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„Hibernation patterns in free-ranging Common hamsters (*Cricetus cricetus*)"

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Table of Content

Abstract **1**

Introduction **3**

Material & Methods **7**

Study site 7

Study period 7

Field techniques 8

Temperature recording 8

Ethical statement 9

Hibernation parameters 9

Seasonal timing 10

Conditional parameters 10

Statistics 11

Results **12**

General patterns 12

Hibernation period 13

Pre-hibernation period 15

Post-hibernation period 16

Conditional consequences 17

Survival rate 19

Discussion **20**

Literature **27**

Appendix **34**

Zusammenfassung 34

Abstract

Common hamsters (*Cricetus cricetus*) are facultative hibernators. These animals rely on a combination of internal (body fat) and external (food hoards) energy reserves to outlive a time of food shortage and low ambient temperatures. After immergence into their burrows (hibernacula) they execute periods of pre-hibernation euthermy, hibernation and post-hibernation euthermy. Hibernation includes alternating periods of deep torpor, characterized by decreased metabolic rate and body temperature and short euthermic phases.

We investigated a free-ranging population living in an urban area in Vienna. Animals were equipped with subcutaneously implanted iButtons. These data loggers recorded body temperature during the time in the hibernaculum, which enabled us to analyze hibernation patterns and to compare timing and duration of different phases between juvenile and adult individuals. All ten focal animals showed regular hibernation patterns but varied in the durations of defined periods.

Age differences were found in hibernation onset, time in torpor and the minimum body temperature during torpor (T_{min}). Juveniles started to hibernate earlier, spent more time in torpor and showed a lower T_{min} than adults probably to compensate their lower energy reserves. Interesting relationships were also found between timing and condition. Animals with higher body mass at immergence showed a later hibernation onset. Later onset was related to longer pre-hibernation euthermy, which could be used to feed on stored food. Animals that showed longer hibernation durations and spent more time in torpor emerged with lower body mass. Thus, the extended hibernation duration could be caused by lower quantity or quality of external energy reserves. Accordingly animals with longer periods of post-hibernation euthermy emerged with an increased body mass. A better condition at emergence could positively affect reproductive success. In general, the results indicate that hamsters with fewer food reserves spent more time in torpor to save energy while animals with more energy reserves could extend the euthermic periods and emerge in a better condition.

Introduction

The Common hamster is a typical synanthropic species and was spread from Western Belgium over Central Europe and many areas in Asia to North Western China. Primarily it inhabited open grassland and fertile steppe habitats (Feoktistova et al. 2013).

Common hamsters show an annual life cycle with an active and a hibernation period. During the active season hamsters show bimodal daily activity patterns with peaks from 4 a.m to 10 a.m and from 4 p.m to 10 p.m (Gebhardt 2005, Kaim et al. 2013). Photoperiod plays an important role during the annual cycle in Common hamster (Monecke et al. 2014). Annual patterns in body mass changes and reproduction are known for this species (Monecke & Wollnik 2005). The transition from the reproductive to the non-reproductive season is triggered by shortening daylength (<15 h) during a sensitive phase in mid-July. Saboureau et al. (1999) showed that a photoperiodically synchronized circannual clock controlled seasonal reproduction. The change in the photoperiod led to gonadal atrophy. In mid-November a second photoperiodically sensitive phase could be determined. In animals exposed to lengthening photoperiod gonadal regrowth could be observed (Monecke & Wollnik 2004).

After vernal emergence during March and April the active season lasts until November when the last animals immerge (Weinhold & Kayser 2006). Sex and age differences in the timing of immergence have been determined, with adult males immerging already in late August (Franceschini-Zink & Millesi 2008, Weinhold 2008). After emergence the mating season starts and lasts from April/May to August (Seluga et al. 1996, Weinhold & Kayser 2006). This restricted period of reproduction is caused by an active season of only 6-7 months (Hufnagl et al. 2011). Common hamsters show a promiscuous mating system with males emerging from the hibernacula before females (Weinhold & Kayser 2006, Franceschini-Zink & Millesi 2008).

In contrast to other hibernators Common hamsters are able to raise one to three litters per year (Franceschini & Millesi 2005, Kayser & Stubbe 2003). Under good environmental conditions female juveniles of first litters are even able to reproduce during their first season (Niethammer 1982, Kayser & Stubbe 2003). More litters also result in a higher reproductive output per season (Hufnagl et al. 2011). In population dynamics Common hamsters follow the r-strategy (Weinhold 2008) producing up to 30 pups during one season (Niethammer 1982). At the end of the active season hamsters immerge into their hibernacula.

After immergence hamsters do not immediately start to hibernate. They stay euthermic in their burrows without showing above-ground activity. The period from immergence until

hibernation onset has been shown to vary among individuals and between the sexes (Siutz et al. 2016). In spring a similar period could be identified. After hibernation is terminated hamsters stay in post-hibernation euthermy until emergence (Siutz et al. 2016).
Hibernation onset depends on age and sex and occurs between late October and early January. Hibernation is terminated with the last arousal between February and April (Siutz et al. 2016).
For winter survival, hibernators show different strategies in the accumulation of energy reserves. Some collect food over the active season to build up food stores (Niethammer 1982, Weinhold & Kayser 2006, Humphries et al. 2003b) while others try to increase their body mass and their proportion of body fat (Davis 1967, Buck & Barnes 1999, Humphries et al. 2003b). During the winter season hibernators live on external or internal energy reserves or use a combination of both (Humphries et al. 2003b) like Common hamsters (Franceschini-Zink & Millesi 2008, Siutz & Millesi 2012).
In both adults and juveniles, males show a higher proportion of body fat than females (Siutz et al. 2012). After the mating season males spend most of their time feeding above ground while females are observed caching food (Siutz et al. 2012). Females have to wean their offspring before they can prepare for the upcoming winter (Hufnagl et al. 2011).
The diet of Common hamsters includes greens, tubers, buds, leaves, flowers but also rhizomes, berries or seeds (Waßmer 2004, Hufnagl 2009). Latter especially are very suitable for storage because seeds decay not as fast as tubers or buds. Hamsters collect food in their cheek pouches and hoard it in distinct chambers in their underground burrows (Hufnagl et al. 2011, Waßmer 2004, Weinhold 2008). Usually these chambers are near the nest and can be located in a depth of up to 2 m accessible over steep tunnels (Weinhold 2008).
In addition to the accumulation of internal and external energy reserves animals also show different physiological strategies. For energy conservation several species, like the Common hamster, can use short torpor bouts or prolonged periods of hibernation to survive during the cold season (Waßmer & Wollnik 1997). Similar hibernation patterns were found in different ground squirrel species. Variability ranged from short torpor bouts to multiday torpor bouts with reduced body temperature near the ambient temperature (Geiser et al. 1990, Michener 1992).
In most mammals and birds one of two different torpor patterns exists. Daily torpor stands in contrast to hibernation or prolonged torpor (Geiser 2004). Daily torpor is characterized by shorter periods of torpor (less than 24 h) with reduced body temperatures resulting in a $T_{b\,min}$ between 10° and 25° C (Geiser & Ruf 1995). Daily torpor alternates with periods of euthermy, which are used for foraging and feeding (Geiser & Ruf 1995, Geiser 2004). Torpor in daily heterotherms is controlled by a circadian system, which enables animals to follow the

daily light cycle (Geiser & Ruf 1995). In hibernators the circadian clock might influence torpor and arousal although it seems to be suppressed until a restart after the hibernation season (Ruf & Geiser 2014).

Periods of metabolic depression and lowered body temperature (torpor) alternate with periods of euthermy (arousals). Together they mark the period of hibernation (Michener 1992, Geiser & Ruf 1995, Waßmer & Wollnik 1997, Millesi et al. 2001). In Common hamster entries into torpor seem to follow a circadian cycle. The start of deep torpor bouts regularly occurs around midnight and follows 24-hour rhythmicity whereas arousals are randomly distributed (Canguilhem et al. 1994, Körtner & Geiser 2000, Waßmer & Wollnik 1997).

