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INFLUENCE OF HOUSING CONDITIONS ON THE HIBERNATION PATTERNS OF EUROPEAN HAMSTERS (*CRICETUS CRICETUS*)

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ABSTRACT

Because most studies on hibernation are made in laboratory conditions but the results are presumed to apply to the wild as well, the objective of this study was to compare the hibernation patterns of European hamsters (*Cricetus cricetus*) in the laboratory with those in semi-natural housing conditions. In order to achieve this, a total of 10 telemetric recordings of body temperature (T_b) from laboratory housing and 18 recordings of animals kept in an outdoors enclosure were obtained. The results were compared according to mean duration of hibernation bouts (HBs) and the frequency and distribution patterns of different types of HBs.

The results show, that although the average ambient temperature (T_a) in the laboratory was consistently higher as compared to the outdoor enclosure, no significant difference in the mean duration of typical multi-day HBs could be found. However, the amount of shorter torpor bouts (< 24 h) was significantly higher in the laboratory as compared to the outdoor enclosure. These shorter torpor bouts occurred at the beginning as well as in the middle of hibernation: during both periods they were found more frequently in the laboratory. Short torpor showing a stepwise decrease of T_b prior to typical multi-day torpor bouts ("test drops"), only occurred in those laboratory studies, where T_a was likewise reduced in steps. These results indicate a significant influence of housing conditions on the hibernation patterns of experimental animals. Results from non-comparative laboratory studies should thus be treated with caution.

Key words: laboratory, outdoor enclosure, comparative study, laboratory artifacts, hibernation pattern, torpor, hamster, test drop, telemetry, *Cricetus*

RUNNING HEAD: Influence of Housing Conditions on Hibernation

INTRODUCTION

For a long time it was believed that hibernating animals reduce their body temperature (T_b) to values near ambient temperature (T_a) at the beginning of winter, remain cooled down throughout winter, and finally warm up to normal T_b at the end of winter. With the beginning of exact studies it became clear that this is not the case. Quite the reverse is true: to date no mammal or bird species has been found to show uninterrupted hibernation (Lyman, 1982; Geiser and Ruf, 1995). Instead of an enduring hypothermia, hibernation is always found to be fragmented into hibernation bouts (HBs) of longer or shorter duration, interrupted by normothermic phases (inter-bout normothermia) also of variable duration. This sequence of hypothermic and normothermic phases represents a typical hibernation pattern, the details of which can be compared between, as well as within, species.

Comparing hibernation patterns between species provides information about the diversity of adaptation strategies to the conditions of a cyclic environment (e.g. French, 1985; Kenagy, 1986; French, 1988; Arnold, 1993). On the other hand, intraspecific comparisons may clarify different adaptations of the sexes or different age groups (e.g. French, 1982; Michener, 1984; Young, 1990; Michener, 1992; Körtner and Geiser, 1998). In the study reported here, intraspecific comparisons of animals kept under different housing conditions were conducted to estimate the impact of experimental design on hibernation patterns.

The closer the housing conditions of experimental animals are to their natural environment, the more likely a natural pattern of behavior (e.g. hibernation patterns) can be expected. For a meaningful interpretation of experimental results, such as the numerous studies on the periodicity of hibernation (e.g. Folk, 1957; Strumwasser, 1959; Daan, 1973; French, 1977; Pohl, 1987; Canguilhem et al., 1994; Grahn et al., 1994; Wollnik and Schmidt, 1995; Waßmer and Wollnik, 1997), it is of great relevancy to exclude artifacts which might be due to artificial housing of laboratory animals. Therefore, the objective of this study was, first, to characterize the time course of hibernation in European hamsters in different housing conditions and, second, to assess artifacts provoked by laboratory housing. In order to achieve this purpose, the hibernation patterns of hamsters kept under semi-natural conditions in an outdoor enclosure were compared to the patterns of hamsters under laboratory housing.

MATERIALS AND METHODS

Animals and housing

31 of the 36 European hamsters used in this study had been obtained from a free-ranging population near Strasbourg (France) in May 1993, 1996 and 1997, respectively. Another five animals came from a laboratory breeding stock of the Medical University in Hannover (Germany) or were bred in the animal research facility of the University of Konstanz (Germany). Details are given in Table 1.

