MASTERARBEIT | MASTER'S THESIS

Titel | Title

Hibernation patterns in free-ranging common hamsters (Cricetus cricetus) with and without additional food stores

verfasst von | submitted by

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angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2025

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 878
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
Betreut von | Supervisor:	ao. Univ.-Prof. Dr. Eva Millesi
Mitbetreut von | Co-Supervisor:	Mag. Dr. Carina Siutz

Danksagung

An erster Stelle möchte ich mich von Herzen bei ao. Univ.-Prof. Dr. Eva Millesi bedanken. Ihre Geduld, ihr Verständnis, ihr fachlicher Rat, der offene Austausch und ihr beständiger Zuspruch haben mich kontinuierlich begleitet und motiviert. Ihr Vertrauen und ihre konstruktiven Rückmeldungen haben diese Arbeit möglich gemacht.

Mein besonderer Dank gilt auch Mag. Dr. Carina Siutz. Sie hat mich in der Feldarbeit und bei der Datenerhebung großartig unterstützt und war jederzeit ansprechbar für Fragen. Sie war stets bereit, ihr Fachwissen zu teilen, und hat mich mit offenem Ohr sowie großer Expertise in wissenschaftlicher Arbeit sehr unterstützt.

Außerdem bedanke ich mich herzlich bei meinen Feldarbeitskolleginnen Margit Valent und Ariane Niebauer für die zuverlässige, angenehme und immer humorvolle Zusammenarbeit. Die gemeinsamen Einsätze im Feld waren nicht nur produktiv, sondern auch menschlich bereichernd.

Zum Schluss möchte ich mich bei meinem Mann und bei meinen Eltern bedanken. Danke an meinen Mann für seine unerschütterliche Unterstützung, sein Verständnis in intensiven Arbeitsphasen und dafür, dass er mir den Rücken freigehalten und mich immer wieder ermutigt hat. Meinen Eltern danke ich von Herzen dafür, dass sie mir mein Studium ermöglicht haben, mich beständig unterstützt und mir das Vertrauen geschenkt haben, meinen eigenen Weg zu gehen.

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Abstract

Hibernation allows small endotherms to endure winter by alternating between multiday deep-torpor bouts (DTBs) and short euthermic intervals. In food-storing hibernators such as the common hamster (*Cricetus cricetus*), the amount and composition of food caches in the burrow can modulate this pattern. We tested whether providing high-quality external energy stores shortly before immergence changes winter heterothermy in free-ranging hamsters, and whether responses differ between sexes. Specifically, we asked if supplementation alters the number and duration of DTBs, the structure of interbouts (IBs), and the occurrence of short and shallow torpor bouts (SSTBs) outside the core hibernation period.

We studied a population in an urban area in Vienna, from autumn 2015 to spring 2016. Shortly before immergence, focal animals received 500 g of sunflower seeds. Subcutaneous temperature loggers recorded body temperature continuously during winter. We used standard, temperature-based categories for the different types of torpor and euthermic periods. Supplemented individuals were compared with non-supplemented individuals. Analyses were conducted separately for males and females.

In males, supplementation clearly reduced hibernation duration. Supplemented males had fewer DTBs, shorter DTB duration, and spent less total time in deep torpor than non-supplemented males. The minimum body temperature during DTBs was, on average, slightly higher in supplemented males. IB structure also shifted: supplemented males showed fewer but longer IBs, while total IB time across the hibernation period was similar between male groups. The mean body temperature during IBs was lower in supplemented males, reflecting shallow torpor bouts during these periods. SSTB expression in males was more pronounced during the pre- and post-hibernation phase: supplemented males showed more SSTBs before the first DTB and after the last DTB, whereas during hibernation, SSTB numbers did not differ between groups.

In females, additional food stores did not affect hibernation patterns. Supplementation did not change the number or duration of DTBs, the total time spent in deep torpor, or the number or duration of IBs. SSTB expression also did not differ between supplemented and non-supplemented females. Overall, the data indicate that access to external energy reserves allows males to confine multiday deep torpor to the coldest weeks, consume the food stores and still save some energy during brief, shallow torpor during the prolonged pre- and post-hibernation periods. These findings are biologically plausible: late-season supplementation provides males with an energetic buffer, enabling them to increase body mass overwinter. This likely improves their condition at early spring emergence, when mating and intrasexual competition start. The absence of an effect of food supplements on torpor expression in females is not surprising, because females secure winter energy primarily through caches and bear late-season

reproductive costs. Added seeds shortly before immergence are therefore more likely to affect timing (e.g., emergence/reproduction) than torpor metrics per se. Females can use the stored seeds in the following season to cope with high energy demands during the reproductive period.

Introduction

In seasonal environments, endotherms face predictable energetic challenges, such as prolonged periods of low ambient temperature and reduced food availability in winter. Many small mammals and several bird species respond with heterothermy, which involves controlled, reversible reductions in body temperature and metabolic rate. This can manifest either as daily torpor or hibernation (Geiser, 2004; Ruf & Geiser, 2015). Daily torpor is a short-term circadian expression aligned with the rest phase of the species (daytime for nocturnal animals and night-time for diurnal ones). Bouts last less than 24 hours, with animals resuming foraging between bouts, and the depression of body temperature and metabolism is much less pronounced than in hibernation. The latter involves a seasonal pattern of deep torpor bouts lasting from days to weeks, interrupted by brief euthermic arousals. Although these arousals are energetically costly and can trigger tissue-level stress, energy conservation remains high because most of the winter is spent in torpor (Geiser, 2004; Ruf & Geiser, 2015; Carey, 2000; Heldmaier et al., 2004).

Hibernation is flexible with respect to energy status: when energy is limited, animals tend to use more multiday deep-torpor bouts (DTBs) and extend the hibernation season, whereas with abundant energy they rely less on DTBs and spend more time euthermic between bouts (Humphries et al., 2003a, 2003b; Willis, 2007; Levesque & Tattersall, 2010; Levy, Dayan & Kronfeld-Schor, 2011; Ruf & Geiser, 2015; Vuarin & Henry, 2014). In common hamsters, access to external stores and higher store quality have been linked to reduced reliance on prolonged DTBs and increased use of short torpor outside the hibernation period, consistent with improved energetic status (Siutz et al., 2017; Siutz et al., 2018a). Here, we differentiate multiday DTBs that structure the hibernation period from short and shallow torpor bouts (SSTBs), which are brief and less energy-efficient per unit time but compatible with late-season foraging and burrow management when food is available (Geiser, 2004; Ruf & Geiser, 2015). Because arousals are costly, wild torpor patterns reflect a trade-off between conserving energy and managing the costs of repeated arousals and state changes, and they are shaped by autumn energy reserves and access to external food as part of seasonal endocrine control (Carey, 2000; Heldmaier et al., 2004; Florant & Healy, 2012; Humphries et al., 2003a, 2003b; Willis, 2007; Levesque & Tattersall, 2010; Vuarin & Henry, 2014).

Minimum body temperature during DTBs can vary with burrow and ambient conditions. We therefore focus on time-allocation metrics (DTB number/duration and euthermic time between bouts) rather than small differences in DTB minima (Boyles et al., 2007; Landry-Cuerrier et al., 2008). In other hibernators, energetic state interacts with microclimate, with animals choosing cooler sites and increasing torpor use when energy is limited, and using warmer sites or remaining euthermic longer

when energy is abundant (Boyles et al., 2007; Landry-Cuerrier et al., 2008). In our study population, animals overwintered in fixed burrows at a single site, so small differences in minimum body temperature during DTBs are interpreted cautiously, and we emphasise changes in time allocation (DTB use versus euthermy).

The common hamster (*Cricetus cricetus*) is a hibernating species that stores food and reduces its body temperature and metabolic rate over winter, relying largely on cached food in its burrow (Wassmer, 2004; Siutz et al., 2012). This species exhibits highly variable torpor patterns within and among individuals, ranging from deep, prolonged bouts to sequences dominated by frequent, short and shallow torpor (Wassmer, 2004). In the free-ranging population at our study site, these patterns were shown to be modulated by sex and age: adult females generally start hibernation later and hibernate for shorter periods than males, while juveniles differ from adults in terms of both timing and duration (Siutz et al., 2016). Such variation likely reflects differences in energy allocation strategies, reproductive demands and access to stores.