Torpor might also play an important role in many other survival strategies (all reviewed in Geiser & Brigham 2012). It could enhance the ability of fat storage of migrating birds (Carpenter & Hixon 1988) or it supported juvenile development during periods of harsh environmental conditions. Chicks of king penguins were able to slow down growth and used heterothermy to endure several months of food shortage (Eichhorn et al. 2011). Female bats used torpor for storing sperm during hibernation. Because of their prolonged oestrus they were able to develop embryos successfully in spring without the presence of males (Racey 1979). Animals could use torpor for water conservation (Warnecke et al. 2008) or to outlive periods of drought (Doucette et al. 2012). Furthermore torpor seemed to be a strategy to avoid inter-specific competition on a limited diet (Levy et al. 2011). In Alpine marmots (*Marmota marmota*) torpor even showed positive effects on intestinal parasites that left for another host because of low T_b (Callait & Gauthier 2000). One of the most intriguing results was found by Geiser & Turbill (2009). They showed that 93.5 % of recently extinct mammal species (n=61) belong to the group of homeotherms. Torpid mammals were able to execute a “sit and wait” strategy and therefore avoided extinction.

But hibernation especially torpor can also have costs for animals. Torpor could affect neuronal tissue damage (Humphries et al. 2003b) or oxidative stress (Carey et al. 2000). Furthermore it negatively influences cellular functions or inhibits the immune system (Munro et al. 2005, Zervanos et al. 2013). Torpor even could inhibit the restorative function of sleep or lead to sleep deprivation. This sleep debt has to be paid during arousals and would be less if the period of torpor was shorter (Daan et al. 1991). Another negative cost of hibernation is memory retention. Millesi et al. (2001) showed a loss of spatial and operant task memory after hibernation in European ground squirrels, while social recognition was unaffected. Torpor also could affect the hippocampal signal transduction. Reduction of synaptic efficacy may lead to a reduction in neuronal connectivity in ground squirrels (Strijkstra et al. 2003).

Population development of Common hamsters changed in the past decades. In Germany during the middle of the 20th century annual trapping rates of two million hamsters were common (Teubner et al. 1996) while in recent time numbers of Common hamsters declined in their western distribution (Ulbrich & Kayser 2004, La Haye et al. 2012). Accordingly the distribution over grasslands and steppe habitats declined, while increasing abundance was found in urban areas with gardens, cemeteries or parks (Feoktistova et al. 2013).

In Poland Common hamsters were found around the Experimental station of the Agricultural University of Lublin with a density of 2.8 individuals per hectare (Banaszek & Ziomek 2010). In Slovakia a new site of Common hamster was found in Košice containing a reproductive micro-population on the area of a cemetery in 2009 (Canady 2013). Like in Feoktistova et al. (2013) it shows that a synurbanization for steppe animals is possible.

In Vienna, Austria a previous study was done on population density (Musil 2010). In a similar area to our study site a density of 14 adult hamsters per hectare in 2006 and a density of 38 adult hamsters per hectare in 2008 was found. Musil (2010) assumed high variation in population densities of Common hamsters resulting from the great ability to adapt to urban environment. Nechay (2000) categorizes 21-50 active burrows per hectare as a very high population density. However borrow and population densities are not directly correlated (Weinhold 2008).

Over-winter survival is necessary for sufficient reproductive output. Survival rates of 62.5 % were found for hamsters living in high population densities (Franceschini & Millesi 2006). Calculations of hibernation mortality dependent on food availability resulted in a survival rate of only 15.4 % but investigations of free-ranging populations showed a real survival rate of 38.5 % (Wendt 1991). Weinhold & Kayser (2006) named several causes for mortality in Common hamster. In addition to mortality during hibernation other threats like predation, parasites and diseases, agriculture and traffic were listed. Shortage of food supply might be the main cause for overwinter mortality, which is calculated with 50-60 % (Weinhold 2008).

The aim of this present study was to investigate hibernation patterns and the timing of immergence and vernal emergence as well as hibernation onset and end in free-ranging Common hamsters. Timing, body temperature patterns and conditional parameters were compared between adult and juvenile individuals.

Materials and Methods

Study site

Free-ranging Common hamsters were studied in an urban area in Vienna, Austria. The hamsters lived on green areas (2.25 ha) of a public hospital (Kaiser-Franz-Josef Spital, Favoriten) located between buildings and streets. The vegetation consisted of separated trees and bushes on the greens, which were divided by visitor pathways (Fig. 1). Throughout the season 300 individuals were captured and marked (adults: 32 females and 41 males; juveniles: 101 females and 126 males). The density of adult hamsters was approximately 32 per ha.

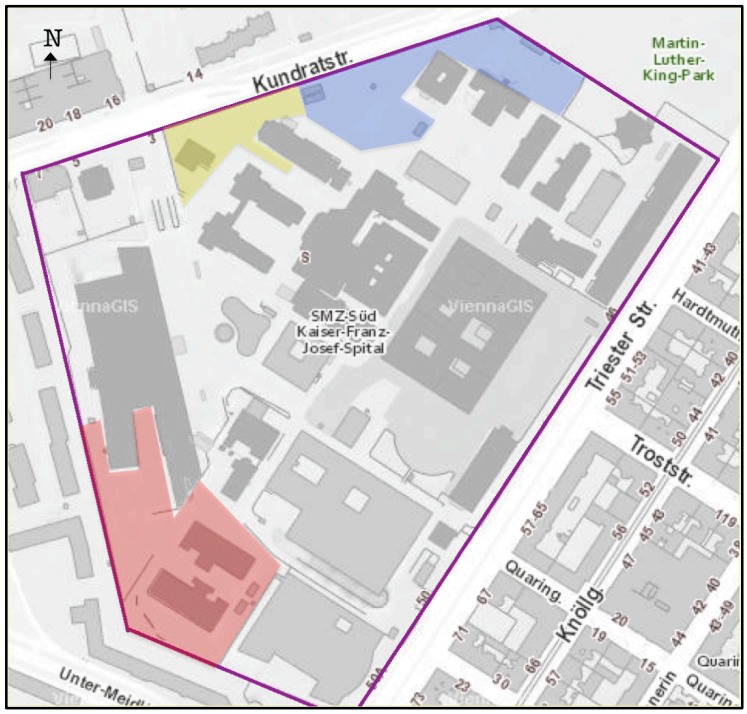

Figure 1: Map of Kaiser-Franz-Josef Spital in Favoriten (Vienna). The violet line edges the hospital area. The dark grey parts are hospital buildings. Colored areas mark the three trapping sites: Red is "Geriatrie" (1.15 ha), yellow is "Kapelle" (0.4 ha) and blue is "Psychiatrie" (0.7 ha).

Study period

The study was part of a long-time investigation in this urban area, which started in October 2011. Focal individuals were monitored during the active season, the hibernation period and at emergence in the following spring. Trapping was done 3-4 times a week during the active season from April until November, either in the morning from sunrise to approximately 11:00 am or in the evening from 5:00 pm until sunset (Roiser-Bezan 2010).

Field techniques

For data collection the capture-mark-recapture technique was applied, using Tomahawk live traps. The traps were baited with crunchy peanut butter and placed in front of the individual burrow entrances (Franceschini-Zink & Millesi 2008). Traps were checked every 20 minutes. Trapped hamsters were released from the traps into cotton sacks equipped with Velcro fasteners for easier handling (Siutz & Millesi 2012). Thus the manipulation was possible without anesthesia and lasted about 5-10 minutes for each hamster.

For each individual the following parameters were recorded: date, time, weather conditions, sex, age (juvenile, yearling or adult), body mass (g), molt (none, little, medium, strong), reproductive status (males: width of testes; females: open/closed vagina and size of teats), as well as the length of head, tibia and hind foot.

Body mass and length of head, tibia and food were used for body fat calculations. A non-invasive method described in Siutz et al. (2012) was applied. This method was previously validated by determining the proportion of body fat in carcasses of dead found hamsters using lipid extraction. Proportion of body fat could be calculated as percentage of total wet mass and enabled to predict the proportion of body fat using a multiple regression model integrating morphometric parameters (Siutz et al. 2012).

Hamsters that were caught for the first time were implanted subcutaneously with a transponder chip near the hind leg for an accurate individual identification. Before being released each hamster was marked with an individual symbol on the rear part of its back for distant recognition. This was done using commercial hair dye, for females in red and for males in black. Thereafter the hamsters were released at the entrance of their burrows (Franceschini-Zink & Millesi 2008).