Before the beginning of the experiments, the animals were individually housed in standard laboratory cages (Makrolon, type IV: 0.55 m (length) by 0.35 m (width) by 0.2 m (height)) under standard laboratory conditions (light-dark cycle with 16 hours light and eight hours darkness (LD 16:8); T_a 20 ± 1 °C). Husbandry was restricted to feeding (twice a week) and a general health check combined with the cleaning of the cages (every three weeks). Between September and October, hamsters were transferred either to a cold room or into the outdoor enclosure.

In the cold room the animals were individually housed in plastic containers of 1 m (length) by 1 m (width) by 1 m (height), the top side of which were open and covered by wire mesh. Each enclosure was filled with soil up to 0.2 m as burrowing material and contained various nest boxes made of plastic.

In the outdoors enclosure the hamsters were individually housed in wire mesh cages of 0.8 m (length) by 0.8 m (width) by 1.1 m (height). Cages were buried 0.6 m into the ground and filled with soil up to ground level. Thus the animals were able to dig their own burrows inside the cages. In order to locate the animals at any time, each cage was equipped with two spiral-shaped antennae fixed into plastic platforms at the bottom and the top of the cage.

In the laboratory, standard rodent food pellets and water were given *ad libitum* whereas in the outdoor enclosure, a mixture of whole wheat and corn grains as well as water were offered *ad libitum* on a feeding rack. The difference in diet was necessary as laboratory pellets grow mold within a few days under outdoors conditions. Food and water were replenished twice a week. During wintertime, feeding racks needed to be refilled only occasionally, which was done very carefully and quietly.

In both environments, general health, body weight and reproductive status was established capturing the animals in live traps once a month followed by a light ether anaesthesia (Ethrane, Abbott GmbH, Wiesbaden, Germany). During the hibernation season this procedure as well as other husbandry was suspended.

Surgery and temperature telemetry

T_b was measured using temperature-sensitive radio transmitters. Transmitters (cylindrical shape, diameter 1.5 cm, height 2.5 cm, weight approx. 8 g) were implanted into the peritoneal cavity of each hamster anaesthetised by intraperitoneal injections of 50 mg

Ketamin (Kemint, Alvetra GmbH, Neumünster, Germany) and 10 mg Rompun (Bayer, Leverkusen, Germany) per kg body weight. For a post-operation period of 10-14 days the animals were housed in polyethylene cages (35 x 55 x 20 cm) at 20 °C and then transferred to the experimental enclosures. No increased morbidity, mortality or other problems resulted from the long-term use of intraperitoneal transmitters.

T_a was measured using additional telemetry transmitters. In the laboratory, the reference transmitter was placed at the floor of the cold room, whereas in the outdoors enclosure, one transmitter was placed at ground level, while a second device was buried 0.6 m into the ground to record soil temperature at the presumed location of the animals' dens.

Statistical analyses

During this investigation, T_b of hamsters and T_a were continuously monitored over a period of 4-8 months at a temporal resolution of 5 min. The following parameters were calculated from the temperature recordings: (1) time of day at the beginning of each hibernation bout (HB), given by the first measurement of T_b below 30 °C: also referred as the "entry" into a HB; (2) time of day at the end of each HB, given by the first measurement above 30 °C: also referred as the "arousal" from a HB; (3) duration of each HB, defined as the interval between entry and arousal; (4) duration of inter-bout normothermia between consecutive HBs, given as the interval between an arousal and the next entry into a HB.

According to Waßmer and Wollnik (1997), three types of HBs were distinguished: (1) long HBs: T_b below 20 °C and bout duration longer than 24 h; (2) short HBs: T_b below

20 °C and bout duration shorter than or equal to 24 h; and (3) short and shallow HBs: T_b above 20 °C and bout duration shorter than or equal to 24 h.

A computer program (Statistica, StatSoft Inc.) was used to compare data across animals and housing conditions. For parametrically distributed data, means ± standard deviations and repeated measures analyses of variance (ANOVA or MANOVA) were used, while nonparametrically distributed data were examined by using medians ± 25 % quartiles and Kruskal-Wallis analyses of variance (KW). When appropriate, Sheffé's multiple *t*-test was used for post-hoc comparisons.