Sex-specific behaviour and energy management have been well documented in this species. During the active season, for example, males feed mainly above ground, whereas females invest more in caching and feed primarily underground. Males also tend to have higher pre-immergence body fat proportions than females (Siutz et al., 2012). Females can produce multiple litters within one season, which compresses the time window for pre-hibernation preparation and can alter the balance between fat reserves and stored food in autumn (Franceschini-Zink & Millesi, 2008; Hufnagl et al., 2011). Consequently, males typically enter winter with larger internal reserves and can rely less on prolonged multiday DTBs during the hibernation period, whereas females maintain a more stable DTB pattern and adjust the timing of emergence and reproduction, consistent with energy-optimisation under sex-specific autumn constraints (Humphries et al., 2003a, 2003b; Levesque & Tattersall, 2010; Franceschini-Zink & Millesi, 2008; Siutz et al., 2016).

Under field conditions, pre-hibernation supplementation produced sex-specific shifts in hibernation and spring timing, indicating partly different energetic strategies in males and females (Siutz et al., 2018a). At the individual level, greater consumption of sunflower-enriched stores was associated with more short and shallow torpor (SSTB) and higher minimum subcutaneous temperatures, without eliminating DTBs (Siutz et al., 2018a; Siutz, Ammann & Millesi, 2018b). At the group level, however, standardising and enriching hoards did not change the number or duration of DTBs (Siutz et al., 2018a). Following prior work in this study system, we use standardised temperature-based categories: deep torpor bouts (DTB: < 20 °C, > 24 h), short torpor bouts (STB: < 20 °C, ≤ 24 h), short and shallow torpor

bouts (SSTB: 20–30 °C, ≤ 24 h), and interbouts (IBs: the entire interval between two DTBs, which can include euthermy and short torpor bouts) (Siutz, Ammann & Millesi, 2018b).

In intensively used agricultural landscapes, simplified crop rotations and herbicide-driven weed suppression can reduce the diversity and quality of potential stores. Diversified crop associations have been shown to improve cache composition and support condition and reproduction in common hamsters (Tissier et al., 2019; Tissier et al., 2021; Gérard et al., 2024). Beyond total caloric intake, cache composition—particularly protein supply and fatty-acid profiles—modulates winter physiology and spring phenology, shaping torpor expression (Ruf & Arnold, 2008; Giroud et al., 2009; Tissier et al., 2019; Tissier et al., 2021; Gérard et al., 2024). Together, these factors can shift the balance between prolonged DTBs during the hibernation period and the use of short or shallow torpor (SSTB) at the margins of winter, especially when additional stores are provided shortly before immergence.

Based on previous studies, we investigated whether supplying additional high-quality external energy stores shortly before immergence alters (i) the hibernation pattern—namely the number and duration of multiday deep-torpor bouts (DTBs) and the timing of euthermic interbout intervals (IBs)—and (ii) the occurrence of short and shallow torpor (SSTB) outside the hibernation period, in free-ranging common hamsters. We also examined whether these effects differ between the sexes. We predicted that supplemented individuals, especially males, would show fewer and shorter DTBs during the hibernation period and a higher frequency of SSTB in the pre- and post-hibernation phases, reflecting improved energetic status. Furthermore, we expected slightly higher minimum body temperatures within DTBs, as well as longer but less frequent euthermic IBs, in supplemented individuals compared to non-supplemented conspecifics. Sex-specific responses were anticipated because males and females differ in their pre-winter balance of fat accumulation, caching effort and reproductive costs. By standardising temperature-based categories and building on prior field work in this study system (Siutz et al., 2017; Siutz et al., 2018a; Siutz, Ammann & Millesi, 2018b), our analyses test how the availability—and, by extension, the composition—of external stores shape winter heterothermy in a food-storing hibernator, distinguishing DTB-structured hibernation from non-hibernation periods that can be fully euthermic or include SSTB.

Material and Methods

Study site and time span

Data collection took place in the area of the Kaiser-Franz-Joseph hospital in the 10th district of Vienna. More precisely, we investigated three focal sites within this urban area: (A) the park area around the chapel, (B) the park area around the psychiatric unit and (C) the park area around the geriatrics unit of the hospital. In total, we used around 2.3 ha of green area. The park vegetation consisted mostly of grass and a few trees and bushes. The focal sites were surrounded by hospital buildings or housing areas and pathways where visitors to the hospital constantly walked by or ambulances drove past.

The fieldwork was carried out from late September to November 2015 until the hamsters immerged into their hibernacula and continued after hibernation was terminated, from March 2016 until May 2016. Trapping was performed in the morning hours from 5:30 a.m. to 11 a.m. and/or again in the evening from 5 p.m. until 9 p.m. These times were chosen due to the known active periods of the common hamster, which are influenced by both seasonal and environmental factors (Siutz et al., 2016; Millesi et al., 2008). On weekends only behavioural observations were carried out. Before hibernation, food supplements were provided (see below). In total, we captured 52 individuals (21 adults and 31 juveniles) in the autumn season of 2015. 18 of those (11 females, 7 males) were chosen as our focal individuals for supplementation.

Field techniques

Trapping technique

Animals were captured using the capture-mark-recapture method with Tomahawk live traps baited with peanut butter. These traps were placed in front of the burrows and checked every 15–20 minutes in order to reduce the stress level of the hamsters (Millesi et al., 2008). Once a hamster was trapped it was released from the trap into a cone-shaped cotton sack for investigations. These cotton sacks were open-ended to enable the hamster to breathe and were laterally equipped with Velcro fasteners, thereby making examination of the lower part possible without anaesthesia (Millesi et al., 2008). Parameters documented were date, time, weather condition, sex (male, female), age (adult: hibernated at least once, juvenile: born in current season), body mass (g), head, tibia and foot lengths (mm) and their reproductive status (only in spring season: testes width in males, closed/open vagina and small/swollen teats in females). Furthermore, for permanent identification, each individual was subcutaneously implanted with a transponder (PIT tag, Data Mars) into the lower part of their back at first capture. To simplify identification for observation we additionally marked each individual by marking their fur with different symbols using commercial hair dye (red for females, black for males).

The whole procedure took about 5-10 minutes and afterwards they were released at the entrance of the burrows where they had been captured at.

Supplementation

At the end of the active season, shortly before the hibernation period, the 18 focal hamsters were provided with 500 g sunflower seeds each. Sunflower seeds had been chosen because of their high amount of polyunsaturated fatty acids and good storability, which makes it a high-quality food for the common hamster (Ruf & Arnold, 2008). These characteristics of sunflower seeds are known to play an important role in the regulation of hibernation patterns in small mammals (Ruf & Arnold, 2008). To ensure that only the focal hamsters collected the sunflower seeds, we placed them in front of the individual's burrow, on a sheet of paper observing them constantly. We were unable to perform supplementary feeding for one female because her burrow could not be identified. This individual was therefore analysed within the non-supplemented female group. Non-supplemented reference data consisted of our unsupplemented focal individuals, as well as additional non-supplemented hamsters from previous years at the same site. Eight individuals were confirmed to be supplemented, for nine others we had to put the sunflower seeds into their burrows since it was not possible to observe the hamsters again before hibernation.

Temperature recording

During the winter season (November-March) the body temperature was recorded using temperature loggers (iButtons) which were implanted shortly before the hibernation period started. Once a hamster was trapped in a Tomahawk live trap it was taken to a veterinary clinic. Under isoflurane anaesthesia the insertion (and after the hibernation period the removal) of the iButton (Ø 15 mm) was carried out. It was implanted subcutaneously in the neck region (Siutz et al., 2012; Siutz et al., 2018a; Siutz et al., 2017). After implantation, the hamster was observed until it had recovered from anaesthesia. The animal was then returned to the field site and released at its burrow. The whole procedure took approximately two hours. Because hamsters were trapped only in the early morning for implantation, this fell within their morning activity period (Siutz et al., 2016; Millesi et al., 2008). In total, we implanted 18 iButtons: eleven females (9 adults, 2 juveniles) and seven males (2 adults, 5 juveniles). 14 of them could be recaptured in spring however one female hamster had lost its iButton, so only 13 could be used for analysis. After the analyses, one male was reclassified as non-supplemented based on his iButton-recorded hibernation pattern and was therefore included in the dataset of non-supplemented hamsters.

