another explanation for the relatively low number of samples containing berries or seeds could be that individuals with cheek pouches full of these valuable items were harder to trap, because they were less interested in the bait placed in the traps. Nevertheless, the data indicate that this caching pattern is a common strategy in the studied hamsters rather than restricted to a few individuals.

Common hamsters were rarely observed feeding above ground. They usually take the food to their burrows and thus shorten their exposure time to predators, social conflicts and inhospitable weather conditions (Buckley & Schneider, 2003; Tauscher & Millesi, 2004). In captivity, juveniles started with this foraging behaviour at the age of about two weeks (Vohralík, 1975), and Tauscher & Millesi (2004) showed that free-living hamsters developed food caching 2-3 weeks after natal emergence.

As soon as reproduction is terminated in late summer or early autumn, hamsters build up food stores. This is in contrast to many other hibernating mammals, which primarily rely on their body fat reserves for overwinter survival (Galster & Morrison, 1976; Humphries et al., 2003a). Common hamsters can use both body fat reserves and food caches, allowing a more flexible preparation for hibernation and a less strict annual schedule compared to non-caching hibernators (Millesi et al., 2004). This is reflected in the extended breeding season and the high individual variation in the duration of the postreproductive period per season (Franceschini-Zink & Millesi, 2008).
In addition, food hoards can be interpreted as a less limited energy reserve compared to body fat, providing a wider range of energetic options (Humphries et al., 2003a & b). Munro et al. (2005) stated that food-storing species should have the energetic flexibility to adjust the depth and duration of torpor bouts primarily as a response to changes in both the size and the quality of their energy reserves. This suggestion may apply to Common hamsters in that sufficient food stores allowed them to vary individual onset of torpor. First results of individual body temperature patterns in the studied population showed that some individuals remained euthermic

in the hibernacula for several weeks and showed both deep and shallow torpor bouts thereafter (Franceschini-Zink & Millesi; Hufnagl & Millesi, unpubl. data). Similar results were found earlier in a telemetry study by Wassmer & Wollnik (1997). However, perishability should affect the choice of food items to store (Gerber et al., 2004). Our study was unable to distinguish between food items that were consumed immediately in the burrow and those stored. Clearly, the tendency to cache declines when decomposition rate increases through time (Gerber et al., 2004). Support for this was found in that well-storable items are cached more selectively.

In spring, food stores could be used during euthermic periods before vernal emergence to prepare for the mating period. This could be more pronounced in males compared to females. Barnes et al. (1986) showed that male Arctic ground squirrels need this time period below ground to complete testicular growth and spermatogenesis. Although testes growth in Common hamsters is not fully completed at vernal emergence, males reactivate the reproductive system in the hibernaculum.
Hence, they may use well-storable food items to prepare earlier and better for the subsequent mating season, being less limited in their energetic options. Evidence for this may be that adult hamster males cached significantly more rhizomes than females. Such sex differences in food caching were also found in Arctic ground squirrels (Gillis et al., 2005). Additionally, the amount of rhizomes in our samples increased towards the end of the active season although this plant component was available throughout the season. Moreover, different contents of rhizomes may play a role. Gillis et al. (2005) stated that rhizomes taken by Arctic ground squirrels (*Polygonum* ssp.) had very high starch contents and anti-inflammatory compounds. Therefore, these plant components provided enough energy when consumed in spring and helped heal wounds due to intrasexual competition.

Juvenile hamsters primarily face the trade-off between growth and preparation for hibernation (Lebl & Millesi, 2008). They have less time to accumulate body fat reserves than older individuals. This is even more pronounced in individuals born late in the season (Franceschini-Zink & Millesi, 2008). They are therefore assumed to depend rather on food caches to survive over winter. Accordingly, juvenile hamsters collected significantly more berries than adult hamsters. On the other hand, significantly more rhizomes were found in adult versus juvenile samples. Perhaps the ease of harvesting played a role for this plant component in adults: experienced hamsters had more practice in collecting rhizomes than juvenile ones.