RESULTS

Because of technical problems and the loss of some animals during the experiments, a total of only 21 complete and 7 partial recordings of T_b during hibernation could be obtained. Figure 1 shows five examples of these results. From the total of 624 HBs, 385 were long HBs, 48 short HBs and 191 short and shallow HBs (Fig. 2).

Duration of hibernation bouts

Duration of HBs varied between 10 minutes and 6.9 days. The average duration of long HBs was 68 h, which corresponds well with previous results on the European hamster (e.g. Gubbels et al., 1989; Wollnik and Schmidt, 1995) and other hamster species (e.g. Kuhnen, 1986; Pohl, 1979). A strong correlation between T_b and the duration of HBs was found (duration (h) = -0.79 ∗ T_m + 89.61; $R_{adj}^2 = 0.62$; N = 615; $p < 0.0001$; where T_m is the minimum of T_b during a HB).

Mean T_a in the outdoor enclosure was significantly lower than in the laboratory (5.82 ± 2.89 vs. 10.03 ± 1.42 °C; one-way ANOVA: $F_{1,374} = 204.03$, $p < 0.001$). This seems to be reflected by significantly shorter HBs in hamsters kept under laboratory conditions (8.17 ± 3.42 vs. 55.88 ± 33.50 h (median ± 25 % quartiles), KW: H (1, N = 624) = 98.19, $p < 0.0001$). A closer look at the frequencies of different HB-classes revealed that this difference was caused by the occurrence of the majority of shorter HBs (< 24 h) in the laboratory studies (Figs. 2 and 3, discussed in greater detail below). Focusing only on the long HBs, a comparison between laboratory and outdoor enclosure housing conditions did not show significant differences (69.52 ± 31.29 vs. 66.28 ± 26.37 h; Fig 3d).

Where both long and short HBs are averaged, the different T_a for the two groups seems to be reflected by significantly shorter HBs in hamsters kept under laboratory conditions (8.17 ± 3.42 vs. 55.88 ± 33.50 h (median ± 25 % quartiles), KW: H (1, N = 624) = 98.19, $p < 0.0001$). However, this difference is related to frequencies rather than duration of HBs, as discussed below.

Frequencies and distribution patterns of different hibernation bouts

The distribution patterns of long, short and shallow HBs showed significant differences between housing conditions (MANOVA, Wilks $\lambda_{3,24} = 0.495$, $p < 0.001$). A post hoc comparison (Scheffé test) showed that this difference was exclusively caused by a higher number of shallow HBs in the laboratory studies as compared to the outdoor enclosure studies (Figs. 2 and 3a). This difference became even more obvious when both short types of HBs (duration ≤ 24 h: short HBs and shallow HBs) were grouped together (ANOVA, $F_{1,26} = 20.85$, $p < 0.0005$; Fig. 3c).

Test drops

Strumwasser (1959) coined the term "test drops" for shallow and short HBs occurring at the beginning of the hibernation season. In their typical form “test drops” show a stepwise decrease in T_b and an increase in bout duration. They were therefore interpreted as a visual sign of an essential adjustment of metabolism towards hibernation. In the present study, only a few animals showed such typical "test drops" (e.g. hamster #4, Fig. 1). In the laboratory studies, 82 % of the hamsters showed some shallow and short HBs prior to the regular occurrence of long HBs, but a stepwise decrease in minimal T_b and increase in torpor duration during consecutive HBs (typical “test drops”) occurred in only two of the three laboratory studies and coincided with a 2-step decrease in T_a (Fig. 1, hamster #4). During the third laboratory study, with no clear “test drops”, T_a was reduced in only one step but was influenced by malfunctions of the T_a control. In the outdoor enclosure with a slow and steady decrease in soil T_a, only 44 % of the hamsters showed shorter HBs prior to multi-day HBs. None of the outdoors hamster showed typical “test drops”.