Hibernation pattern

IButton recordings enabled us to distinguish between the distinct phases of heterothermia during the hibernation period (Figure M1).

Definitions

Hibernation patterns in the common hamster (*Cricetus cricetus*) are characterized by varying depths and durations of torpor, with the most common phases being deep torpor bouts (DTBs), short torpor bouts (STBs), and shallow torpor bouts (SSTBs) (Siutz & Millesi, 2017; Siutz et al., 2018a). Additionally, food supplementation has been shown to influence the duration and depth of torpor, with sex-specific differences in response to food availability (Siutz et al., 2018b).

Deep torpor bout (DTB): defined by a body temperature below 20 °C for a time period of more than 24 hours.

Short torpor bout (STB): defined by a temperature below 20 °C and a time period of a maximum of 24 hours or shorter.

Short and shallow torpor bout (SSTB): defined by a temperature between 20 to 30 °C and a time period of a maximum of 24 hours or shorter.

Interbout (IB): period between DTBs, including SSTBs and STBs if they occurred between two periods of DTB.

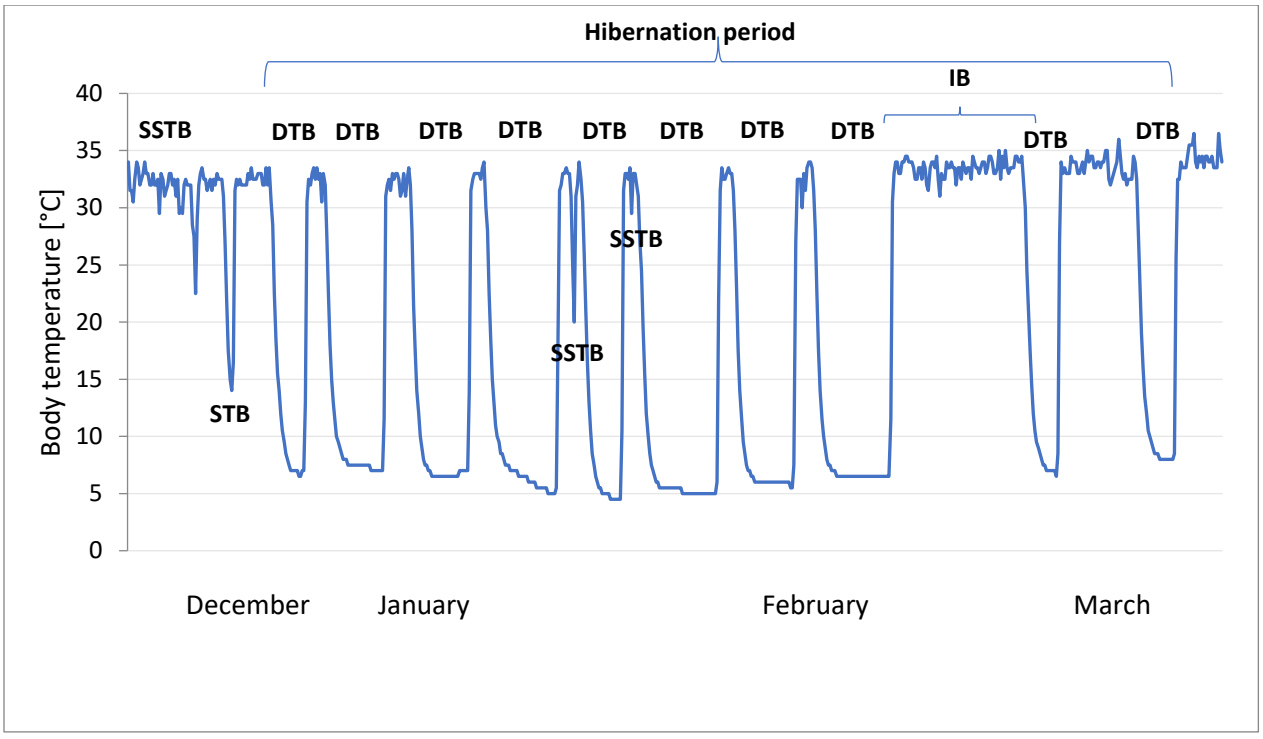

Figure M1 Hibernation pattern of juvenile female hamster (iButton recording), showing the different torpor bouts

Observations

After implantations, we observed the hamsters until they started to hibernate in their burrows. Once a hamster terminated its surface activity and immerged into its burrow, we blocked their burrow

entrance with soil and leaves. We could confirm the date of immergence by the indications of the temperature patterns, when its body temperature fell below 35 °C, as described by Siutz et al. (2018a). After the hibernation period (from March onwards) we monitored the burrows again to document the emergence date of each individual hamster.

Non-supplemented animal data

For comparison with non-supplemented hamsters, we used a reference dataset of 27 individuals (14 males, 13 females). It comprised our unsupplemented focal animals together with additional non-supplemented hamsters from previous iButton studies provided by the Department of Behavioural Biology, University of Vienna. All data were collected at the same site or in nearby areas in the winters 2009/10, 2012/13, 2013/14, and 2014/15.

Statistics

Statistical analysis was performed using IBM SPSS Statistics 24. Normal distribution of the data was tested with Shapiro-Wilk tests. When data was normally distributed, the Student's *t* test for unpaired groups was used to compare different parameters between supplemented and non-supplemented hamster within males and females (DTB, STB, SSTB, IB). For heterogenetic data the Mann-Whitney-U-test was used. Relationships between parameters were tested with the Pearson's and Spearman's rho correlations. Significance level was set at $p \leq 0.05$. Tables and graphics are shown as means ± standard deviation unless noted otherwise.

Ethical Statement

All procedures performed on animals were approved by the Austrian Ministry of Science, Research and Economy, the Ethical Committee for Animal Welfare (GZ BMWFW-66.006/0013-WF/VI3b/2015), City of Vienna (MA22-2484/10, MA22-310/11) and the University of Vienna (2015-010).

Results

Deep torpor bouts (DTB)

DTBs are defined by a body temperature below 20 °C for a period longer than 24 hours. All animals, with and without additional food stores, showed DTBs alternating with euthermic periods (Tab. 1).

Table 1 Number of individuals showing DTBs (n), mean number of DTBs (#), mean duration of DTBs (h) and total time spent in deep torpor (d) in supplemented and non-supplemented male and female hamsters. Mean ± SD

	n	DTB (#)	DTB duration (h)	Total time (d)
supplemented males	6	12.2 ± 2.1	76.6 ± 9.3	39.3 ± 10.5
non-supplemented males	14	20.6 ± 4.3	114.6 ± 15.9	98.1 ± 23.7
supplemented females	6	19.5 ± 2.7	116 ± 21.6	95.5 ± 27.4
non-supplemented females	13	18.4 ± 4.3	109.1 ± 17.7	83.8 ± 24.0

The number of DTBs differed significantly between supplemented and non-supplemented males. Males with additional food stores showed fewer DTBs than non-supplemented ones (t= -4.334, p ≤ 0.0001) (Tab. 1, Fig. 1). In females, however, the number of DTBs did not differ between individuals with and without additional food stores (t=0.549, p = 0.590) (Tab. 1, Fig. 1).