Neither adult males nor females changed their food preferences with reproductive status. Although the gathered plant components changed marginally between the compared time periods, they reflected seasonal availability more than energetic needs. However, adult males tended to cache less leaves in the breeding versus postbreeding period.
Females stayed close to their burrows during gestation and particularly lactation (Franceschini-Zink & Millesi, 2008). Accordingly, they gathered plant components mainly near their burrows (leaves). The main food items at our study site apparently provided sufficient nutrients for gestation and milk production, as evident in the reproductive success of the investigated individuals. Higher energetic needs during the reproductive period could be reflected in increased food intake (Kenagy, 1989b; Pieta, 1997), but we were unable to measure the quantity of collected food items per day.

Although the grassland at our study site in Vienna was less diverse and productive compared to meadows in the countryside, some plant species suitable for the hamsters occurred in high density and in good quality from spring until autumn. Accordingly, no outstanding seasonal changes in food preferences – independent of age and reproductive status – were found. In general, the data demonstrate the adaptability of this species to various environmental conditions, reflected in high reproductive success and overwinter survival rates.

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Zusammenfassung

Wie viele andere Tiere auch, hat der Feldhamster (*Cricetus cricetus*) mit Habitatsfragmentierung und -verlust zu kämpfen (Nechay, 2000; Weinhold & Kayser, 2006). Primär bewohnte er fruchtbare Steppengebiete (Wendt, 1989; Nechay, 2000; Monecke, 2004). Da diese jedoch mittlerweile größtenteils in Ackerland umgewandelt wurden, erwies sich der Hamster als klassischer Kulturfolger und besiedelt nun vorrangig landwirtschaftlich genutzte Flächen (Niethammer, 1982; Wendt, 1989; Nechay, 2000; Spitzenberger, 2001; Monecke, 2004). Dabei ist zumeist auch schon für eine ausreichende Nahrungsgrundlage der kleinen Nager gesorgt (Niethammer, 1982; Wendt, 1989; Nechay, 2000; Weinhold & Kayser, 2006).
Am Ende des letzten Jahrhunderts kam es dennoch zu einem raschen Rückgang der Feldhamsterbestände - vor allem in ihrem westlichen Verbreitungsgebiet (Mitchell-Jones et al., 1999; Monecke, 2004; Neumann & Jansman, 2004). Als mögliche Ursachen für die Bestandsrückgänge werden einerseits die Intensivierung der Landwirtschaft mit vermehrtem Einsatz von Düngemitteln sowie von Herbiziden und Rodentiziden und andererseits die intensive Bejagung bis hin zum Ende des vorigen Jahrhunderts dieses mancherorts - aufgrund von Massenvermehrungen - als Fraßschädling aber auch als Pelzlieferant angesehenen Tieres diskutiert (Wendt, 1989; Nechay, 2000; Spitzenberger, 2001; Kayser & Stubbe, 2003; Monecke, 2004; Neumann & Jansman, 2004; Weinhold & Kayser, 2006). Dies führte zu dem heute stark fragmentierten Verbreitungsgebiet des Feldhamsters und der genetischen Isolation einzelner Populationen (Wendt, 1989; Weinhold & Kayser, 2006). Dementsprechend ist diese Tierart als „gefährdet“ eingestuft und durch die FFH-Richtlinie der EU geschützt (Mitchell-Jones et al., 1999).
In Folge der fortschreitenden Habitatzerstörung sind einzelne Hamsterpopulationen mittlerweile auch im städtischen Bereich - in Gärten, Parkanlagen, Friedhöfen oder Industriegebieten - anzutreffen (Mitchell-Jones et al., 1999; Nechay, 2000; Spitzenberger, 2001; Weinhold & Kayser, 2006). So nutzt auch die von uns in einer Langzeitstudie (2001-2008) untersuchte Feldhamsterpopulation die Grünflächen einer Wiener Wohnhausanlage. Die Tiere leben hier auf einer künstlich angelegten und somit eher artenarmen Wiese, umgeben von Bäumen und Sträuchern. Dieses stark anthropogen beeinflusste Habitat zeichnet sich durch eine relativ hohe Populationsdichte aus (Franceschini & Millesi, 2001). Neu errichtete Straßen und Gebäude könnten allerdings die Zu- und Abwanderung einzelner Individuen und damit den genetischen Austausch mit anderen Populationen unterbinden. Ziel dieses Langzeitprojektes war es daher, die Entwicklung der Bestände zu dokumentieren und zu untersuchen wie Feldhamster mit urbanen Gegebenheiten zurechtkommen. Die Tiere wurden mit Lebendfallen gefangen, untersucht, individuell markiert und anschließend wieder freigelassen. Als Alterskategorien wurden Juvenile (im aktuellen Jahr geboren) und Adulte (nach mindestens einer Winterschlafperiode) unterschieden.