Temperature recording

In autumn, 18 focal hamsters (6 adult females, 8 juvenile females and 4 juvenile males) were caught and brought to a veterinary clinic. Temperature loggers (iButtons) were programmed to measure temperature in 90 min-intervals, covered with Elvax (ethylene vinyl acetate resins) and paraffin, sterilized. The iButtons (15 mm in diameter) were subcutaneously implanted in the neck region under isoflourane anesthesia. After implantation and recovery from anesthesia (1-3 h) the hamsters were returned to the field site and released at their burrows.

Further recapture attempts and observations of focal and non-focal animals in the study area were carried out until their immergence into the hibernacula. Burrow monitoring was continued to monitor surface activity of hamsters. For this purpose the entrances of burrows were blocked with loose materials like leaves, twigs or grass. Active hamsters removed these materials, indicating activity above ground.

To ensure the recapture of all emerged focal individuals in the following spring, daily burrow monitoring was carried out starting in February 2015. Active hamsters removed these materials, indicating vernal emergence.

Ten of 18 focal animals could be recaptured (3 adult females, 5 juvenile females and 2 juvenile males). Removal of the iButtons was done using the same procedure as during implantation in autumn. Data logger readout was edited by provided computer software.

Ethical statement

All procedures performed on animals were approved by the Austrian Ministry of Science, Research and Economy, City of Vienna (2546/08, 1216/09, 2484/10), the Ethical Committee for Animal Welfare (GZ BMWF-66.006/0020-II/3b/2012) and the University of Vienna (2014-008, 2015-010).

Hibernation parameters

The following parameters were defined to analyze individual hibernation patterns (Tab. 1). The individual's immergence date marked the starting point of time underground followed by a period of pre-hibernation euthermy (Fig. 2). The first deep torpor bout (DTB) marked the hibernation onset followed by alternating torpor bouts and arousal episodes, characterizing hibernation. Rewarming after the last torpor bout marked the end of the hibernation phase and was followed by a period of post-hibernation euthermy, lasting until vernal emergence (Fig. 2).

Table 1: Hibernation parameters of Common hamsters.

Parameter	Description
DTB - number - length	Deep torpor bout Total number of DTBs. DTBs are defined by lowering the body temperature under 20° C for a period of at least 24 h (Waßmer & Wollnik 1997) Duration of a DTB, mean/individual
Time in torpor	Time, the animals spend in a state of torpor, lowering the body temperature approximately to the ambient temperature
DTB length	Duration of a DTB, mean/individual
T_{min}	Minimal body temperature during the period of deep DTBs, mean/individual
Hibernation duration	Time span between the onset of the first and the end of the last DTB
Hibernation onset	Date of the first DTB
Hibernation end	Date of the last DTB ending

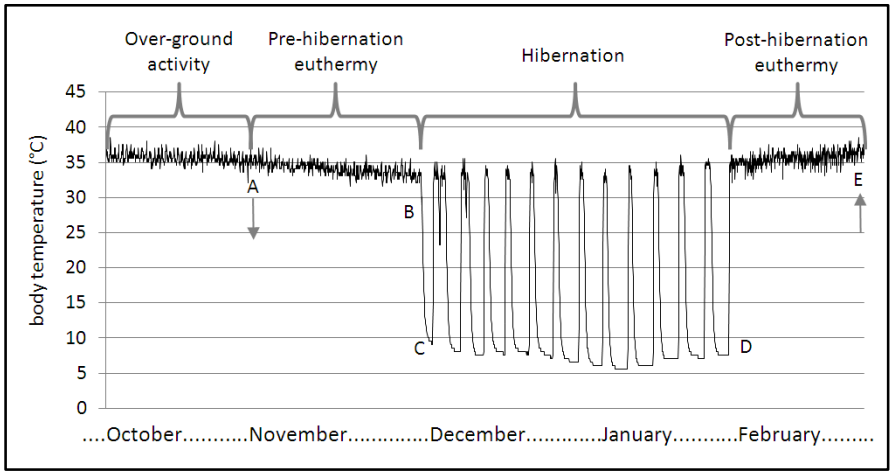

Figure 2: Hibernation pattern of an adult female hamster. A: Day of immergence. During pre-hibernation period hamsters showed a state of normothermy. B: First DTB characterizing hibernation onset. C: Body temperature during torpor, followed by an arousal. D: Last arousal marking the end of hibernation. E: Post-hibernation period terminated at the day of vernal emergence.

Seasonal Timing

Burrow monitoring was carried out to determine the exact dates of immergence and emergence. That enabled the calculation of certain periods during winter (Tab. 2).

Table 2: Time parameters of Common hamster showing the length and the timing of certain periods during the season.

Parameter	Description
Immergence date	Day of the year, when animals immerged into the hibernacula and terminated above ground activity
Pre-hibernation euthermy	Time span (d) from immergence until the first DTB
Post-hibernation euthermy	Time span (d) from the end of the last DTB until vernal emergence
Emergence date	Day of the year, when animals emerged from the hibernacula
Time in hibernaculum	Total number of days animals stayed underground, including pre-hibernation euthermy, hibernation duration and post-hibernation euthermy
Non-hibernating period	Sum of pre-hibernation euthermy and post-hibernation euthermy (d)

Conditional parameters

The following parameters were defined to compare the condition of the hamsters before and after hibernation as well as the changes in body mass and proportion of body fat during winter. Immergence body mass was defined as the body mass at time of the last capture in the season if the hamster immerged into the hibernaculum within 10 days thereafter. The proportion of body fat at immergence was calculated using morphometric parameters measured during the last capture (Siutz et al. 2012).

Emergence body mass was determined at first capture in spring. Vernal burrow monitoring ensured that the hamsters were captured within 10 days after they had emerged from their hibernacula. Proportion of body fat at emergence was calculated accordingly to that before immergence.

To calculate changes in body mass and proportion of body fat over winter two parameters were defined. Δbm was defined as emergence body mass minus immergence body mass and Δbf was defined as proportion of body fat at emergence minus proportion of body fat at immergence.

Statistics

All parameters were analyzed in hours and expressed as days for better clarity. For analysis of DTB length and T_{min} individual means were taken, while all other parameter values were absolute.

For statistical analysis of hibernation patterns in Common hamsters, SPSS 22.0 (IBM) was used. The Shapiro-Wilk test showed that data were normally distributed. To test for relationships among different parameters Pearson's correlations were applied. For group comparisons Student's t-test was used.

Sample size differed for correlations and tests because not all focal animals could fulfill all requirements. Some tests required a certain age group. Several animals were excluded from certain correlations because data points were missing. Adult males were excluded from statistical analysis because for this class no data was available.

Results

General patterns

In autumn the timing of immergence into the hibernaculum varied among individuals and occurred between 18. Oct. and 20. Nov. (mean = 4. Nov. ± 12 d, n = 10). Focal animals spent 40 ± 18 d (n = 10) in pre-hibernation euthermy. After the hamsters had terminated hibernation they stayed in their burrows for up to 43 d (19 ± 11 d, n = 9; post-hibernation euthermy) until they emerged between 7. Apr. and 12. May (mean = 22. Apr. ± 12 d, n = 9). In total animals spent about 170 ± 19 d (n = 9) in their hibernaculum. During this period hamsters did not hibernate for 35 ± 12 % of the time (n = 9).

All studied animals showed hibernation patterns with regular deep torpor bouts (DTBs). The hibernation phase started with the first DTBs occurring between 28. Nov. and 4. Jan. (mean = 13. Dec. ± 13 d, n = 10) and ended with the last arousal from DTBs between 13. Mar. and 27. Apr. (mean = 2. Apr. ± 14 d, n = 10). The hibernation phase lasted for 110 ± 22 d with 88 ± 19 d (80 %) spent in torpor. The hamsters showed between 13 and 27 DTBs (mean = 19 DTBs) during hibernation with a mean torpor bout length of about 4.6 ± 0.7 d.

Individuals showed a high individual variation in hibernation duration, time in torpor, the number of DTBs and time in hibernaculum (Tab. 3). Examples of hibernation patterns are shown in Fig. 3.

Table 3: Individual results for hibernation parameters as hibernation duration, time in torpor, number of DTBs and time in hibernaculum. F = female, M = male, J = juvenile, A = adult, n = 10.
[A] = hibernation patterns of these animals are shown in Fig. 3.
[B] = the value of "Time in hibernaculum" is missing, because the emergence date of one individual could not be determined exactly.