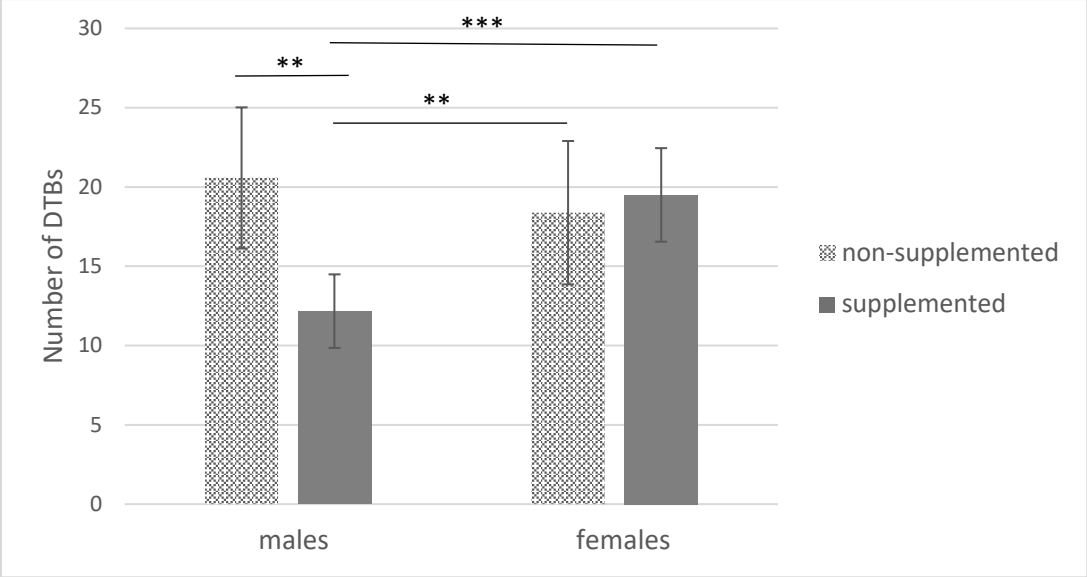

Figure 1 Number of deep torpor bouts (DTB) in males and females with and without additional food stores, * p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001, Mean ± SD

Correspondingly, supplemented males spent significantly less time in deep torpor than non-supplemented ones (t= -5.467, p ≤ 0.0001) (Tab. 1). Mean DTB duration differed between

supplemented and non-supplemented males. DTBs of supplemented males were shorter than those of non-supplemented ones (t= -6.257, p < 0.001) (Tab. 1).

The female groups behaved very similarly referring to the time spent in deep torpor (t=0.901, p = 0.380) and DTB duration (t=0.690, p = 0.499) (Tab. 1).

Regarding sex differences, supplemented males showed significantly fewer DTBs than both non-supplemented and supplemented females (both p < 0.001).

Body Temperature during Deep Torpor

To compare hibernation patterns in more detail, individual minimum and mean body temperature during deep torpor was calculated and compared between supplemented and non-supplemented hamsters. Minimum body temperature in non-supplemented males was significantly lower than in supplemented males (z= -1.988, p = 0.047) (Fig. 2). Furthermore, mean body temperature during DTBs tended to be lower in non-supplemented compared to supplemented males (z= -1.900, p = 0.057) (Fig. 3).

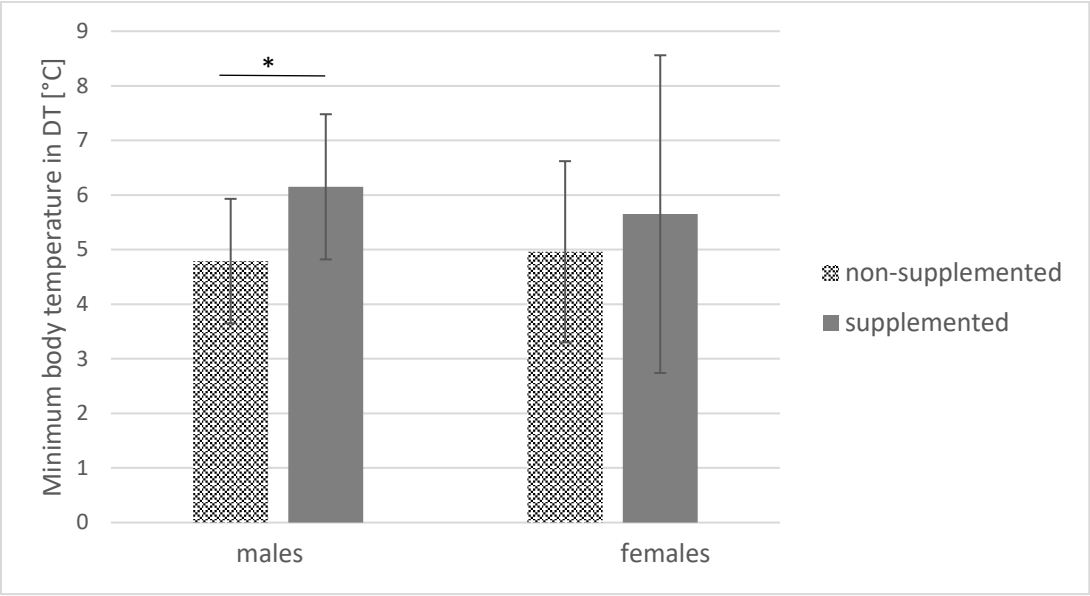

Figure 2 Minimum temperature during deep torpor in males and females with and without additional food stores, * p ≤ 0.05, Mean ± SD

In females neither minimum nor mean body temperature during DTBs differed between the groups (Fig. 2 and 3).

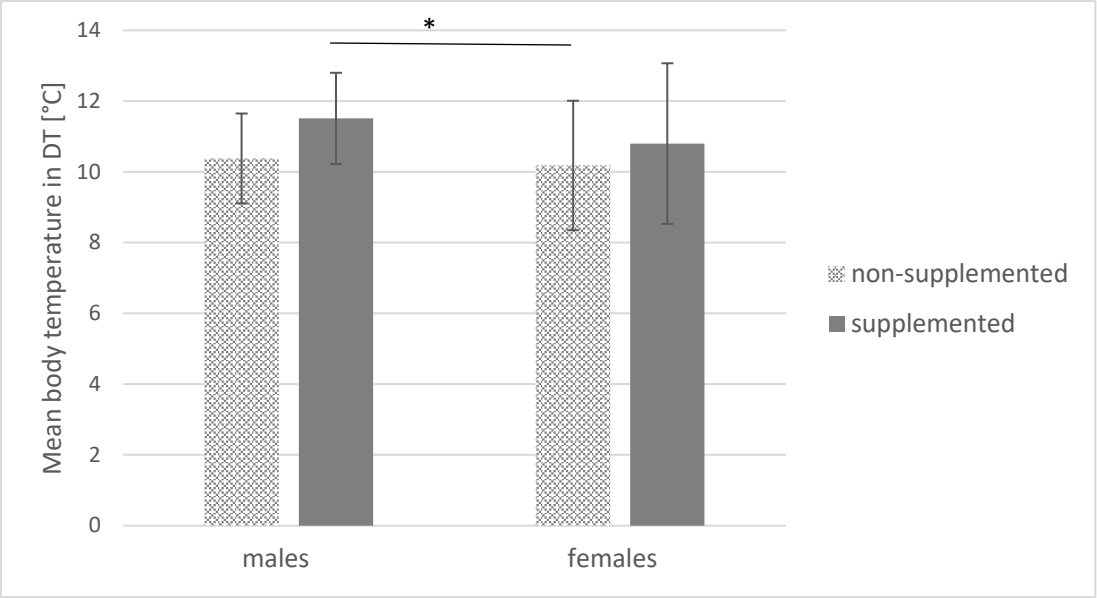

Figure 3 Mean body temperature in deep torpor (DTB) in males and females with and without additional food stores, * $p \leq 0.05$, Mean ± SD

Supplemented males were found to have significantly higher mean body temperature than non-supplemented females ($z= -2.370$, $p = 0.018$).

Short torpor bouts (STB)

STBs are defined by a temperature below 20 °C for a maximum period of 24 hours. STBs were shown by only a few animals in both groups. In supplemented and non-supplemented males, only one individual in each group, and in supplemented and non-supplemented females, two individuals in each group expressed STBs (Tab. 2).

Table 2 Number of STB (#), total duration of STB (h) and minimum temperature (°C) in supplemented and non-supplemented male and female hamsters. Numbers in parentheses refer to the number of STBs expressed by the respective individual. Mean ± SD

	n	STB (#)	Duration (h)	Minimum temperature (°C)
supplemented males	1	1	10.5	19.6
non-supplemented males	1	1	19	18.2
supplemented females	2	4 (3/1)	81 ± 21	15.1 ± 0.5
non-supplemented females	2	2 (1/1)	22.5 ± 6.25	16.3 ± 2.25

Short and shallow torpor bouts (SSTB)

SSTBs are defined by body temperatures between 20 °C and 30 °C for a period of less than 24 hours. The body temperature patterns of most animals, with and without additional food stores, included SSTBs (Tab. 3).