Feldhamster beenden ihren Winterschlaf - je nach Witterung und geographischer Lage - zwischen März und Mai (Monecke, 2004; Franceschini & Millesi, 2004; Weinhold & Kayser, 2006; Franceschini et al., 2007; Franceschini-Zink & Millesi, 2008). Männchen beginnen die aktive Phase im Allgemeinen vor den Weibchen (Niethammer, 1982; Franceschini & Millesi, 2004). Mit dem Auftauchen der Weibchen aus dem Winterschlaf beginnt auch die Paarungszeit, die bis in den Spätsommer andauern kann (Grulich, 1986; Nechay, 2000; Monecke, 2004; Franceschini & Millesi, 2004; Franceschini et al., 2007; Franceschini-Zink & Millesi, 2008).

Feldhamster weisen - mit bis zu drei Würfen pro Saison - ein für Winterschläfer erstaunlich hohes Reproduktionspotential auf (Franceschini-Zink & Millesi, 2008). Mehrere Würfe pro Saison bedeuten auch mehr Nachkommen in dem betreffenden Jahr (Franceschini-Zink & Millesi, 2008). Zusätzlich zeigten frühere Studien, dass Weibchen, die den Winterschlaf früh im Jahr beendeten, mehr Würfe und somit auch mehr Nachkommen aufziehen konnten (Franceschini-Zink & Millesi, 2008). Daher scheint der Beginn der aktiven Saison den Fortpflanzungserfolg entscheidend zu beeinflussen.
Während der reproduktiven Phase selbst können Weibchen Zeit gewinnen, indem sie sich in einem postpartum Östrus wieder verpaaren. Dadurch kommt es zu einer Überlappung von Laktationsphase des ersten und Trächtigkeitsphase des zweiten Wurfes (Vohralik, 1974; Grulich, 1986; Franceschini-Zink & Millesi, 2008).
Nach der Entwöhnung des letzten Wurfes beginnen sich die Weibchen auf den Winterschlaf vorzubereiten (Wendt, 1989; Nechay, 2000; Wassmer, 2004; Weinhold & Kayser, 2006; Franceschini-Zink & Millesi, 2008). Feldhamster reichern vor Winterschlafbeginn nicht nur vermehrt Körperfett an, sondern tragen mit ihren großen Backentaschen auch Vorräte in ihre Bauten ein (Wendt, 1989; Vander Wall, 1990; Nechay, 2000; Wassmer, 2004; Weinhold & Kayser, 2006). Eine hohe Variation in der Dauer dieser Vorbereitungszeit konnte bereits festgestellt werden (Franceschini-Zink & Millesi, 2008). Generell beginnt die Winterschlafperiode zwischen Anfang September und Ende Oktober (Nechay, 2000; Monecke, 2004; Franceschini-Zink & Millesi, 2008).