ID	Sex	Age	Hibernation duration (d)	Time in torpor (d)	DTBs (#)	Time in hibernaculum (d)
121-14[A]	M	J	94	73	19	142
287-14	M	J	88	71	14	166
123-14	F	J	118	94	21	168
132-14	F	J	127	107	20	154
176-14	F	J	149	125	27	206
217-14	F	J	104	93	16	[B]
317-14[A]	F	J	111	91	19	186
2-14	F	A	131	89	24	169
23-14	F	A	77	59	13	161
44-14[A]	F	A	97	79	19	181

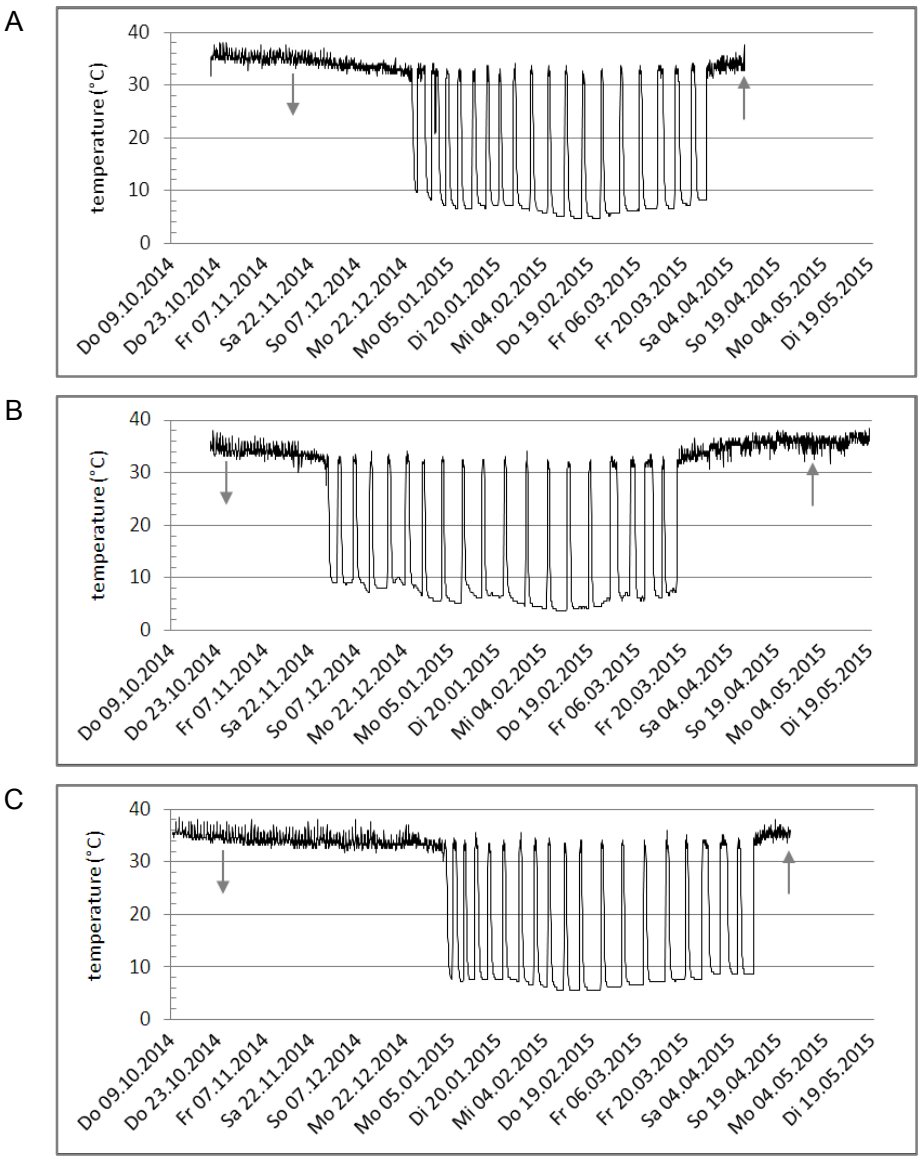

Figure 3: Hibernation patterns of three Common hamsters in the season 2014/2015. A: Juvenile male. B: Juvenile female. C: Adult female. Arrow down marks the date of immergence and arrow up marks the date of emergence. Individual values are shown in Tab. 3.

Hibernation period

Hibernation duration, time in torpor and number of DTBs were highly correlated. Hamsters that hibernated for longer periods also spent more time in torpor ($r_P = 0.932$, $p = 0.000$, $n = 10$) and showed more DTBs ($r_P = 0.921$, $p = 0.000$, $n = 10$). Accordingly animals that spent more time in torpor also showed more DTBs ($r_P = 0.791$, $p = 0.006$, $n = 10$).

The timing of hibernation onset was related to several hibernation parameters. Individuals that started to hibernate late in the season hibernated for shorter periods ($r_P = -0.797$, $p = 0.006$, $n = 10$), spent less time in torpor ($r_P = -0.783$, $p = 0.007$, $n = 10$) and tended to have fewer DTBs ($r_P = -0.586$, $p = 0.075$, $n = 10$). No relationship could be found between the timing of hibernation onset and hibernation end ($r_P = -0.326$, $p = 0.358$, $n = 10$).

Hibernation onset also differed between the age groups. In female hamsters, adults started to hibernate later than juveniles (T-test: t = -2.476, p = 0.048, n = 3/5). Adult females started hibernating on 22. Dec. ± 15 d while in juvenile females the hibernation period began already on 4. Dec. ± 6 d.

Juvenile females spent significantly more time in torpor than adult females (T-test: t = 2.462, p = 0.049, n = 5/3; Fig. 4). All other hibernation parameters did not differ significantly between the age groups.

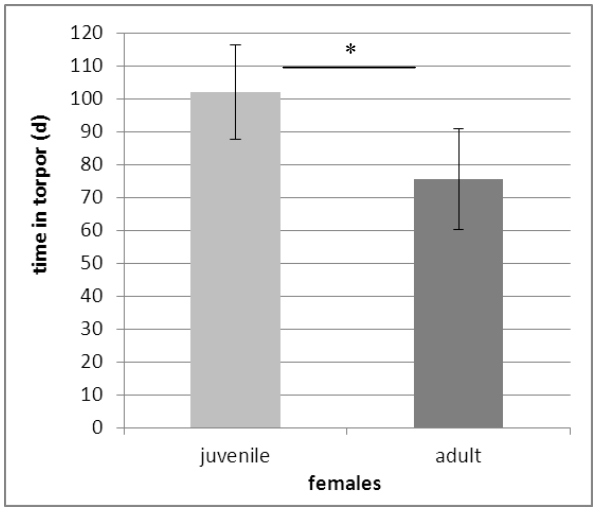

Figure 4: Time in torpor in juvenile and adult female hamsters.

Another difference among age groups was found within the hibernation period. During deep torpor bouts juveniles showed lower values of T_{min} than adults (T-test: t = -2.365, p = 0.046, n = 7/3; Fig. 5).

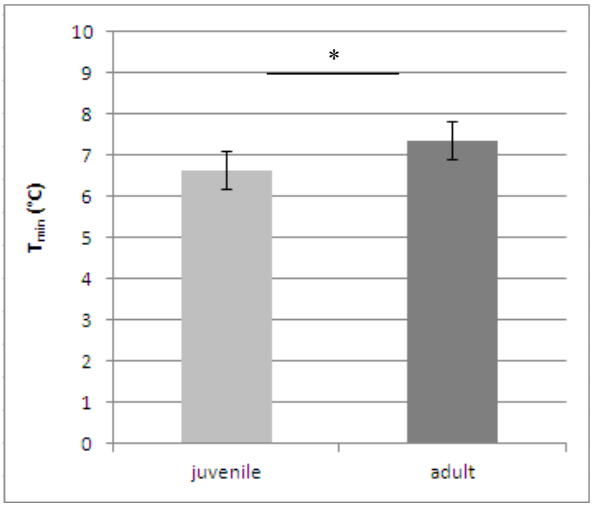

Figure 5: Mean minimum body temperature (T_{min}) during the period of deep torpor bouts in Common hamsters.