Table 3 Number of individuals showing SSTBs (n), the number of SSTB (#), mean duration of SSTB (h) and total time spent in SSTB (d) in supplemented and non-supplemented male and female hamsters. Mean ± SD

	n	SSTB (#)	SSTB duration (h)	Total time (d)
supplemented males	5	42 ± 40.4	3.4 ± 1.8	6.4 ± 6.2
non-supplemented males	12	5.1 ± 12.0	6.9 ± 5.9	1.0 ± 1.9
supplemented females	4	8 ± 12.1	2.9 ± 2.5	1.2 ± 1.8
non-supplemented females	9	14.8 ± 26.7	3.7 ± 3.0	2.8 ± 5.7

Males with additional food stores showed a tendency to have more SSTBs than non-supplemented ones (z= -1.981, p = 0.059) (Tab. 3, Fig. 4).

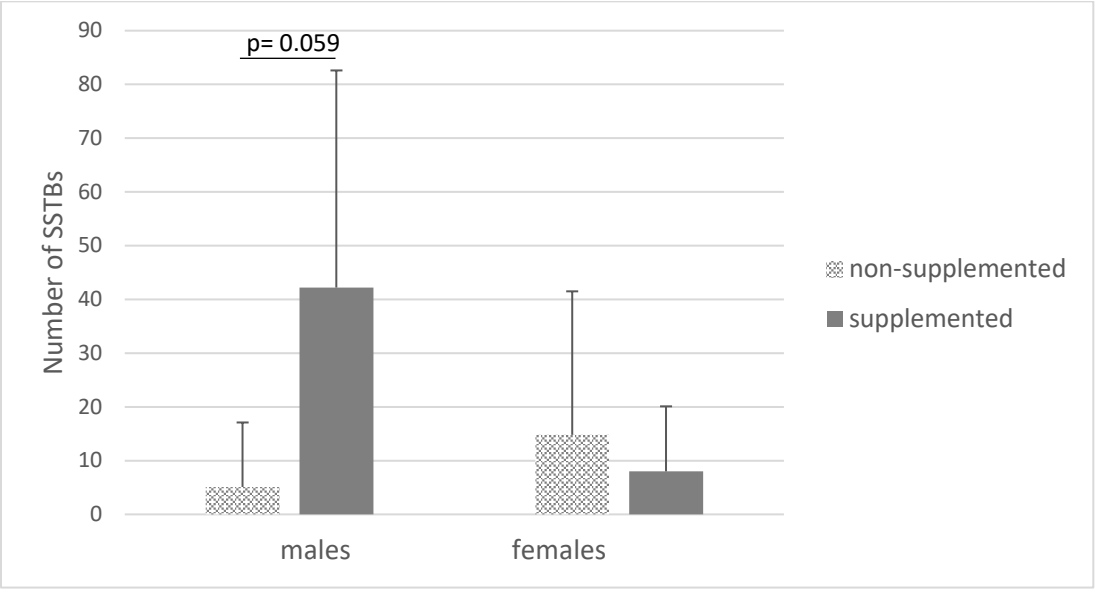

Figure 4 Number of short and shallow torpor bouts (SSTB) in males and females with and without additional food stores, Mean ± SD

Females showed no difference in the number of SSTBs whether they had additional food stores or not (z= -0.224, p = 0.823) (Tab. 3, Fig. 4). When comparing the total time spent in SSTB the male groups differed slightly. Supplemented males spent more time in SSTB than non-supplemented ones (z= -1.781, p = 0.075). For the females, no difference was found (z= -0.446, p = 0.656) (Tab. 3).

Furthermore, we found no significant differences between the groups in the duration of SSTBs neither in males (z= -1.416, p = 0.157) nor in females (z= -0.626, p = 0.532) (Tab. 3).

Body Temperature during SSTB

Comparisons of body temperature during SSTB showed that non-supplemented and supplemented individuals of both sexes did not differ in minimum and mean body temperature ($p > 0.05$ in all cases; Tab. 4).

Table 4 Mean body temperature (°C) and minimum body temperature (°C) during SSTBs in supplemented and non-supplemented male and female hamsters. Mean ± SD

	Mean Temperature (°C)	Minimum Temperature (°C)
supplemented males	30.2 ± 0.7	24.9 ± 2.2
non-supplemented males	27.9 ± 2.2	23.8 ± 2.7
supplemented females	30.4 ± 2.2	23.4 ± 5.2
non-supplemented females	29.5 ± 1.2	24.7 ± 2.7

Timing of SSTBs during time in burrow

The time spent in the burrow from immergence in autumn until vernal emergence was divided into three phases. The pre-hibernation period lasted from immergence until the first DTB. Thereafter the hibernation period started, lasting until the end of the last DTB. Finally, the post-hibernation period was defined as the period from the termination of hibernation until emergence in spring. Comparing supplemented and non-supplemented males and females revealed that supplemented males tended to show more SSTBs during the pre-hibernation period than non-supplemented ones ($z= -1.941$, $p = 0.052$) (Fig. 5). In addition, supplemented males had significantly more SSTBs than non-supplemented females during the pre-hibernation period ($z= -2.149$, $p = 0.032$). No differences were found between the other groups ($p > 0.102$ in all cases). During the hibernation period, however, the number of SSTBs was similar in all groups. Throughout the post-hibernation period, supplemented males showed significantly more SSTBs compared to supplemented females ($z= -2.079$, $p = 0.038$) and non-supplemented females ($z= -2.589$, $p = 0.010$) (Fig. 5). During the post-hibernation, non-supplemented males did not differ from any other group ($p > 0.112$ in all cases).

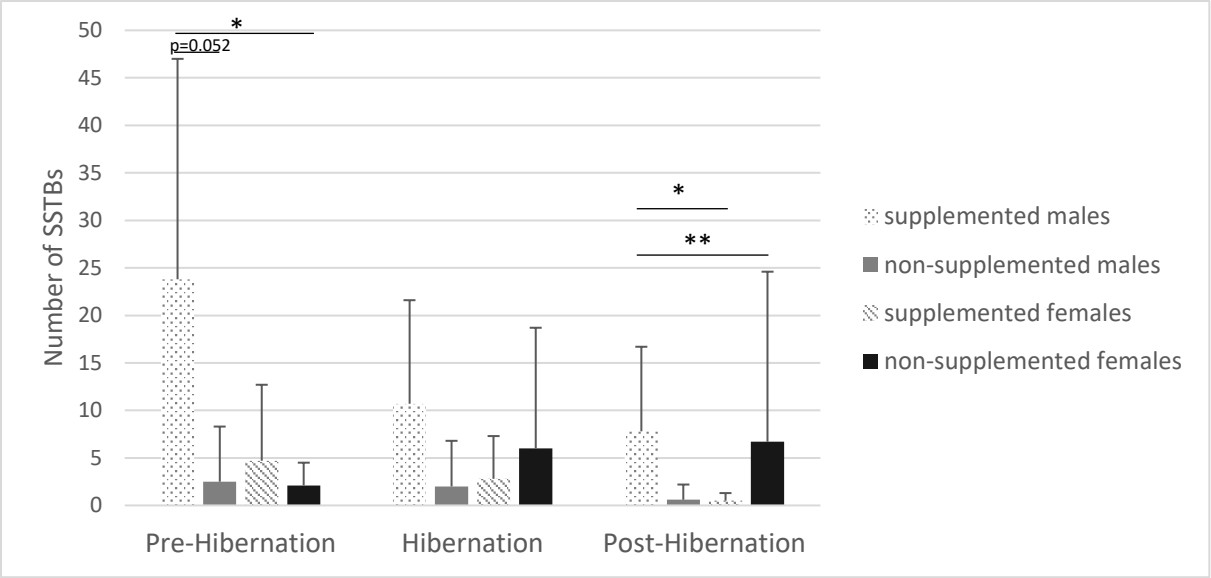

Figure 5 Distribution of short and shallow torpor bouts (SSTB) in males and females with and without additional food stores during the different periods of hibernation, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, Mean ± SD

The number of SSTBs did not differ between the periods of pre-hibernation, hibernation and post-hibernation in supplemented and non-supplemented males and females (Bonferroni-corrected $p < 0.017$ in all cases).

Interbouts (IB)

Since all the animals showed DTBs, all of them also had Interbouts (IB) between DTBs (Tab. 5). IBs are defined as the time between two DTBs, including STBs and SSTBs occurring during this period and hence, body temperatures below 30 °C. In contrast, arousals are defined as the time between two DTBs with body temperatures above 30 °C.