Der besonders kalte Winter 2005/06 (der kälteste seit 1987 mit einer Schneedecke bis in den März hinein; Zentralanstalt für Meteorologie und Geodynamik, Wien, Österreich, Online-Archiv) ermöglichte es uns klimatische Einflüsse auf saisonale Aktivitäten sowie den Fortpflanzungserfolg weiblicher Feldhamster zu untersuchen. Die während der Saison 2006 gewonnen Daten wurden dazu mit Ergebnissen aus früheren Jahren (2003-05) verglichen.
Im Frühjahr 2006, tauchten die Weibchen zwei Wochen später aus den Winterschlafbauten auf als in den Jahren davor. Folglich setzte auch die Paarungszeit 2006 entsprechend später ein als 2003-05. Im Jahr 2006 konnte eine signifikant niederere Fortpflanzungsrate festgestellt werden als in früheren Jahren. Es wurden nur halb so viele Jungtiere geboren wie in den Saisonen 2003-05. Hauptverantwortlich dafür waren die ersten Würfe in der Saison 2006, die wesentlich weniger Jungtiere enthielten als in den Jahren davor. Aufgrund der geringeren Wurfgröße konnten die Mütter offenbar mehr in ihren Nachwuchs investieren, da die Jungtiere der frühen Würfe 2006 bei ihrem ersten Auftauchen aus dem Nestbau signifikant schwerer waren als 2003-05.
Um den zeitlichen Rückstand aufzuholen, hatten 2006 die meisten Weibchen (86%) einen postpartum Östrus, während es 2003-05 nur rund ein Drittel war. Diese Strategie erwies sich als erfolgreich, da die Geburt der zweiten Wurfserie 2006 etwa zur selben Zeit erfolgte wie in den vorangegangenen Jahren.
Die Vorbereitungszeit für den Winterschlaf, war jedoch 2006 deutlich kürzer als in den Jahren davor. Dies lag vor allem daran, dass Weibchen 2006 nicht - wie aufgrund des späteren Aktivitätsbeginns zu erwarten - ihren Winterschlaf weiter in den Herbst verschoben, sondern sich - wie in früheren Jahren - Ende September in ihre Winterschlafbauten zurückzogen. Der geringere Reproduktionserfolg und damit auch -aufwand 2006 könnte den Weibchen eine kürzere Vorbereitungsphase für den Winterschlaf ermöglichen. So zeigten bereits Franceschini-Zink & Millesi (2008),

dass Weibchen mit geringem Reproduktionserfolg früher mit dem Winterschlaf begannen als Individuen mit mehr Nachkommen.
Diese verkürzte Vorbereitungszeit machte sich jedoch - wenig überraschend - im Körpergewicht der Weibchen zu Winterschlafbeginn bemerkbar. 2006 hatten die Weibchen bei Winterschlafbeginn das geringste Körpergewicht aller Studienjahre. Dies könnte darauf hinweisen, dass diese Tiere vermehrt auf Futtervorräte - anstatt auf Körperfettreserven - setzten. Diese Vermutung wird durch die erstaunlich hohen Überlebensraten über den Winter 2006/07 bestätigt. Während 2003-05 rund ein Drittel der Weibchen im nächsten Frühling wieder gefangen wurden, waren es 2006 doppelt so viele. Allerdings dürfte hier den klimatischen Bedingungen eine entscheidende Rolle zukommen: Im Gegensatz zu einem kalten Winter 2005/06 war der Winter 2006/07 außergewöhnlich mild. Dies könnte dazu geführt haben, dass einige Tiere während der Wintermonate ihren Bau verließen - wie es auch bei anderen Populationen beschrieben wurde (Nechay, 2000; Wassmer, 2004; Weinhold & Kayser, 2006) - und Nahrung sammelten (Grulich, 1986; Wendt, 1989 und 1991). Diese Annahme wird dadurch gestärkt, dass einige Weibchen ihr Körpergewicht über den Winter halten konnten und manche bis zu ihrem Wiederfang im Frühling sogar an Gewicht zulegten.
Zusammenfassend kann festgehalten werden, dass ungünstige Wetterbedingungen zu zeitlichen Verschiebungen des Jahreszyklus und dadurch zu niederen Fortpflanzungsraten führen können, jedoch günstiges Wetter im Winter sich positiv auf die Überlebensrate auswirken und - wie in unserem Fall - vorangegangene Defizite im Reproduktionserfolg kompensieren kann. Die Populationsdichte im Frühling 2007 war etwa gleich hoch wie die 2006. Die Ergebnisse zeigen außerdem, dass Feldhamster auch im urbanen Habitat opportunistische Reproduktionsstrategien aufweisen.

