NAT. CROAT. | VOL. 6 | No 2 | 217–231 | ZAGREB | June 30, 1997

ISSN 1330-0520
UDK 598.323.2+591.543.42(494)

HIBERNATION OF RECENTLY CAPTURED *MUSCARDINUS, ELIOMYS* AND *MYOXUS*: A COMPARATIVE STUDY

PETER VOGEL

Institut de Zoologie et d'Ecologie animale, Université de Lausanne,
CH-1015 Lausanne, Switzerland

Vogel, P.: Hibernation of recently captured *Muscardinus, Eliomys* and *Myoxus*: a comparative study, Nat. Croat., Vol. 6, No 2., 217–231, 1997, Zagreb

Prehibernation behaviour and hibernation pattern was investigated in three species of Gliridae, *Muscardinus avellanarius, Eliomys quercinus* and *Myoxus glis* in order to test the allometric relationship between torpor bout length and body weight. Food preferrance, weight increase and beginning of torpor bouts were studied. The mean of the longest torpor bouts was calculated for the two undisturbed species, *Muscardinus* and *Eliomys*, and it was significantly inversely correlated with body weight.

Key words: hibernation, torpor, arousal, Gliridae, *Muscardinus, Eliomys, Myoxus*

Vogel, P.: Hibernacija netom uhvaćenih *Muscardinus, Eliomys, Myoxus*: usporedbena studija, Nat. Croat., Vol. 6, No 2., 217–231, 1997, Zagreb

Istraživano je prehibernacijasko ponašanje i hibernacija kod tri vrste puhova, *Muscardinus avellanarius, Eliomys quercinus* i *Myoxus glis* da bi se testirao alometrijski odnos između duljine perioda torpora i tjelesne težine. Proučavan je izbor hrane, povećanje tjelesne težine i početak perioda torpora. Za dvije neometane vrste, *Muscardinus* i *Eliomys*, izračunata je aritmetička sredina najdužih perida torpora, koja je bila u znatnoj inverznoj korelaciji s tjelesnom težinom.

Ključne riječi: hibernacija, torpor, buđenje, Gliridae, *Muscardinus, Eliomys, Myoxus*

1. INTRODUCTION

Mammalian hibernation, which may last up to nine months, is always structured in a characteristic pattern: torpor bouts of several days are interrupted by bouts of euthermia of several hours (FRENCH 1985). Evidenced from electroencephalograms, the periodic arousal occurs before falling asleep (DAAN et al. 1991, TRACHSEL et al. 1991). This is also evident from the change in body temperature which rises in *Muscardinus* between two torpor bouts to sleeping temperature but not to activity temperature (VOGEL & FREY 1995). These normothermic phases are not fully explained, but according to the most probable hypothesis this phase is used to eliminate some chemical imbalance accumulated during periods of low body temperature (FRENCH 1982). This agrees with the observation of FRENCH (1985) who showed a positive correlation between the duration of euthermia and body weight: the heavier a mammal, the longer this period. Euthermia lasts only 2 hours in a 30 g *Muscardinus* (VOGEL & FREY 1995), but about 24 hours in the 4.5 kg *Marmota marmota* (ARNOLD 1988), easily explained by the mass-specific metabolic rate.

Another problem of the hibernating pattern is the length of the torpor bouts. FRENCH (1985) showed a reverse relationship with body mass: the smaller the hibernator, the longer the torpor bout. This result is contradictory to a prediction based on two facts: 1) Smaller mammals have a higher specific metabolic rate which should lead to a shorter period between two bouts of arousal, if arousal functions in cell regulation; 2) heating up the body mass of a 4.5 kg marmot requires much more energy than that of a 30 g dormouse, independent of metabolic rate, which only influences speed. Therefore, the interruption of hibernation is more problematic in big than in small mammals. A third argument comes from observations on the torpor length in free ranging common dormice (VOGEL & FREY 1995): the mean duration of the torpor bouts is 10.8 days. According to the equation of FRENCH (1985), who takes into account only the 5 longest torpor bouts in standard conditions of 5 °C, the length for this body size should be 20 days, which is rather unusual for this species.

As no physiological theory explains this relationship the question arises whether the significant differences found by FRENCH (1985) are not due to differences among mammalian families rather than the consequence of body size per se. FRENCH compared small bats, medium- sized Zapodidae and large ground squirrels. In order to test this relationship in an independent data set, free from phylogenetic differences among families, I decided to compare three species of the family Gliridae of different body size: *Muscardinus avellanarius* (15–35 g), *Eliomys quercinus* (45–120 g) and *Myoxus glis* (70–190 g).