Table 5 Mean number of IBs (#), mean duration of IBs (h) and total time spent in IB (d) in supplemented and non-supplemented male and female hamsters. Mean ± SD

	IB (#)	Duration (h)	Total time (d)
supplemented males	11.2 ± 2.1	38.1 ± 6.5	17.4 ± 2.6
non-supplemented males	19.6 ± 4.3	27.6 ± 13.1	22 ± 9.8
supplemented females	18.5 ± 2.7	23.5 ± 6.2	17.5 ± 3.1
non-supplemented females	17.4 ± 4.3	27.3 ± 11	18.7 ± 6.5

The number of IBs differed significantly between the male groups as non-supplemented males showed more IBs than supplemented ones ($p = 0.001$) (Tab. 5). Furthermore, the mean duration of IBs differed significantly among males, supplemented ones had a longer mean duration of IBs than non-

supplemented males (z= -1.979, p = 0.048). Nevertheless, the total time spent in IBs did not differ between these groups (z= -0.412, p = 0.680) (Tab. 5).

For the females, no significant differences in IB expression were found between individuals with and without additional food. Thus, the number of IBs (t= 0.549, p = 0.590), the mean duration of IBs (t= -0.745, p = 0.466) and the total time spent in IB (t= -0.388, p = 0.703) were similar in both groups (Table 5).

Body Temperature during IBs

Minimum body temperature during IBs did not differ between male groups (t= -1.092, p = 0.289) but mean body temperature during IBs was lower in supplemented males than in non-supplemented ones (z= -2.023, p = 0.043) (Fig. 6).

Mean body temperature during interbouts differed significantly between non-supplemented males and supplemented females (t= -2.562, p = 0.028; Fig. 6).

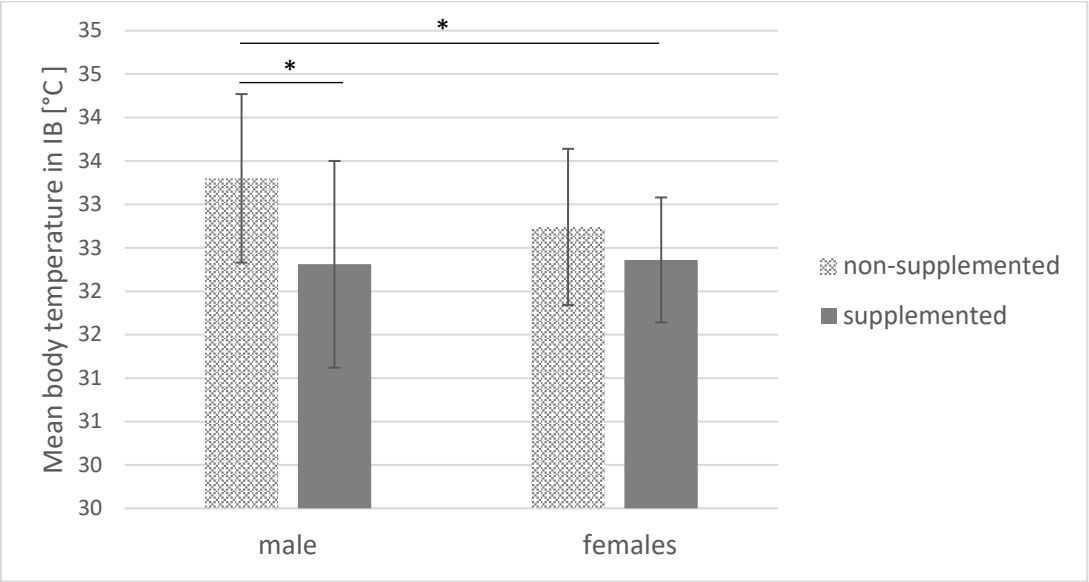

Figure 6 Mean body temperature during Interbouts (IB) in males and females with and without additional food stores, * p ≤ 0.05, Mean ± SD

Within female groups neither for the minimum (z= -0.880, p = 0.379) nor for the mean body temperature during IB (t= -0.889, p = 0.386) significant differences were detected (Fig. 6).

Discussion

Our field data suggest that food supplementation prior to hibernation affects winter heterothermy in the common hamster (*Cricetus cricetus*), with clear effects observed in males and comparatively weaker or absent effects observed in females during the hibernation period. In males, supplementation was associated with fewer deep torpor bouts (DTBs), shorter DTB duration, and less time spent in deep torpor overall, and the minimum body temperature during DTBs (measured subcutaneously) was slightly higher on average. In contrast, there was no significant difference in female DTB metrics between supplemented and non-supplemented individuals. Interbout structure also shifted in males (fewer, longer interbouts), while females showed little change. These outcomes are broadly consistent with patterns reported for heterothermic mammals, in which greater energy availability reduces reliance on deep torpor and extends euthermic phases. However, this relationship is sex-dependent in common hamsters, and in our population females showed no corresponding change (Geiser, 2004; Ruf & Geiser, 2015; Levesque & Tattersall, 2010; Levy, Dayan & Kronfeld-Schor, 2011; Vuarin & Henry, 2014; Siutz et al., 2016). The same population and winter were analysed previously with different metrics and seasonal partitions (Siutz et al., 2018a; Siutz, Ammann & Millesi, 2018b). Here, we reanalyse the same dataset with an explicit focus on hibernation (DTBs) versus pre- and post-hibernation (SSTBs) and interpret sex-specific differences accordingly. In males, supplementation reduced reliance on prolonged deep torpor during the hibernation period. DTBs occurred less often and were shorter, and a larger share of time was spent in euthermic interbout intervals. This pattern aligns with energy-optimisation theory, whereby abundant resources and/or warmer microclimates enable individuals to maintain higher torpor minima within DTBs and spend more time in euthermy. This can reduce not only energetic expenditure, but also the recognised non-energetic consequences of torpor and arousals, such as reduced immune surveillance requiring euthermic restoration, neural downscaling with potential cognitive consequences, oxidative/cellular stress during rewarming and limitations on above-ground behaviours that are important for foraging, maintaining territory and mating (Humphries et al., 2003a, 2003b; Levesque & Tattersall, 2010; Landry-Cuerrier et al., 2008; Vuarin & Henry, 2014; Boyles et al., 2007). Consistent with sex-specific overwintering strategies in this species, females cache extensively and may shorten or delay hibernation following late litters, often prioritising euthermy to restore condition (Franceschini-Zink & Millesi, 2008; Siutz et al., 2016; Hufnagl et al., 2011). In food-storing hamsters, females can carry caches into early spring and draw on them during gestation and lactation. Consequently, extra energy acquired before winter may show up as earlier emergence and reproduction rather than as changes in winter torpor.

In food-storing hibernators, the balance between internal fat and external caches determines the extent to which torpor is used (Humphries et al., 2003a). In our study, access to high-quality stores was associated with fewer and shorter DTBs in males. The response is graded rather than on/off. As autumn energy reserves (fat plus cached food) increase, DTBs become fewer and shorter during the hibernation period, and more time is spent euthermic between bouts. This pattern is consistent with work on the eastern chipmunk (Tamias striatus), a food-storing hibernator. In free-ranging chipmunks, experimental increases in hoard size reduced the use of prolonged torpor and increased euthermic time, and a complementary cost–benefit framework showed that animals flexibly trade off torpor against available energy (Humphries et al., 2003a; Humphries et al., 2003b). Seasonal measurements in the same species further indicate that individuals with sufficient stores remain euthermic for longer and use torpor intermittently rather than relying on multiday bouts (Levesque & Tattersall, 2010). Sex-specific autumn strategies likely shape these outcomes. In common hamsters, males typically forage above ground and build up food caches only during the postreproductive period before immergence. Therefore they benefit directly from body fat stores, whereas females have a longer and energetically more costly reproductive period, especially those that raise three litters and are therefore still lactating in September. This limits fat accumulation, increases reliance on caching, which females show throughout the season, and favors retention of the DTB pattern with earlier spring timing when supplemented (Franceschini-Zink & Millesi, 2008; Siutz, Franceschini & Millesi, 2016; Hufnagl et al., 2011; Millesi et al., 2008; Siutz et al., 2012; Siutz et al., 2018).