Pre-hibernation period

The later the hamsters immerged into the hibernacula the shorter was the phase of pre-hibernation euthermy (r_P = -0.699, p = 0.024, n = 10). Individuals that spent longer periods in pre-hibernation euthermy started to hibernate later in winter (r_P = 0.748, p = 0.013, n = 10). No relationship was found between the duration of pre-hibernation euthermy and immergence body mass.

Immergence body mass was significantly correlated with hibernation onset in that individuals with higher immergence mass started to hibernate later in winter (r_P = 0.784, p = 0.037, n = 7; Fig. 6). This relationship could not be found with proportion of body fat at immergence (r_P = 0.661, p = 0.106, n = 7) although immergence body mass and body fat were positively correlated (r_P = 0.791, p = 0.034, n = 7). Neither body mass nor proportion of body fat at immergence was related to any of the hibernation parameters (p > 0.1 in all cases).

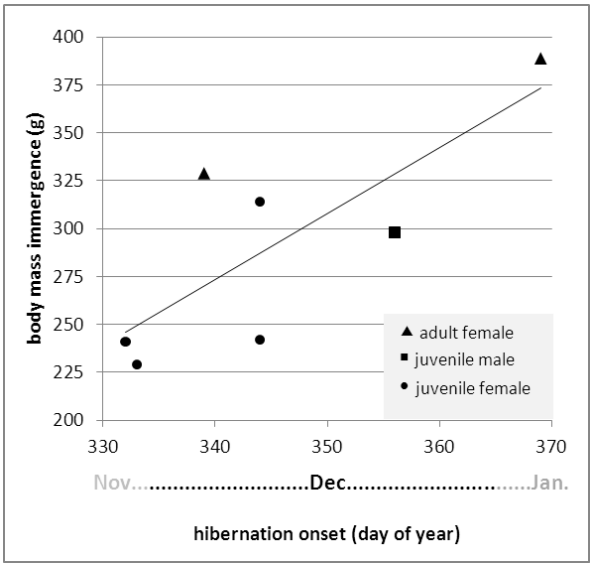

Figure 6: Relationship between body mass at immergence and hibernation onset.

Post-hibernation period

The end of hibernation was highly correlated with hibernation duration and correspondingly the time spent in torpor as well as the number of DTBs. Hamsters which terminated hibernation later had longer hibernation durations (r_P = 0.830, p = 0.003, n = 10), spent more time in torpor (r_P = 0.739, p = 0.015, n = 10) and correspondingly showed more DTBs (r_P = 0.899, p = 0.000, n = 10). After the hibernation period the animals stayed underground in post-hibernation euthermy until they emerged from their burrows. Hibernation duration and post-hibernation euthermy showed no significant relationship.

Emergence dates were negatively correlated with hibernation onset (r_P = -0.659, p = 0.054, n = 9) demonstrating that hamsters which started to hibernate late in winter emerged earlier in spring. The individuals' emergence dates were highly correlated with hibernation duration, time in torpor and the number of DTBs. Hamsters that hibernated for longer periods emerged later in spring (r_P = 0.801, p = 0.009, n = 9). The same relationships were found between emergence date and time in torpor (r_P = 0.738, p = 0.023, n = 9) or the number of DTBs (r_P = 0.780, p = 0.013, n = 9).

In total animals that emerged later in spring spent more time in hibernaculum (r_P = 0.766, p = 0.016, n = 9) whereas animals that immerged later in autumn spent less time in hibernaculum (r_P = -0.791, p = 0.011, n = 9). However an early immergence was related to a longer euthermic period in the hibernaculum (r_P = -0.681, p = 0.043, n = 9).

Conditional consequences

At vernal emergence body mass and the proportion of body fat of the focal animals was determined. Hamsters that had hibernated for longer periods (r_P = -0.619, p = 0.075, n = 9) and accordingly spent more time in torpor (r_P = -0.641, p = 0.063, n = 9) tended to have lower emergence body mass. The number of DTBs however, was negatively related to emergence body mass (r_P = -0.728, p = 0.026, n = 9).

Animals that terminated hibernation late in the season also had a lower body mass at emergence (r_P = -0.808, p = 0.008, n = 9; Fig. 7). No such relationships could be found for the proportion of body fat at emergence although body mass and body fat at emergence tended to be related (r_P = 0.633, p = 0.068, n = 9). Animals that spent longer periods in post-hibernation euthermy emerged with a higher body mass (rP = 0.827, p = 0.006, n = 9).

No relationship was found between conditional parameters at immergence and emergence.

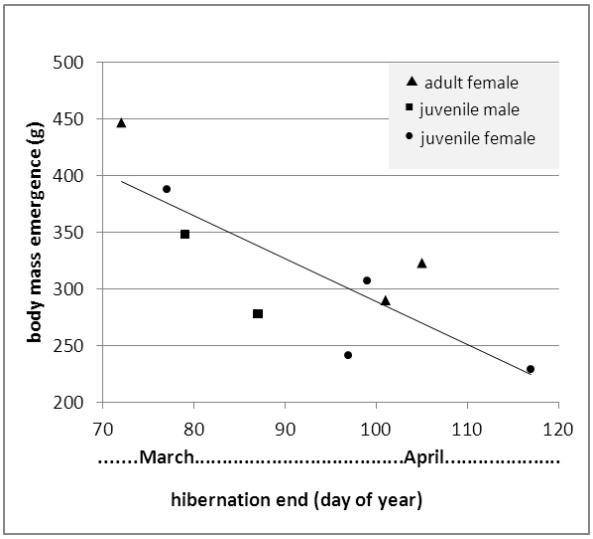

Figure 7: Relationship between body mass at emergence and end of hibernation.

We further calculated the changes in body mass and the proportion of body fat comparing before and after the time in the hibernaculum. While ∆bm was not related to any hibernation or conditional parameter ∆bf showed significant correlations with bfIM (r_P = -0.875, p = 0.023, n = 6; Fig. 8A) and the onset of hibernation (r_P = -0.818, p = 0.047, n = 6; Fig 8B). Hamsters with less fat at immergence were able to gain body fat over winter, while fatter individuals lost fat. Furthermore an early hibernation onset was related to an increase of body fat whereas animals that started hibernating later showed a loss in body fat over winter.

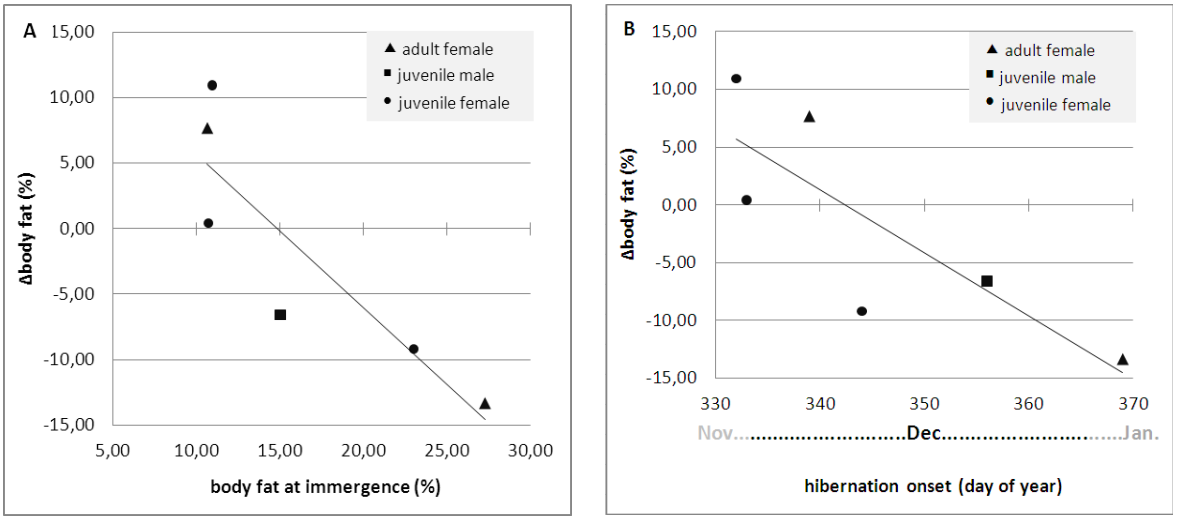

Figure 8: Relationships between ∆bf and body fat immergence (A) as well as ∆bf and hibernation onset (B).