All these species have been studied in the past (*Muscardinus*: HERTER 1928, VOGEL & FREY 1995; *Eliomys*: PAJUNEN 1970, 1974, DAAN 1973, *Myoxus*: KOENIG 1960, KÖNIG 1960, VIETINGHOFF-RIESCH 1960), but none of these authors kept these species simultaneously. Therefore, the opportunity to have three species in identical conditions was also used to compare and discuss some facts of the pre-hibernation behaviour.

2. MATERIAL AND METHOD

Six animals of each species (5 for the experiments and 1 as reserve) were captured during September and October 1995 in Switzerland. A list of the animals and their origin is given in table 1. During pre-hibernation they were kept in an outdoor animal room at ambient temperature. Each animal had its own cage. They were fed walnuts, hazelnuts, acorns, sweet chestnuts, sunflower seeds and fruit (apples, pears, plums). In order to test species specific food preferences (Table 2), different food items were simultaneously offered to all animals. Some of the common dormice caught in September and having a low juvenile weight (13–17 g) did not increase their body mass. Therefore they were replaced by animals trapped in October.

The cage size was increased with body size. The common dormice were placed in wooden cages with a glass front and the dimensions (in cm) 45 (length) × 45 (depth) × 30 (height), the garden dormice in a wooden cage of 40 × 40 × 55 and the fat dormice in metal cage of 60 × 40 × 100. The mesh size of the wire-lattice was 12 mm, obviously not mouse or shrew proof. The bottom was covered with 5 cm of humid earth, some leaves for nesting and branches for climbing.

The wooden nest boxes for *Muscardinus* had an inner dimension of 7.5 × 6.5 × 6.5 cm, for *Eliomys* 10 × 10 × 8 cm and for *Myoxus* 12 × 12 × 12 cm. In the latter, the wall

Table 1. List of experimental animals (*Muscardinus* M1–M5, *Eliomys* E6–E10, *Myoxus* G11–G15), capture localities, date of capture, mass at capture and mass at onset of hibernation.

Animal	Sex	Locality	Altitude [m]	Capture	Mass cap. [g]	Mass hib. [g]	Mass gain [g]	Mass gain %
M1	M	Forel	700	30.9.95	17.3	26.7	9.4	54.3
M2	F	Aclens	505	14.10.95	14.6	28.3	13.7	93.8
M3	M	Forel	700	24.9.95	19.8	28.4	8.6	43.4
M4	M	Forel	700	22.10.95	20.6	27.4	6.8	33.0
M5	F	Forel	700	22.10.95	17.7	26.5	8.8	49.7
Mean M					18.0	27.5	9.5	54.9
SD M					2.4	0.9	2.6	23.2
E6	F	Villetta	1240	22.2.04	52.7	105.3	52.6	99.8
E7	F	Marchairuz	1383	14.2.04	44.4	109.5	65.1	146.6
E8	F	Marchairuz	1383	20.2.04	50.0	100.7	50.7	101.4
E9	F	Marchairuz	1383	5.4.04	95.4	120.2	24.8	26.0
E10	F	Marchairuz	1383	15.2.04	45.8	125.0	79.2	172.9
Mean E					57.7	112.1	54.5	109.4
SD E					21.4	10.2	20.1	56.0
G11	F	Villetta	1240	25.8.95	68.2	133.0	64.8	95.0
G12	F	Roche	530	3.9.95	120.4	174.0	53.6	44.5
G13	M	Genolier	516	10.9.95	103.5	171.0	67.5	65.2
G13	M	Villeneuve	700	4.9.95	102.0	160.0	58.0	56.9
G15	F	Villeneuve	700	10.9.95	133.0	192.0	59.0	44.4
Mean G					105.4	166.0	60.6	61.2
SD G					24.4	21.7	5.6	20.9

Table 2. Comparative food preferences during perehibernation period in animals fed *at libitum*.

Food	Muscardinus	Eliomys	Myoxus
Hazelnuts fresh	+++	++	++
Walnuts open	++	++	+++
Acorn	–	–	++
Sunflower seeds	++	+	–
Apple	+	+	+++
Pear	++	++	++
Raspberry (*Rubus* sp.)	+	+	+
Elder (*Sambucus*)	–	–	–
Mushroom (*Boletus*)	–	–	–
Meal worms (*Tenebrio*)	–	+++	–

Scale: – not consumed; + low; ++ medium; +++ high preference

was double spaced and filled with dry rotten wood in order to increase thermal and phonic isolation, leading to outer dimensions of 20 × 20 × 20 cm.

While *Eliomys* and *Muscardinus* started to hibernate normally, *Myoxus*, although showing a spectacular increase of body weight (Table 1), did not enter hibernation. It was concluded that for the hibernation of this species a place without any disturbance was a necessary condition. Therefore all the experimental animals of the three species were transferred at the end of November to a humid cellar of a non-heated, uninhabited building. The natural photo period was perceptible at low light intensity due to two small plastic windows. The mean ambient temperature and its range measured in the empty nest box was in December 4.5 °C (1.4–8.7), January 4.4 °C (2.4–6.9), February 3.3 °C (0.6–6.1) and March 6.6 °C (1.8–11.9).