DISCUSSION

Test drops

In the present study, exemplary "test drops" showing a gradual decrease of T_b and increase of HB duration were only found in two of three laboratory studies. In these experiments, T_a was lowered in two steps from 20 to 8 °C (Fig. 1, hamster #4). A similar exemplary stepwise decrease of T_b during the first HBs was found in the American chipmunk *Tamias striatus* in the laboratory study of Pivorun (1976). In the same study, the author also examined *Eutamias minimus*. In the beginning of hibernation this chipmunk species showed some short HBs and/or shorter long HBs, which was termed "pre-plateau stage" by the author. In the case of *Tamias striatus*, T_a was lowered from 16 to 13, 10, 8, 6, and 3 °C, while for *Eutamias minimus*, T_a was reduced in only two steps to reach the final 10 and/or 8 °C.

Similar findings were reported for the American ground squirrel *Spermophilus columbianus*, according to an unpublished laboratory study by Paul J. Young (pers. comm). In the beginning of hibernation these animals were subjected to a T_a of 15 °C, which was slowly lowered over 90 days to 0 °C. In a second group of animals, whose experiment started immediately with a T_a of 5 °C, contrary results were found. After a single HB of shorter duration the ground squirrels reached the average bout length of approx. 15 days.

In free-ranging ground squirrels, preliminary short HBs of less than 24 h were never found, although an increase in the duration of HBs from the beginning of hibernation until midwinter could be detected (Young, 1990; Michener, 1992; and pers. comm. in litt. by both authors). Körtner and Geiser (1998) reported short HBs (< 24 h) in the beginning of hibernation of the mountain pygmy-possum *Burramys parvus*. However, a closer look at their Figure 6a (p. 175) revealed only three events of shorter HBs, which were probably not drawn from the same animal.

The existing literature and the results of this study suggest that the exemplary appearance of "test drops" is provoked by an initially high and then continuously or stepwise sloping T_a in laboratory studies. Therefore it seems justified to address them as laboratory artefacts. This conclusion does not negate the important scientific insights triggered by the interpretation of the "test drop" phenomenon, wrong though that interpretation might have been. The perception of this laboratory artefact stimulated important hypotheses on thermoregulation such as the cyclic resetting of setpoints or the programmed stepwise suppression of thermoregulatory nuclei in the hypothalamus (e.g. Hammel, 1967; Leucke and South, 1972).

Short and shallow hibernation bouts

In their study on the hibernation of the European hedgehog *Erinaceus europaeus*, Fowler and Racey (1990) found short and shallow HBs at a rate of 20 % in the middle of hibernation. The authors coined the term "transient shallow torpor" to stress the difference to the “test drop” concept. In the present study "transient shallow torpor" was even found at a rate of more than 60 % after long HBs had appeared. This high percentage accounted exclusively for a higher percentage of short HBs in the middle of hibernation as compared to the beginning.

In European hamsters kept under a light-dark cycle in the laboratory, entries into long and short HBs show the same daily timing while entries into shallow HBs occurred approximately 5 h later (Waßmer and Wollnik, 1997). Accordingly, short HBs may represent interrupted long HBs, indicating a disturbance of hibernation. This assumption is supported by the fact that short HBs occurred in the outdoor enclosure by far most in hamster #19 who spent the winter in a laboratory cage above the soil and was therefore exposed to very harsh temperatures (Fig. 1; hamster #19).

Most other studies in the laboratory (e.g. Canguilhem et al. 1994; Grahn et al., 1994) as well as in outdoor enclosures (e.g. Saboureau et al., 1991; Barnes and Ritter, 1993; Wollnik and Schmidt, 1995) regularly found "transient shallow torpor" within the hibernation patterns of various species. In contrast to this, none or only a few short or shallow HBs were reported from free ranging hibernators (e.g. Young, 1990; Michener, 1992; Arnold, 1993; Körtner and Geiser, 1998 and pers. comm. by Paul J. Young and Gail R. Michener).

Regardless of their sequential position in the time course of hibernation, both types of shorter HBs pooled together occurred significantly more frequently in the laboratory as compared to the outdoor enclosure housing (Figs. 3a and 3c). It is therefore highly probable that the regular occurrence of "transient shallow torpor" in the laboratory studies indicates an impairment of the natural hibernation behaviour due to the conditions of artificial housing.