Time in pre-hibernation euthermy was related to ∆bf (r_P = -0.829, p = 0.042, n = 6; Fig. 9A) demonstrating animals with short periods of pre-hibernation euthermy had a higher proportion of body fat in spring, whereas animals staying longer in pre-hibernation euthermy lost body fat over winter. Different was the relationship between ∆bm and post-hibernation euthermy. Short periods of post-hibernation euthermy were related to a loss of body mass whereas animals that stayed longer in post-hibernation euthermy were able to gain body mass (r_P = 0.908, p = 0.012, n = 6; Fig. 9B). Neither ∆bm nor ∆bf showed relationships with any other period of seasonal timing.

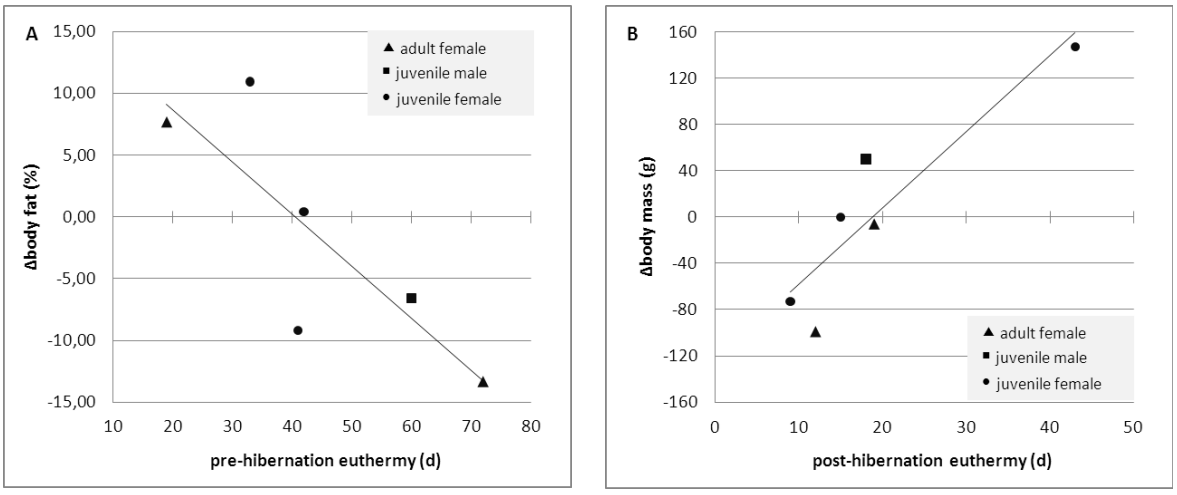

Figure 9: Relationships between ∆bf and pre-hibernation euthermy (A) as well as ∆bm and post-hibernation euthermy (B).

Survival rate

The survival rate for all marked individuals in the study area was 39.4 % (n = 66). For animals equipped with an iButton, the survival rate was 55.5 % (n = 18). 33.3 % of the other hamsters (n = 48) could be recaptured. More details of survival rates in different sex and age classes are shown in tab 4. In the subsequent spring 31.8 % of juvenile males and 47.1 % juvenile females could be recaptured. The only adult male caught in autumn could not be recaptured, whereas 33.3 % adult females were recaptured in spring.

Table 4: Survival rates split in sex and age classes. Values in brackets represent individuals equipped with iButtons.

	Autumn 2014	**%**	**Spring 2015**	**%**
Total	66 (18)	100	26 (10)	39.4
Adult females	9 (6)	13.7	3 (3)	4.6
Adult males	1 (0)	1.5	0 (0)	0
Juvenile females	34 (8)	51.5	16 (5)	24.2
Juvenile males	22 (4)	33.3	7 (2)	10.6

Discussion

This study investigated overwintering behavior in free-ranging Common hamsters, including the hibernation phase. We were able to recapture 10 of 18 animals equipped with iButtons. All of them showed regular hibernation patterns including alternating deep torpor bouts and arousals.

Former investigations of Common hamster under laboratory (Waßmer & Wollnik 1996, Mikovits 2013) and semi-natural (Wollnik & Schmidt 1995, Waßmer 2004) conditions showed high individual differences in hibernation performance. Waßmer & Wollnik (1997) distinguished between three types of hibernation bouts: Short and shallow hibernation bouts (SSHB), short hibernation bouts (SHB) and deep hibernation bouts (DHB = DTB). This high variance in performing SSHBs, SHBs and DHBs could have been caused by supplied food outside the burrows during the winter season. To feed on these external energy reserves animals had to leave their burrows, which was defined as time above ground in Waßmer (2004). As a result these hamsters could reduce their time in torpor and therefore avoid negative costs. In free-ranging Common hamsters in Vienna no above ground activity was observed and after immergence the hibernacula entrances were closed with soil (Musil 2010, Siutz et al. 2016). Accordingly these animals like those in our study have to exclusively use their internal energy reserves and stored food resulting in regular hibernation patterns with deep torpor bouts (Siutz & Millesi unpublished).

Current terminology defines hibernation as a period of alternating deep torpor bouts and short arousal episodes (Geiser 2004). Hence we applied the term of DTBs, which were characterized by a body temperature of less than 20° C for periods longer than 24 h (Waßmer & Wollnik 1997, Weinhold & Kayser 2006). During DTBs hibernators can reduce their body temperature below 10° C (Geiser 2004) with a minimum in Arctic ground squirrels (*Spermophilus parryii*) of -2.9° C (Barnes 1989, Buck et al. 2008). Our focal animals showed a minimum body temperature T_{min} of 6.9° ± 0.5° C and a mean DTB length of 4.6 ± 0.7 d. The body temperature of hamsters decreases in relation to ambient temperature (Waßmer 2004). These periods of deep torpor last for 3-4 days with a maximum duration of 7 days (Waßmer 2004, Gubbels et al. 1989). The lowest body temperature recorded in our study was 3.1° C in a juvenile female.

All hamsters in our study showed periods of pre-hibernation euthermy, hibernation and post-hibernation euthermy until vernal emergence. The durations of these periods, however, varied among individuals. Hamsters that immerged early in the season showed longer euthermic periods in their hibernacula. Late immergence on the other hand was related to a shorter pre-hibernation euthermy and generally less time in hibernacula. Early immergence

could reduce predation risk in European ground squirrels (Millesi et al. 2008). Our focal animals spent up to 72 d in pre-hibernation euthermy, a long period very few is known about. We assumed that immergence could be triggered by a certain threshold of body fat and a certain amount of stored food to terminate above ground activity. Animals could live on these internal and external energy reserves and therefore extend pre-hibernation euthermy. Animals that had high body mass at immergence or spent more time in pre-hibernation euthermy started later with hibernation and accordingly reduced hibernation duration resulting in less time spent in torpor and fewer DTBs. Reduction of torpor might be advantageous because of the mentioned costs torpor could induce (Strijkstra et al. 2003, Munro et al. 2005, Zervanos et al. 2013).

During the active season foraging behavior differed between sexes in Common hamsters. Females were observed almost exclusively caching food while males were feeding above ground most of the time (Siutz et al. 2012). Thus it is likely that females had larger food hoards in their hibernacula and used to feed on them (Weinhold & Kayser 2006) during an extended period of pre-hibernation euthermy (Siutz et al. 2016). In contrast to adult females, adult males and juveniles showed shorter periods of pre-hibernation euthermy probably because of a lack of food reserves. This lack of external energy reserves resulted in longer hibernation durations (Mikovits 2013, Siutz et al. 2016). While males owed this circumstance their foraging behavior and frequent burrow changes during the active season (Siutz et al. 2012) juveniles were short in time to build up food hoards until autumn. Accordingly juveniles immerged later than adults to compensate their disadvantage by extending the time above ground (Siutz et al. 2016). Pluch et al. (2013) showed that even among juveniles, heavier and fatter individuals tended to immerge earlier.

Terminated by the last arousal, hibernation was followed by the period of post-hibernation euthermy. Similar to pre-hibernation euthermy, durations of post-hibernation euthermy of our focal animals varied strongly and no differences between the age groups were found. This result was supported by Siutz et al. (2016) showing that both, adult males and females stayed euthermic in their burrows after the hibernation phase and fed on their remaining food hoards until emergence.