Ein weiterer Aspekt dieser Arbeit war es, erste Einblicke in die von Hamstern benötigten Nahrungsressourcen bzw. die im Untersuchungsgebiet genutzten Nahrungsquellen zu gewinnen. Da die Tiere den Inhalt ihrer Backentaschen oftmals in den Fallen entleerten, war es möglich, die Nahrungsbestandteile einzusammeln und auf die darin enthaltenen Pflanzenarten sowie -bestandteile (Blätter, Wurzeln, Samen, Beeren, Knospen oder Blüten) zu bestimmen.
Die meisten Proben enthielten die im Untersuchungsgebiet am häufigsten vorkommenden Pflanzenarten: Gras, Löwenzahn und Klee. Von diesen Arten wurden zumeist die Blätter (in 80% der Proben) gesammelt, alle anderen Pflanzenarten und -bestandteile waren in weitaus geringerer Häufigkeit vorhanden.
Wie erwartet, kam es zu saisonalen Änderungen in der Nahrungszusammensetzung aufgrund der jahreszeitlich schwankenden Verfügbarkeit der einzelnen Bestandteile: Während Knospen signifikant öfter im April und Mai gesammelt wurden, waren Beeren hingegen nur in Proben ab Anfang Juni 2006 enthalten.
Juvenile Hamster sammelten signifikant mehr Beeren als adulte Tiere, Adulte hingegen mehr Wurzeln als Juvenile. Ein Grund dafür könnte in der guten Haltbarkeit der Beeren über den Winter liegen. Jungtiere - vor allem spät in der Saison geborene - sind in der Vorbereitung für den Winterschlaf zeitlich weitaus mehr limitiert als adulte Tiere (Franceschini-Zink & Millesi und Lebl & Millesi, 2008). Sie müssen mehr in ihr Wachstum investieren und haben daher, kaum die Möglichkeit ausreichend Körperfett für den Winter aufzubauen. Daher sind adäquate Futtervorräte für den Winter für sie besonders wichtig. Dabei werden sichtlich gut lagerbare Nahrungsbestandteile bevorzugt.

Unter den adulten Hamstern sammelten die Männchen deutlich mehr Wurzeln als Weibchen. Hamster können diesen lange haltbaren Pflanzenbestandteil während euthermer Phasen im Herbst und Frühling nutzen (Niethammer, 1982). Dabei haben die Tiere entweder ihren eigentlichen Winterschlaf noch nicht begonnen bzw. bereits beendet und sind unterirdisch aktiv, verlassen jedoch nicht den Bau (Petzsch, 1937; Wassmer & Wollnik, 1997; Wassmer, 2004). So können die Tiere im Frühjahr einerseits ungünstige Wetterperioden überdauern und sich andererseits schon unterirdisch auf die bald beginnende Paarungszeit - mit der Ausbildung der Hoden - vorbereiten (Barnes et al., 1986; Wendt, 1989). Hier scheinen Futtervorräte eine entscheidende Rolle zu spielen und Männchen mit entsprechend guten Vorräten bereits vor dem Auftauchen aus dem Winterschlaf einen Vorteil zu verschaffen.
Hinsichtlich des Fortpflanzungsgeschehens fanden wir keine signifikanten Veränderungen in der Nahrungszusammensetzung. Trächtige Weibchen sammelten ähnliche Pflanzenarten und -teile wie Laktierende. Daraus lässt sich schließen, dass diese Pflanzen (Löwenzahn, Klee und Gras) ausreichend Nährstoffe enthielten bzw. der erhöhte Bedarf an Nährstoffen während der Fortpflanzungszeit durch eine gesteigerte Nahrungsaufnahme gedeckt werden konnte. Ähnliche Ergebnisse lieferten auch Studien von Erdhörnchenarten (Kenagy, 1989; Pieta, 1997).

In dieser Studie konnte gezeigt werden, dass Feldhamster mit dem anthropogen beeinflussten Nahrungsangebot im urbanen Lebensraum gut zurechtkommen, auch wenn sich dieses stark von den ursprünglichen Habitaten und landwirtschaftlich genutzten Flächen unterscheidet. Jedoch kann - trotz der hohen Anpassungsfähigkeit dieser Tierart - ein derart stark anthropogen beeinflusstes Habitat nicht den natürlichen Lebensraum des Feldhamsters ersetzen. Zum langfristigen Fortbestand dieser Art wären Schutzmaßnahmen - in erster Linie in natürlichen Habitaten - und ein hamsterfreundliches Management in der Landwirtschaft dringend erforderlich.