GENERAL DISCUSSION

The European hamster has a body size of approximately 300 g. As this species does not accumulate body fat before winter, it is exclusively dependent on storing food before the onset of hibernation (Nechay et al., 1977). In addition, this species is known to drop hibernation under unfavourable conditions, e.g. in years of mass reproduction (gradations) (Petzsch, 1952). Taking this precondition of the species' autecology into account, the European hamster seems to be capable of a mixed strategy between the classical hibernators and the species showing daily torpor (Geiser and Ruf, 1995): Presumtiously under optimal conditions, they display a classical hibernation pattern (e.g. hamster #20, Fig. 1). If hamsters face less favourable circumstances, this pattern might be modified to show a significant amount of "transient shallow torpor" (e.g. hamster #19, Fig. 1), express only short HBs (e.g. hamster #23, Fig. 1) or even no HBs at all (e.g. hamster #28, Fig. 1). In order to avoid confusion with the comparison between housing conditions, all examples of these different hibernation strategies were drawn from the outdoor enclosure studies.

Astonishingly, according to the statistical comparison of the frequencies of short HBs and the combined shorter HBs, the amount of disturbances seems to be much higher in the laboratory as compared to the outdoor enclosure studies (Figs. 3a and 3c). This might be due to several technical and other artifacts in a typical animal house such as noise (Strumwasser 1959) - especially ultrasonic noise, alterations of the air pressure by the ventillation system, malfunctioning control of T_a and lighting condition or standardized laboratory food.

Although the detected differences could also be influenced and masked by age effects (Michener, 1984), biased by an unbalanced sex ratio (Michener, 1992) and different genetic background within the experimental animals (Geiser and Ferguson, 2001), most of these factors can be rejected in this study. All animals in the study were at least half a year of age and fully mature. There are no indications of age effects in the European hamster besides differences between juveniles and adults (Ruzic, 1976). The majority of hamsters in the study were male (23 out of 36; Table 1). Although there was a highly biased sex ratio between groups: 12 out of 13 females were from the outdoor enclosure studies (Table 1), no biase in the frequency and distribution of short HBs could be found. Neither the comparison of single laboratory studies to each other or the outdoor studies nor the comparison between the pooled studies yielded any hint of biased results due to the genetic background of hamsters. It is therefore justified to assign the detected differences in the distribution and frequency of shorter HBs to differences to the housing conditions.

FINAL CONCLUSIONS

The European hamster with its unique opportunistic features may be not the best example for drawing a general conclusion on the significance of poorly designed laboratory studies. However, this study indicates even in this species, that conclusions drawn from non-comparative laboratory studies alone should be treated with caution.

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FIGURE LEGENDS

Fig. 1: Hibernation patterns of five European hamsters. The upper solid line shows the time course of body temperature; the lower dotted line the time course of ambient temperature.

Hamster #4 hibernated in the laboratory. The lower panel shows the temperature of the cold room. Temperature control failed three times, on December 13th, March 4th and March 30th. Recording of body temperature failed for short periods of time (interrupted time course of upper panel). Recording of hamster #4 started on November 11th.

Hamster #19 hibernated above the soil, therefore the lower panel represents ambient temperature at ground level. Accordingly, the ordinate of this graph starts at -5 °C instead of 0 °C. Recording of hamster #19 started on November 23rd. During some hibernation bouts measuring failures occurred. In these cases the last undisturbed value was kept up until the malfunction disappeared. Both animals (#4 and 19) frequently show short hibernation bouts in between the typical multi-day bouts, indicating a high level of disturbance.

Ambient temperature for hamsters #20, 23 and 28 was recorded in the soil (0.6 m depth). Hamster #20 shows a regular hibernation pattern, consisting exclusively of multi-day hibernation bouts. This was the typical pattern found in the outdoor enclosure recordings. However, the recordings of hamster #23 and #28 show the variability of hibernation patterns under the same housing conditions. In the hibernation of hamster #23, only 4 short hibernation bouts occurred, while hamster #28 did not show any hypothermia at all. Nevertheless, the statistical comparison of hibernation patterns revealed significant differences between housing conditions.