To be ready for reproduction at female emergence males use this period for spermatogenesis (Michener 1992, Buck et al. 2008). Barnes et al. (1986) showed that testicular recrudescence and spermatogenesis only occurred at normal body temperature. Thus animals stayed euthermic in their underground hibernacula although hibernation was already terminated. Although we found no significant sex difference our data indicated that male yearlings (juveniles from last season) emerged before the females in spring. To compete with adult males, yearlings emerged with nearly the same body condition resulting

from longer hibernation durations and perhaps more food reserves. Thus these yearlings could reproduce successfully after the emergence of females (Siutz et al. 2016). In almost all female hamsters ovarian activity was initiated in their hibernacula as indicated by an open vagina at emergence (Siutz et al. 2016).

Emergence was strongly related to hibernation parameters like time in torpor, DTBs and hibernation duration. More DTBs, more time in torpor and longer hibernation durations led to a later end of hibernation and a later emergence date in the following spring. Increased time in hibernation and delayed emergence were also related to lower emergence body mass, which could be caused by a shortage in energy resources. If animals were limited in food hoards, extended periods of hibernation would save energy but during hibernation body fat is used mainly to warm up during arousal episodes. Individuals with small food caches would probably not be able to compensate mass loss during hibernation by feeding on external reserves after hibernation. Accordingly these animals showed shorter periods of post-hibernation euthermy and a delayed emergence until food is available above ground (Siutz & Millesi unpublished).

In Common hamsters males emerge earlier than females (Weinhold & Kayser 2006, Franceschini-Zink & Millesi 2008, Siutz et al. 2016), similar to many other hibernators (Michener 1984, Young 1990, Munro et al. 2005, Healy et al. 2012, Buck et al. 2008, Gür & Gür 2015). The timing of emergence and the body condition are very important for the subsequent mating season. Early emergence increased reproductive success in adult Columbian ground squirrels while late emerging animals were not reproductively successful (Young 1990). Male Richardson's ground squirrels used the time of post-hibernation euthermy to feed on their accumulated food caches to prepare for the subsequent mating season (Michener 1992). Male Arctic ground squirrels emerged with nearly the highest body mass during the active season. During the following 10 d of mating season they lose 21 % of their body mass (Buck & Barnes 1999).

The mating season in Common hamsters lasts for several months and is characterized by high intrasexual competition among males (Weinhold & Kayser 2006). To improve their body condition individuals fed on their food hoards during the period of post-hibernation euthermy. Sufficient food hoards enabled hamsters to extend the post-hibernation euthermy (Siutz et al. 2016). Previous studies showed that female hamsters that emerged earlier could also mate earlier and thus were able to have more litters and offspring in this season. Correspondingly spring emergence was positive correlated with individual reproductive output (Franceschini-Zink & Millesi 2008). In addition, juveniles of litters born early in the season showed higher survival rates because they had more time for growth and preparation for the upcoming winter and they even might be able to reproduce in their first season (Franceschini-Zink & Millesi 2008).

During pre-hibernation fattening hibernators are able to increase their weight up to 100 % by accumulating body fat. Huge differences were found in the rate of mass gain comparing fat-storing hibernators with 40-100 % of their body mass and food-storing hibernators with 15-20 % (Levesque & Tattersall 2010). In free-ranging Common hamsters body mass and accordingly the proportion of body fat could only be evaluated during the active season. In our study we were able to measure body mass and the proportion of body fat before and after the time in hibernacula. None of these two parameters showed any significant relationships with hibernation parameters. This could be caused by the relatively low sample size in our study. Another reason might be found in food hoards in that we could not determine quality or quantity of these underground reserves. Most mammalian hibernators accumulate body fat for the subsequent winter. Only few species among the group of granivores including the Common hamster accumulate food to survive times of food shortage (Humphries et al. 2003b). In Eastern chipmunks a strong correlation between autumnal body mass and the expression of torpor bouts was found. Animals that were able to gain more mass during the end of the season spent more time in torpor (Levesque & Tattersall 2010). Studies in captive species showed that even if food was provided ad libitum throughout the winter body mass decreased during hibernation periods (Levesque & Tattersall 2010).

In another study (French 2000) Eastern chipmunks (*Tamias striatus*) were supplied with different amounts of food at the beginning of hibernation. Durations of torpor bouts at the end of hibernation were negatively related to the amount of provided food. Animals given the highest amount of food (5000 g sunflower seeds) terminated hibernation early and stayed euthermic until spring. But even these animals showed periods of heterothermy although the amount of food would have been sufficient to avoid torpor bouts completely. They might not realize the magnitude of their resources and therefore still execute torpor (French 2000). Investigation of free-ranging Eastern chipmunks supplied with food before hibernation showed a decrease of executed torpor bouts. Furthermore these animals had a higher T_{min} during deep torpor bouts (Humphries et al. 2003a). These results indicated the reduction of torpor if sufficient energy reserves were available.

Studies of Common hamsters showed that animals still executed periods of torpor despite sufficient amounts of food were available (Otsu & Kimura 1993, Mikovits 2013). We could show that animals that spent longer periods in post-hibernation euthermy emerged with a higher body mass. Again no relationship was found between the period of post-hibernation euthermy and body fat. These animals might have enough external energy reserves to enhance their condition until emergence. Correspondingly they were able to start the mating season in an improved body condition.

Body mass and body fat content changed during the winter period. We assumed that amount and quality of food hoards are responsible for a high variance among Δ-values of focal

animals. Some individuals were able to increase both body mass and body fat content while others decreased in both. Higher body fat at emergence implied only a higher body fat content in relation to body mass. The total fat could still have decreased. However, we could find animals that were able to gain body fat content probably because a relational loss in body mass. Other animals almost showed no difference before and after time in hibernacula. This difference might be related to a variation in quantity and/or quality of individual food stores. Unfortunately we had no knowledge about amount and composition of individual food hoards.

High body fat at immergence, late hibernation onset and an extended period of pre-hibernation euthermy were related to a higher relative loss in body fat. These individuals had higher internal body fat reserves and therefore they were able to extend the period of pre-hibernation euthermy avoiding negative effects of torpor (Humphries et al. 2003b, Zervanos et al. 2013). Correspondingly the onset of hibernation was delayed and shorter periods of hibernation and post-hibernation euthermy might be the consequences.

Short post-hibernation euthermic phases were associated with mass loss over winter while individuals that showed long post-hibernation euthermy gained body mass. This seemed reasonable because, as already mentioned, animals probably used this period to feed on their remaining food reserves to increase their body mass. Individuals with more food reserves could afford a longer euthermic period before emergence, leading to a higher body mass at the onset of the active season. Enhanced body condition at emergence has previously shown to be positively related to reproductive success during the mating season (Franceschini-Zink & Millesi 2008). Thus these relationships could be explained by different amounts or composition of food hoards (Siutz et al. 2016).

When comparing age classes we found no differences in the date of immergence but adult females seemed to execute the longest periods of pre-hibernation euthermy. Siutz et al. (2016) found a huge variation among sex and age cohorts in the duration of pre-hibernation euthermy although all classes spent a similar time in their hibernacula. Together, similar immergence and differences in pre-hibernation euthermy among adult and juvenile females resulted in a variation in timing of hibernation onset. Adult females showed a later hibernation onset than juvenile females. Therefore juveniles spent more time in torpor and by that could save energy. Usually more time in torpor would result in longer hibernation duration, which was interestingly not the case. Thus we assume that juveniles spent more time in torpor while adults extended the arousal episodes during hibernation. One adult focal individual showed an interruption of hibernation, which might be the reason we found no significant result comparing arousal durations. The strategy of extended arousals could reduce the costs of torpor but would require a sufficient amount of internal and external

energy reserves, which was more likely in adults compared to juveniles. Hibernators that rely on body fat might increase the time spent in torpor because of limitation of this internal energy reserve (Humphries et al. 2003b) while food-storing hibernators could adjust the time spent in torpor to the available external energy reserves (Humphries et al. 2003a, Siutz et al. 2016, Siutz & Millesi unpublished).