During hibernation, all animals had access to nuts, sunflower seeds and apples. Moreover *Eliomys* were given meal worms (larvae of *Tenebrio molitor*) which they consumed during the rare activity periods. *Myoxus'* food was supplemented with a large portion of acorns and sweet chestnuts. Water was given ad libitum. As hibernation in *Myoxus* did not occur as long as food was present, at beginning of January the food stock was not renewed.

Nest temperature was recorded by a Grant Squirrel data logger with 16 channels, 15 devoted to the experimental animals, one channel to an empty nest box as control for the ambient temperature. The recorder was placed in a corridor leading to the experimental room. In November nest temperature was recorded every five minutes, resulting in a logging capacity of two weeks. As the transmission of the data to a portable computer was a significant disturbance, the program was changed to a recording interval of 12 minutes with a single monthly data transfer combined with a visual control of the cages and eventual renewal of water.

The data were plotted on graphs and the length of torpor bouts determined to a precision of 12 min. The beginning of a torpor bout was defined by the decreasing nest temperature, and the end of the torpor by the onset of a regular body temperature rise of at least 0.2 °C/12 min, leading to the next bout of euthermia.

The analysis of the body temperature changes on particular days showed that data transfer combined with food replenishment and cleaning of the water dish caused some disturbance, waking up several animals. Synchronous waking up of several animals on two afternoons is probably due to children playing noisily outside the experimental house on school free days.

Complementary observations on the hibernation of 11 *Myoxus* are presented here, because they help to interpret our experimental results on fat dormice. On February 2, 1996, workers discovered in a military depot situated in a forest behind Lausanne a container with several hibernating dormice. In order to prevent damage of the military material, but to keep the fat dormice alive, the container was transferred to an empty military depot. On April 3 our institute was informed and I was allowed to check the situation. The room with the container was without any food and the windows were dormice proof. As a consequence the situation was partially equivalent to our experimental animals, first disturbed by human intervention and then remaining undisturbed during 2 months of the hibernation period without food.

3. RESULTS

3.1 Behaviour during the pre-hibernating period

Food preference: The simultaneous presentation of different food items to all the individuals showed differences in food preference among the species (Table 2). In *Muscardinus*, hazelnuts are most favoured. In *Myoxus*, the greatest preference was for walnuts and apples/pears. *Eliomys* preferred meal worms (larvae of *Tenebrio molitor*). Common dormouse and fat dormouse rejected meal worms in autumn, these were consumed, however, in moderate frequency in spring by 2 of the 5 fat dormice.

Pre-hibernation mass increase: During the four weeks following capture in September, body mass began to increase immediately in *Eliomys* and in *Myoxus*, but not in *Muscardinus*. Suspecting a physiological disorder, the light common dormice were released and new animals were captured again in October. At that time, the freshly captured animals were all as light as the released ones. Mass increase obviously takes place only shortly before the onset of hibernation. A comparison of the final mass (Table 1) shows a mean gain of 55 % (33–93 %) in *Muscardinus*, 109 % (26–173 %) in *Eliomys* and 61 % (44–95 %) in *Myoxus*.

Nest construction: At the introduction to the cage, each animal was given a wooden nest box filled with dry leaves. Supplementary dry leaves, moss and pieces of paper tissue were placed on the ground. *Muscardinus* did not modify the initial content of the nest box, though in nature they build a fine spherical nest of vegetable material. *Eliomys* entered the soft material and minced the tissues to very small pieces. *Myoxus* did not modify the offered nest box content.

Onset of hibernation: *Eliomys* was the first species to start daily torpor at end of September and entered hibernation in October. *Muscardinus* followed only in November. Under standard conditions with food ad libitum, *Myoxus* did not enter hibernation and showed no daily torpor.

3.2 Period of hibernation

The hibernation pattern of all experimental animals is presented in Figure 1. In 4 of 5 *Muscardinus* hibernation took place without problems. But in one animal, nest temperature showed an incredible fluctuation, first interpreted as a physiological disturbance. For this reason the problematic animal was exchanged at the end of December with the reserve animal. At the end of January the temperature showed the same chaotic style and it was then clear that it was a problem of the particular channel of the instrument. As a consequence, the sample size of common dormice was reduced to 4 animals.

Hibernation in all 5 *Eliomys* was without problem. After some of the arousals the animals left the nest and consumed meal worms. In March some longer euthermic period were observed, but hibernation was not finished at the beginning of April when the experiment was stopped.