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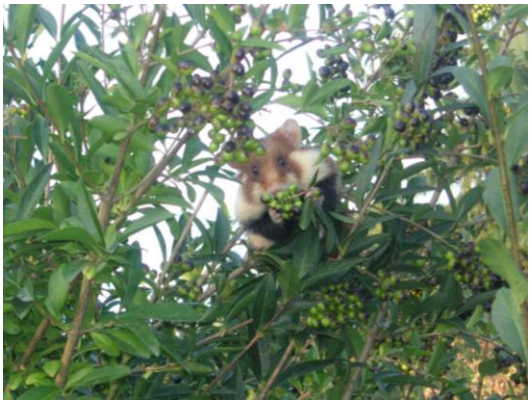
Photo gallery

Study site in southern Vienna, Austria:
a park area associated with apartment complexes.

Typical hamster burrow (left), with pathways between the entrances (right).

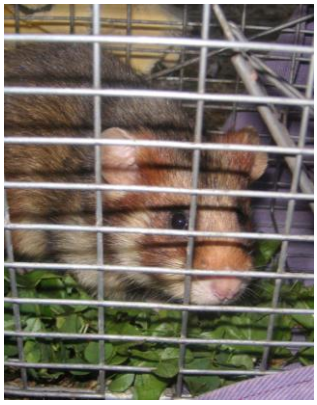
Hamster released in front of its burrow.

Juvenile hamster emerging from the natal burrow.



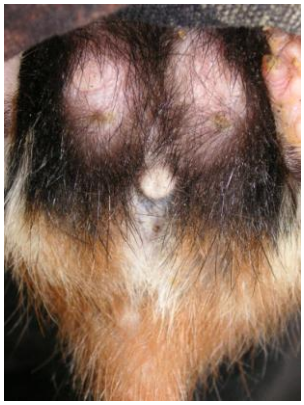
Foraging hamsters, with full cheek pouches (left)
and on top of a privet bush (right).





Juvenile Common hamster in front of (left) and in a Tomahawk live trap (middle). Adult hamster in the trap with expelled cheek pouch contents (leaves from clover) (right).

Hamster in the cotton sack, being weighted.



Investigating teat and vulval status in a female hamster.

Measuring testes width in a male hamster.

Individual fur marking with red hair dye.

Hamster being released from the cotton sack after investigation.

Foraging hamster with red fur marking, allowing individual recognition at distance.

Curriculum vitae

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Berufserfahrung

März-April 2009	**Universität Wien - Department für Verhaltensbiologie** Tutorin für die „Übungen zur Physiologie der Tiere“
September 2008	**Magistrat der Stadt Wien - MA 49, Forstamt** Führungen für Schulklassen im Erholungsgebiet Wienerberg
seit April 2007	**Verein „Freunde der Perchtoldsdorfer Heide“** Aufbereitung von Schulungsunterlagen, Organisation und Abhaltung von Führungen (je nach Nachfrage)
seit April 2005	**Verein „Freunde der Perchtoldsdorfer Heide“** Monitoring von europäischen Zieseln (10Tage/Saison)
seit Mai 2004	**Schönbrunner Tiergarten GmbH - Besucherservice** Führungen für Kinder, Einschulung neuer Mitarbeiter, Erarbeitung von Programmkonzepten (25Stunden/Monat)

Kongressbeiträge

HUFNAGL, S. & MILLESI, E. (Poster): Seasonal changes in diet composition of Common hamsters (*Cricetus cricetus*). 82nd Annual Meeting of the German Society of Mammalogy, 14.-18. September 2008, Wien/A.

HUFNAGL, S. & MILLESI, E. (Vortrag): Seasonal constraints and reproductive performance in Common hamsters. 15th Meeting of the International Hamsterworkgroup, 11.-14. Oktober 2007, Kerkrade/NL.

HUFNAGL, S. & MILLESI, E. (Poster): Seasonal effects on reproductive timing and success in female Common hamsters. 14th Meeting of the International Hamsterworkgroup, 1.-3. Oktober 2006, Münsterschwarzach/D.