High density and the possibility of multiple litters in our study population likely accentuate sex-specific responses. This expectation is consistent with sex-specific behaviour and timing in this species. Adult females typically begin hibernation later than males and hibernate for shorter periods. Reproductive effort in late summer and autumn reduces the time available for fattening and caching (Siutz et al., 2016; Franceschini-Zink & Millesi, 2008). For males, arriving with additional stores at immergence provided a larger energetic buffer, reduced reliance on prolonged deep torpor, and was accompanied by body-mass increases over winter (Siutz et al., 2012; Siutz et al., 2018a). From an evolutionary perspective, these differences are expected. Males must compete for mates soon after spring emergence, so selection favours individuals that reach spring in good condition and can invest in early activity and mate searching. Consistent with this, supplemented males increased body mass over winter and emerged heavier than unsupplemented males (Siutz et al., 2018a). Females enter reproduction immediately after emergence; mating and gestation begin quickly, all females gain mass during pregnancy and typically lose mass during lactation, so net mass gain after emergence is limited despite the early increase (Franceschini-Zink & Millesi, 2008; Hufnagl et al., 2011). Accordingly, supplemented females advanced emergence and conception while maintaining DTB structure,

consistent with buffering reproductive costs under time constraints (Siutz et al., 2016; Siutz et al., 2012). In the same population, a subsequent season reported approximately twice as many litters in supplemented compared with unsupplemented females (Siutz et al., unpublished data).

Shallow torpor dynamics provide additional context. Supplemented males showed more short and shallow torpor bouts (SSTBs), particularly during the pre- and post-hibernation periods, whereas within the hibernation period group differences were limited. Deep torpor entails the lowest metabolic rate per unit time, while SSTBs save less energy per unit time but remain compatible with above-ground activity when food is available. Males shortened the hibernation period to the coldest part of winter, used stores accumulated shortly before immergence during the surrounding weeks, and increased their body mass over winter. In that context, additional SSTBs before and after the shortened hibernation phase likely provided modest energy savings without committing to multiday DTBs and could occur alongside foraging. That this pattern was expressed by males but not females is consistent with sex-specific strategies in this species: females often compress autumn preparation due to late litters and invest more in caching, whereas males are observed to feed mainly above ground during the active season, show less pronounced caching and switch burrows more frequently. Under high energy availability shortly before immergence, males can therefore minimise hibernation and emerge in better condition, while females maintain DTB structure and advance spring timing.

In males, interbout (IB) intervals were fewer but longer in supplemented than in unsupplemented individuals. Because an IB spans the entire interval between two DTBs and can include short torpor episodes (SSTBs), shifts in mean IB temperature mainly reflect the proportion of such short bouts within IBs rather than changes during strictly euthermic intervals (Siutz, Ammann & Millesi, 2018b). Small adjustments within the burrow, such as chamber position, plugging, or insulation, may also influence IB temperature (Wassmer, 2004). In other taxa such as hibernating bats and chipmunks, energy status shapes microclimate selection and time allocation (Boyles et al., 2007; Landry-Cuerrier et al., 2008). When energy is limited, these species choose cooler sites and increase torpor use. When energy is abundant, they use warmer sites or remain euthermic for longer (Boyles et al., 2007; Landry-Cuerrier et al., 2008). In our hamster population, animals overwintered in fixed burrow systems at a single urban site and hibernaculum temperatures were similar across years. We therefore interpret shifts in mean IB temperature as compositional changes within IBs, that is, a higher share of short torpor, rather than as microclimate selection (Siutz, Ammann & Millesi, 2018b). In females, IB number and duration did not differ between supplemented and unsupplemented groups, and mean IB temperature showed no consistent treatment effect. In females, this unchanged IB pattern fits their autumn energy strategy: late litters constrain pre-hibernation fattening, increase reliance on caching, and favour maintaining

DTB/IB structure rather than changing it (Franceschini-Zink & Millesi, 2008; Siutz et al., 2016). Taken together, in males the combination of higher minimum body temperature during DTBs, fewer but longer IBs, and a lower mean IB temperature indicates that supplementation altered body temperature patterns in both DTBs and IBs.

Nutritional mechanisms provide an additional explanation. In food-storing hibernators, the intake of food before winter and the body's reserves are actively regulated and closely linked to seasonal endocrine control (Florant & Healy, 2012). This provides a direct link between the quality of the diet and the expression of torpor. While our supplement increased availability, sunflower seeds also altered composition due to their high content of n-6 polyunsaturated fatty acids (PUFAs), particularly linoleic acid. In hibernating animals, diets rich in n-6 PUFAs are associated with lower minimum torpor temperatures and altered arousal dynamics (Ruf & Arnold, 2008; Munro, Thomas & Humphries, 2005). In fat-storing hibernators, higher dietary linoleic acid has been proposed to stabilise cardiac function during arousal and re-entry into DTB, thereby reducing the risk of arrhythmias. This mechanism may also apply to food-storing species (Ruf & Arnold, 2008). This is consistent with seasonal adjustments in membrane phospholipids and shifts in the balance of lipid versus carbohydrate oxidation, which are linked to oxidative balance (Ruf & Arnold, 2008; Giroud et al., 2009; Florant & Healy, 2012). In previous work on this population, standardising and enriching hoard size with sunflower seeds did not alter the group-level frequency or duration of deep torpor bouts. However, at the individual level, greater consumption of enriched seeds was associated with more short and shallow torpor (SSTB) and higher minimum subcutaneous temperatures, without eliminating DTBs (Siutz et al., 2018a; Siutz, Ammann & Millesi, 2018b). Because our supplement increased both energy availability and fatty-acid composition, we cannot disentangle quantity from quality effects and therefore cannot attribute the observed patterns to PUFAs alone (Ruf & Arnold, 2008; Florant & Healy, 2012; Munro, Thomas & Humphries, 2005; Giroud et al., 2009). In short, availability primarily constrains whether and how much deep torpor is used (Humphries et al., 2003a, 2003b; Siutz et al., 2018), whereas dietary composition can fine-tune winter torpor expression (DTB metrics and SSTB distribution within interbouts) (Siutz et al., 2017; Munro, Thomas & Humphries, 2005; Ruf & Arnold, 2008; Giroud et al., 2009). However, diets rich in polyunsaturated fatty acids (PUFAs) can increase the risk of peroxidation. Seasonal shifts in oxidative status have been reported in small hibernators (Ruf & Arnold, 2008; Giroud et al., 2009).

From a physiological perspective, moving away from a state of very deep torpor could reduce cumulative cellular costs despite the fact that arousals are linked to oxidative and inflammatory stress at the tissue level (Carey, 2000; Heldmaier, Ortmann & Elvert, 2004). The higher minimum body temperature during DTBs in supplemented males suggests a winter pattern with fewer extreme lows

and potentially a reduced cellular stress burden. It remains to be tested whether this translates into improved survival or reproduction, but it is known that energy status, endocrine control of intake and dietary lipid profiles all shape winter physiology and spring phenology (Florant & Healy, 2012; Ruf & Arnold, 2008; Giroud et al., 2009; Siutz et al., 2018a).

Our conclusions are subject to two limitations. Firstly, the number of animals in each of the four sex-by-treatment groups (male-supplemented, male-control, female-supplemented and female-control) was small. Several comparisons, particularly those involving SSTBs, were confined to specific seasonal phases or lay close to conventional significance thresholds. Given the small sample sizes, we interpret p-values together with effect sizes and uncertainty. A subsequent season showed similar qualitative patterns, but confirmation with larger, contemporaneous cohorts is still needed. Secondly, as our non-supplemented controls derive from earlier years at the same site, unmeasured between-winter variation (e.g. ambient conditions, soil temperatures and disturbance) could introduce noise, which is a known issue in field energetics (Levesque & Tattersall, 2010; Landry-Cuerrier et al., 2008). Hibernaculum temperatures at the site were similar across years, which mitigates but does not eliminate this concern. In addition, we did not quantify pre-existing hoards in female burrows before supplementation, so initial cache size could have contributed to individual variation. Future work should measure pre-immergence hoards and follow marked individuals across multiple winters to separate year effects from treatment effects.