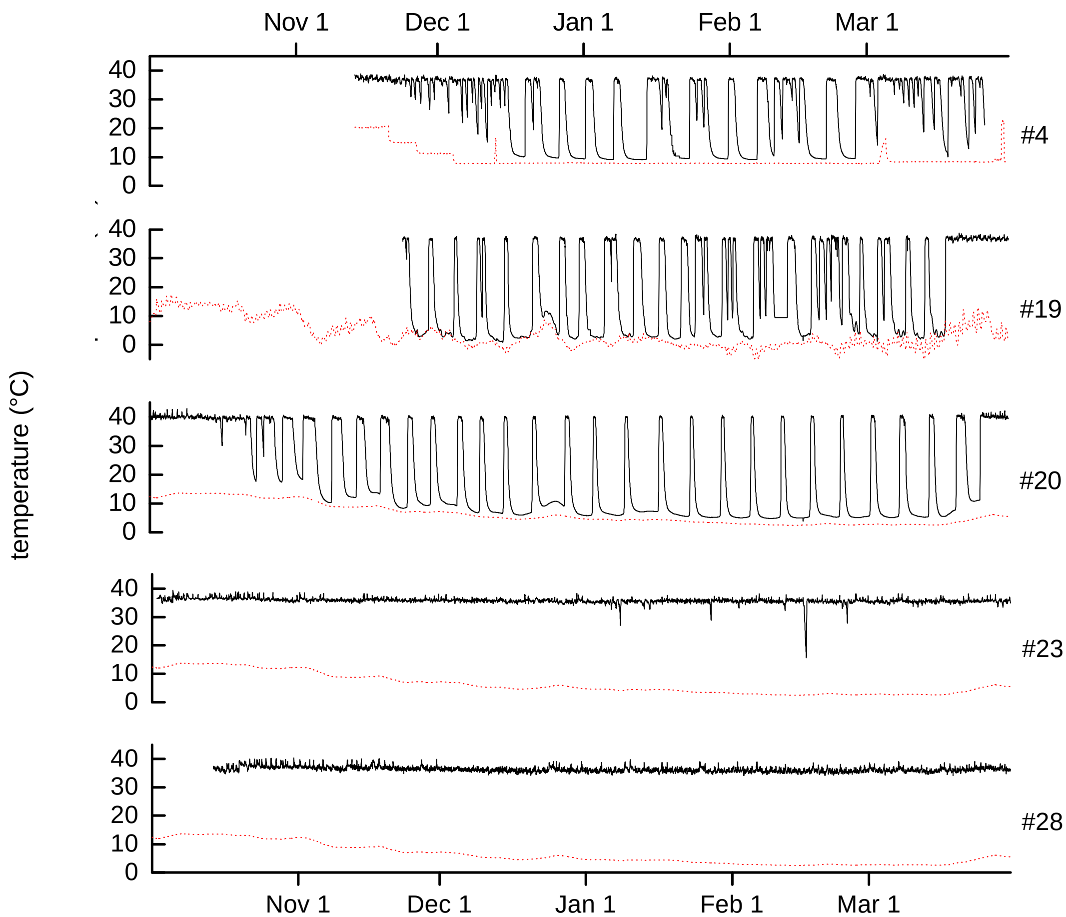
Fig. 2: Frequencies of different hibernation bouts in the hibernation of 28 European hamsters, kept in the laboratory and an outdoor enclosure. Hamsters #11, 15 and 28 did not show any hibernation bouts. The predominance of shallow hibernation bouts in the laboratory is clearly visible. In the outdoor enclosure, most short hibernation bouts occurred in the hamster, which hibernated above ground (#19) under very harsh ambient temperatures. Abbreviations: ShHBs: shallow hibernation bouts (body temperature above 20 °C); SHBs: Short hibernation bouts (shorter than 24 h); LHBs: Long hibernation bouts (longer than 24 h).

Fig. 3: Box plots of the frequencies of different hibernation bouts in the hibernation of 28 European hamsters, kept in the laboratory and an outdoor enclosure. The Boxes show the range between 25-75% quartiles around the median (indicated by an open square). Error bars indicate the minimum-maximum data range. Shallow hibernation bouts (body temperature above 20 °C); Short hibernation bouts (shorter than 24 h); LHBs: Long hibernation bouts (longer than 24 h). Shallow hibernation bouts alone (a) and pooled together with short hibernation bouts (b) as shorter hibernation bouts (c) occurred significantly more frequent in the laboratory studies.