During the investigation of sex and age differences in hibernation patterns of Common hamsters Siutz et al. (2016) were able to include the class of adult males and found several results similar to our study. They could show that adult females started hibernation later than other classes and accordingly showed the shortest hibernation duration. Adult females also spent less time in torpor than juveniles supporting our results. Comparing only adult hamsters the difference of days spent in torpor was even highly significant. Feeding above ground in males against food caching in females during the active season probably resulted in a higher proportion of body fat in males and larger food hoards in females before immergence. Due to higher internal energy reserves males were able to immerge earlier than females and spent hibernating up to 80 % of the winter season (Siutz et al. 2012).

Contrasting results were found in studies of different ground squirrel species (Buck et al. 2008, Gür & Gür 2015). Adult females started hibernation first, followed by adult males and juveniles. Prior immergence of adults is typical among hibernating ground squirrels because in reliance on body fat juveniles need more time than adults for fattening and growth before their first hibernation period (Michener 1984).

In addition to longer heterothermic periods juvenile hamsters also showed a lower T_{min} during DTBs. Lower body temperature during torpor is associated with higher energy savings but also could increase the negative effects of torpor. Arousals were needed for recovery from physiological costs related to prolonged torpor. Neuronal tissue damage, oxidative stress, reduction of neuronal connectivity, negatively affected cellular functions as well as reduced immunocompetence have been shown to be potential costs of torpor (Humphries et al. 2003b, Strijkstra et al. 2003, Zervanos et al. 2013).

Gür & Gür (2015, Anatolian ground squirrel) found a lower body temperature (T_{min}) in juveniles during hibernation. They assumed that differences in depth or insulation of hibernaculum might lead to these results. We cannot exclude that these factors might play a role in Common hamsters but we assume a similar quality of burrows for juveniles and adults. The utilization of perennial hibernacula by different individuals is well known from previous studies (Weinhold & Kayser 2006). Hibernacula of Common hamsters showed a depth of 1-2 meters and are used for more than one season if hibernation was successful.

In woodchucks (*Marmota monax*) similar differences between age classes were found in relation to time in torpor and T_{min}. These may be caused by higher internal energy reserves noticeable as higher body mass in adult animals (Zervanos et al. 2013). Age- and size-

related differences in T_{min} and timing of hibernation end were found in Yellow-bellied marmots (*Marmota flaviventris*). While adults could terminate hibernation earlier juveniles executed torpor until food was available. Adults stayed euthermic and were able to live on their body fat reserves (French 1990).

Small hibernators had higher survival rates in comparison to non-hibernators (Turbill et al. 2011). In hibernating sciurids pre-immergent body mass might be important for the overwinter survival especially in juveniles (Murie & Boag 1984). In Common hamsters predation and winter mortality are two main mortality factors in life. These are followed by accidents with vehicles and diseases while historically reasons like hunting for fur or for pest control do not play an important role in recent times (Weinhold 2008). 50-60 % of hamster population may not survive the winter period (Weinhold 2008). An investigation of free-ranging adult hamsters showed winter mortality of 61.5 % and in addition a calculated mortality rate of 85 %, dependent on their amount of hoarded food (Wendt 1991).
In our study area the animals showed a survival rate of 39.4 %. If we focused only on animals equipped with iButtons we even found a survival rate of 55.5 %. These results implied that iButtons had no negative influence on the survival rate of Common hamsters. Other studies using iButtons showed recapture rates of even 62 % in Golden-mantled ground squirrels (Healy et al. 2012). In Richardson`s ground squirrels body temperature was measured by radio collars (a non-invasive method), which were located thrice a day and transmitted data of body temperature. Again no negative influence on survival rate in animals was found (Michener 1992).

In conclusion Common hamsters showed a high individual variation in hibernation and in timing of euthermic and heterothermic periods during winter. Our study provides a detailed analysis of hibernation patterns in free-living Common hamsters. Body condition at immergence was related to the timing of hibernation onset resulting in an earlier onset of juveniles compared to adults. Juveniles also spent more time at lower body temperatures in torpor than adults despite potential costs of deep torpor. Post-hibernation euthermy was found in all animals and is used to enhance body condition at emergence. Differences in body mass and body fat could cause differences in timing and duration of periods in hibernacula. Further investigations are needed to examine the role of quantity and/or quality of food stores on torpor expression.

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Appendix

Zusammenfassung

Der europäische Feldhamster (*Cricetus cricetus*) ist ein fakultativer Winterschläfer. Im Gegensatz zu den meisten Winterschläfern, die sich nur auf ihr Körperfett als Energiereserve verlassen können, sind Feldhamster in der Lage während der aktiven Saison Vorräte zu sammeln und in ihren Bauen zu lagern. Abhängig von Alter und Geschlecht beenden sie die aktive Phase zwischen August und November und bleiben bis zum Frühjahr in ihren unterirdischen Bauen (Hibernacula). Die Zeit im Hibernaculum ist durch charakteristische Phasen gekennzeichnet, eine eutherme Phase vor Winterschlafbeginn, der Hibernationsphase und einer euthermen Periode nach dem Winterschlaf. Während des Winterschlafs alternieren Torporphasen mit kurzen euthermen Phasen (Arousals). In dieser Studie wurden Winterschlafmuster sowie Timing und Dauer der einzelnen Phasen untersucht und zwischen adulten und juvenilen Tieren verglichen. Weiters wurden Zusammenhänge zwischen Körpergewicht vor und nach dem Winter und den Hibernationsparametern ermittelt.

Die Untersuchung wurde in Wien an einer freilebenden Hamsterpopulation zwischen Juni 2014 und Juni 2015 durchgeführt. Dabei kam die Fang-Wiederfang-Methode zum Einsatz, um Geschlecht, Alter und das Körpergewicht der Tiere zu ermitteln. Mit Hilfe morphometrischer Messungen konnte zusätzlich der Körperfettanteil kalkuliert werden. Zehn von 18 Tieren, denen iButtons subkutan implantiert wurden, konnten im Frühjahr 2015 wieder gefangen werden. Anhand der Aufzeichnungen konnte die Körpertemperatur, in 1.5 h Intervallen über den gesamten Zeitraum im Hibernaculum untersucht werden.

Während der Zeit im Hibernaculum zeigten alle zehn Versuchstiere regelmäßige Winterschlafmuster und alle beschriebenen Phasen. Adulte Tiere wiesen im Vergleich zu juvenilen einen späteren Beginn des Winterschlafs sowie kürzere Torporphasen bei höherer Körpertemperatur auf. Größere Vorratsmengen und ein höherer Körperfettanteil sind mögliche Gründe für diese Unterschiede. Juvenile Tiere könnten aufgrund ihrer geringeren Reserven dazu gezwungen sein, längere Torporphasen bei niedrigerer Körpertemperatur einzuhalten. Die daraus resultierende Energieersparnis geht jedoch mit den Kosten von Torpor wie Zellschädigungen oder einem geschwächten Immunsystem einher.

In den beiden euthermen Phasen, vor und nach dem Winterschlaf, konnte jeweils eine große Variation in der Dauer zwischen den einzelnen Individuen festgestellt werden. Besonders interessant war dabei der Zusammenhang mit dem Körpergewicht. Ein hohes Körpergewicht beim Abtauchen verzögerte den Beginn des Winterschlafs. Diese Tiere nutzten vermutlich die eutherme Phase im Bau um von ihren Vorräten zu fressen und somit ihre körperlichen Voraussetzungen für den Winterschlaf zu verbessern. Eine längere eutherme Phase nach

dem Winterschlaf war mit einem höheren Gewicht im Frühjahr verbunden, wogegen Tiere die viel Zeit im Torpor verbrachten und somit lange Winterschlaf hielten mit einem niedrigeren Körpergewicht auftauchten. Hamster mit ausreichenden Vorräten waren offenbar in der Lage sich einen konditionellen Vorteil für den Beginn der aktiven Phase und die sofort anschließende Paarungszeit zu verschaffen. Diese Studie zeigt, dass Timing im Leben des Feldhamsters eine große Rolle spielt. Alter, Geschlecht und der körperliche Zustand gegen Ende der aktiven Saison nehmen Einfluss auf die Dauer der einzelnen Phasen, die im Hibernaculum verbracht werden. Zusätzlich ist die Menge der gesammelten Vorräte für das Überleben aber auch für die konditionelle Verfassung im Frühjahr von großer Bedeutung. Sie bildet die Grundlage für eine erfolgreiche Paarungszeit und einhergehend einen höheren reproduktiven Erfolg.