For a subset of individuals, seeds were placed in the burrow without the caching process being observed directly, so the amount consumed by each animal likely varied. Furthermore, since IBs include STBs and SSTBs by definition, differences in mean IB temperature primarily reflect IB composition rather than temperature reductions during strictly euthermic intervals (Siutz, Ammann & Millesi, 2018b). To separate microclimate effects from energetic drivers, and to quantify how availability and composition jointly shape torpor thresholds, it would be valuable to replicate the study with same-year controls at the same site. This could include direct verification of caching and consumption with camera traps, audits of hoards after winter, and continuous logging of burrow microclimates (Boyles et al., 2007; Siutz et al., 2017).

From a conservation perspective, supplementation can influence the hibernation behaviour of food-storing hibernators, with pronounced effects in males. However, outcomes depend on sex and the specific habitat. Diversified plantings and weed-rich communities can improve the quality and diversity of potential food stores. Protein-rich, diversified, crop-based diets have also been shown to enhance hibernation and subsequent reproduction in hamsters (Tissier et al., 2019; Tissier, Kletty, Robin &

Habold, 2021; Gérard, Robin, Kletty & Habold, 2024). At the population level, habitat loss and landscape simplification are the main limitations; supplementation alone rarely offsets them, so management should be implemented alongside habitat measures to increase food availability and improve its composition (e.g., protein and fatty-acid profile) (Kletty et al., 2020; Descamps & De Vocht, 2025).

From a management perspective, lipid-rich seeds (e.g., sunflower seeds) may modulate torpor expression without addressing emerging protein limitations. A more effective way of improving condition and reproductive output in agricultural landscapes is to promote protein-rich weeds, legumes, or soybean-based rotations (Tissier et al., 2019, 2021; Gérard et al., 2024). In reintroduction projects, low female reproductive rates are a critical bottleneck. Targeted supplementation around emergence and early spring can improve female reproductive success by enhancing condition and advancing timing (Tissier et al., 2019, 2021; Gérard et al., 2024). By contrast, a small pilot supplementation between the first and the next litter did not alter reproductive output in this population (unpublished observation).

Taken together, our study shows that in a food-storing hibernator, pre-hibernation access to external energy reserves reduces the expression of deep torpor primarily in males and elevates the minimum body temperature during DTBs, whereas female deep-torpor metrics remain largely unchanged, consistent with sex-specific overwintering strategies (Franceschini-Zink & Millesi, 2008; Siutz et al., 2016; Hufnagl et al., 2011). This pattern is expected under energy-optimisation frameworks in which abundant resources and favourable microclimates allow animals to maintain higher torpor minima and spend longer euthermic periods, thereby minimising arousal and thermogenesis costs (Humphries et al., 2003a, 2003b; Levesque & Tattersall, 2010; Vuarin & Henry, 2014; Boyles et al., 2007). Evidence from food-storing small mammals shows that restricting access to caches increases the likelihood of hibernation and the occurrence of short, shallow torpor, while effects on deep-torpor number and duration are not consistent across species (Humphries et al., 2003a; Munro, Thomas & Humphries, 2005; Vuarin & Henry, 2014). From a conservation perspective, although lipid-rich seeds (e.g. sunflower seeds) may influence the expression of torpor, they do not address the emerging protein limitation in common hamsters. Therefore, fostering protein-rich weeds or legumes, or soybean-based crop rotations, is a more promising way to improve the health and reproductive output of animals in intensive farming areas (Tissier et al., 2019, 2021; Gérard et al., 2024). Rather than expecting farmers to plant specifically for hamsters, measures can be integrated into existing rotations by promoting protein-rich legumes (e.g., soybean) and maintaining weed-rich field edges, which together improve dietary protein supply and diversify potential food stores (Tissier et al., 2019; Tissier et al., 2021; Gérard et al., 2024) and address the protein limitation highlighted for wild populations (Descamps & De Vocht,

2025). Future studies should manipulate the size and composition of the cache experimentally, and couple continuous subcutaneous temperature measurements with burrow microclimate data to quantify energetic thresholds influencing torpor decisions in the field. Overall, our results support the idea that torpor optimisation in food-storing hibernators is based on energy availability, and highlight that nutritional quality, as well as quantity, shapes overwintering strategies and their management implications.

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Appendix

Zusammenfassung

Winterschlaf ermöglicht es kleinen endothermen Tieren, den Winter zu überstehen, indem sie mehrtägige Episoden tiefen Torpors (DTB) mit kurzen euthermen Intervallen abwechseln. Bei Vorratssammlern wie dem Feldhamster (*Cricetus cricetus*) können Menge und Zusammensetzung der Vorräte dieses Muster beeinflussen. Ziel dieser Studie war es zu prüfen, ob die Bereitstellung zusätzlicher hochwertiger Futtervorräte kurz vor der Einwinterung das Winterschlafmuster freilebender Hamster verändert und ob sich die Reaktionen zwischen den Geschlechtern unterscheiden. Konkret fragten wir, ob die Zufütterung die Anzahl und Dauer der DTBs, die Struktur der Interbout-Intervalle (IBs) sowie das Auftreten kurzer und flacher Torporepisoden (SSTBs) verändert.

Hierzu untersuchten wir von Herbst 2015 bis Frühjahr 2016 eine Feldhamsterpopulation in einem urbanen Habitat in Wien. Kurz vor Beginn der Winterschlafphase erhielten ausgewählte Tiere jeweils 500 g Sonnenblumenkerne. Subkutan implantierte Temperaturlogger zeichneten die Körpertemperatur den gesamten Winter über kontinuierlich auf. Wir verwendeten standardisierte, temperaturbasierte Kategorien zur Auswertung (DTB < 20 °C und > 24 h, STB < 20 °C und ≤ 24 h, SSTB 20–30 °C und ≤ 24 h sowie Interbout (IB) als Intervall zwischen zwei DTBs, das STB/SSTB einschließen kann). Die zugefütterten Individuen wurden mit nicht zugefütterten Tieren vom selben Standort verglichen.

Bei den Männchen reduzierte die Zufütterung die Winterschlafphase deutlich. Zugefütterte Männchen hatten weniger DTBs, kürzere DTB-Dauer und verbrachten insgesamt weniger Zeit im tiefen Torpor als nicht zugefütterte Hamster. Die minimale Körpertemperatur während der DTBs war im Mittel etwas höher. Auch die IB-Struktur verschob sich: Zugefütterte Männchen zeigten weniger, aber längere IBs, während die gesamte IB-Zeit über den Hibernationszeitraum hinweg in den Gruppen ähnlich blieb. Die mittlere Körpertemperatur während IBs war bei supplementierten Männchen niedriger. Dies deutet auf einen höheren Anteil kurzer Torporereignisse innerhalb der IBs hin. Die SSTB-Expression nahm bei den Männchen sowohl am Beginn als auch am Ende des Winters zu, zugefütterte Männchen zeigten mehr SSTBs vor der ersten und nach der letzten DTB. Während der eigentlichen Winterschlafphase unterschied sich die SSTB-Zahl zwischen den Gruppen hingegen nicht.

Bei den Weibchen blieb das Muster des Winterschlafs stabil. Die Zufütterung veränderte weder die Anzahl noch die Dauer der DTBs, die Gesamtzeit im tiefen Torpor oder die Zahl bzw. Dauer der IBs; auch die Ausprägung der SSTB unterschied sich nicht zwischen zugefütterten und nicht zugefütterten Weibchen. Insgesamt deuten die Daten darauf hin, dass der Zugang zu externen Energiereserven es Männchen ermöglicht, Winterschlaf auf die kältesten Wochen zu beschränken und in den angrenzenden Prä- und Posthibernationsphasen vermehrt kurze Torporepisoden mit geringer Temperatursenkung zu nutzen. Diese Befunde sind biologisch plausibel: Die Zufütterung wirkt bei

Männchen als Energiepuffer und ermöglicht ihnen ihr Körpergewicht während des Winters zu erhöhen. Die verbesserte Kondition zu Frühlingsbeginn kann ein entscheidender Vorteil sein, wenn Aktivität, Paarung und Auseinandersetzungen zwischen den Männchen einsetzen. Dass Weibchen ihre Winterschlafmuster nicht verändern, ist nicht überraschend, weil sie ihre Überwinterungsenergie primär über Vorratshaltung absichern. Zusätzliche Samen kurz vor der Einwinterung beeinflussen daher eher das saisonale Timing (z. B. Emergenz/Reproduktion) als Torpormetriken.