Table 1: Origin, Sex and Housing Conditions of Hamsters

Abbreviations: DD (constant darkness); OE (outdoor enclosure); LD (light-darkness), LL (constant light).

	LD1 Laboratory 1	LD2 Laboratory 2	LL1 Laboratory 3	OE1 Semi-Natural 1	FG2 Semi-Natural 2
Number and Origin of Hamsters	4 captive-bred	4 wild catches	3 wild catches 1 captive-bred	12 wild catches	12 wild catches
Sex	4 Male	4 Male	3 Male 1 Female	6 Male 6 Female	6 Male 6 Female
Photoperiod	Short Day (LD 8:16)	Short Day (LD 8:16)	LL	Natural Photoperiod or DD	Natural Photoperiod or DD
Ambient Temparature (T_a)	8 ± 1°C	8 ± 1°C	8 ± 1°C	Natural T_a	Natural T_a
Initial Decrease in T_a	Irregular	3 Steps	3 Steps	slow continuosly sloping	slow continuosly sloping
Food	Rodent Pellets	Rodent Pellets	Rodent Pellets	Grain Mix	Grain Mix



Nov 1
Dec 1
Jan 1
Feb 1
Mar 1
temperature (°C)
40
30
20
10
0
#4
#19
#20
#23
#28

Fig. 1

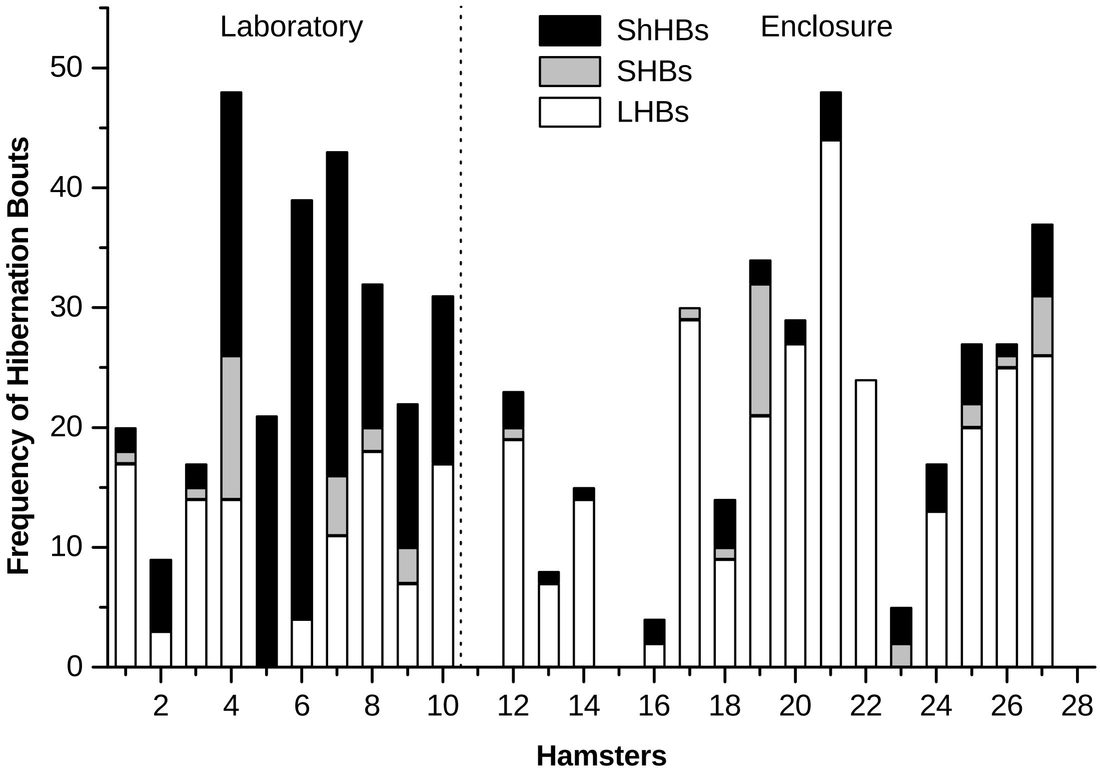

Laboratory
Enclosure
ShHBs
SHBs
LHBs
Frequency of Hibernation Bouts
Hamsters
0
10
20
30
40
50
2
4
6
8
10
12
14
16
18
20
22
24
26
28

Fig. 2

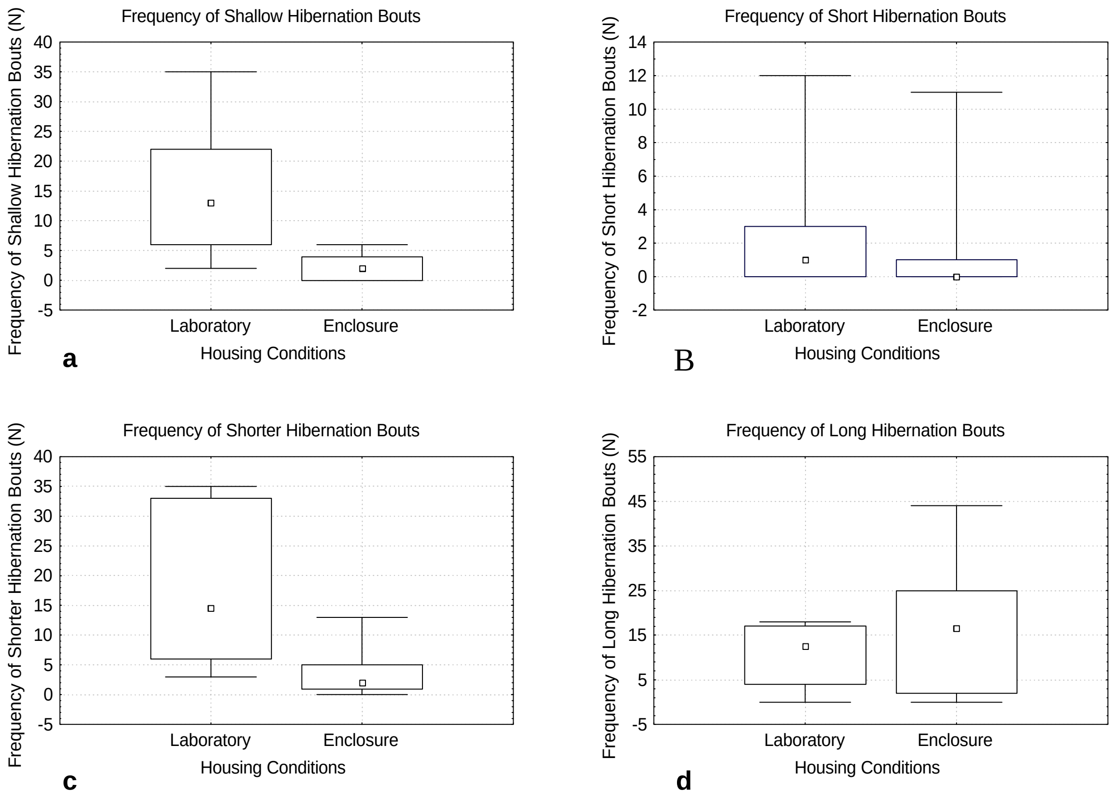

Frequency of Shallow Hibernation Bouts
Frequency of Shallow Hibernation Bouts (N)
40
35
30
25
20
15
10
5
0
-5
Laboratory
Enclosure
Housing Conditions
a
Frequency of Short Hibernation Bouts
Frequency of Short Hibernation Bouts (N)
14
12
10
8
6
4
2
0
-2
Laboratory
Enclosure
Housing Conditions
B
Frequency of Shorter Hibernation Bouts
Frequency of Shorter Hibernation Bouts (N)
40
35
30
25
20
15
10
5
0
-5
Laboratory
Enclosure
Housing Conditions
c
Frequency of Long Hibernation Bouts
Frequency of Long Hibernation Bouts (N)
55
45
35
25
15
5
-5
Laboratory
Enclosure
Housing Conditions
d

Fig. 3