The *Myoxus* that were fed every second week in November did not enter hibernation. When fed once a month (beginning December and first January) daily torpor began, probably when they ran out of food, and the classic pattern of hibernation began later (Figure 2). The pattern suggested that the fat dormice had finally acclimatised to the experimental conditions, possibly as a result of a completely undisturbed situation; therefore the food for *Myoxus* was not renewed. According to FRENCH (1985), species with heavy fat deposits do not feed during hibernation and can normally be kept over 10 months without food (FRENCH 1985).

The pattern in February analysed on March 2 was unexpected: In 3 of the 5 *Myoxus*, the regular pattern of periodic arousal had stopped (Figure 1). In fact only one had survived the period of food depression. Three of them had been dead for at least two weeks because only skin and skeleton remained. Small predators or scavengers had obviously consumed the soft parts. The fourth animal was freshly dead, with a weight of 78 g. It was left in the nest box for further observation: after 10 days the weight had fallen to 45 g, and after another week the remaining skeleton and skin weighed 32 g. In traps set in the room two shrews (*Crocidura russula*) and one bank vole (*Clethrionomys glareolus*) which are known to consume dead mice in snap traps were captured. The 12 mm wide meshes of the wire-lattice allowed these animals to enter in the cages. The question then arose: Was hibernation disturbed by the shrews to such a point that the fat dormice ran out of energy?

The accidental event in the military depot may help to give an answer. In this case, 11 fat dormice had chosen to hibernate not in the forest, but in the building. The wooden container which was selected as hibernaculum (Fig. 3) had the inner

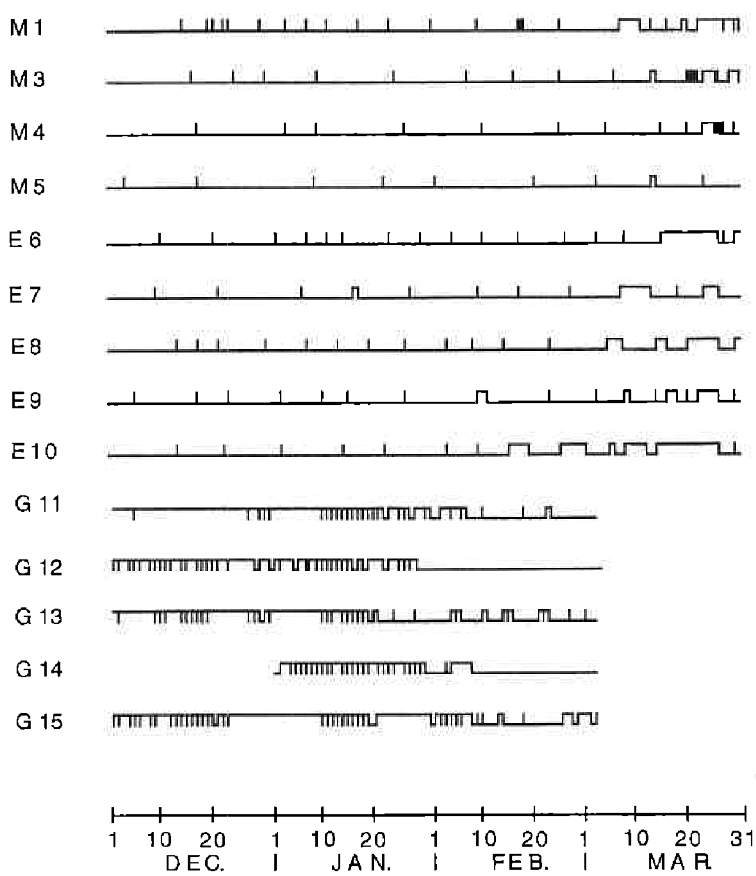

Fig. 1. Pattern of hibernation revealed by nest temperature in *Muscardinus* (M), *Eliomys* (E) and *Myoxus* (G). Top line = euthermia, bottom line = hibernation, vertical bar from top line = daily torpor, vertical bar from bottom line = periodic arousal. G 14 entered nest box only in January. G 13 is the only survivor of *Myoxus*.

dimensions of 32 × 32 × 20 cm and was filled to 1/4 with thick iron screws of 6 cm length. The workers did not think of the consequences of a transfer to another military building, resulting in stress by forced change of hibernaculum place, the inability of escaping from the new site and the absence of food and water. However, unlike our 5 experimental fat dormice, they could remain in their own hibernaculum and were not confined to a foreign nest box. Nine dormice remained in the container, two others were found in the room behind a board. Of the 11 animals, 6 were dead, 5 were alive. Two of the dead were eaten, obviously by the dormice themselves. The room was mouse proof, no shrew or vole could enter. In this situation, without any food, two months led to death for more than half of the dormice.

The mean mass of the 5 surviving *Myoxus* was 84.7 g (72.6–115.4 g). In 9 days it rose to 136.7 g, (113.0–157.5 g) equivalent to an increase of 63 %!

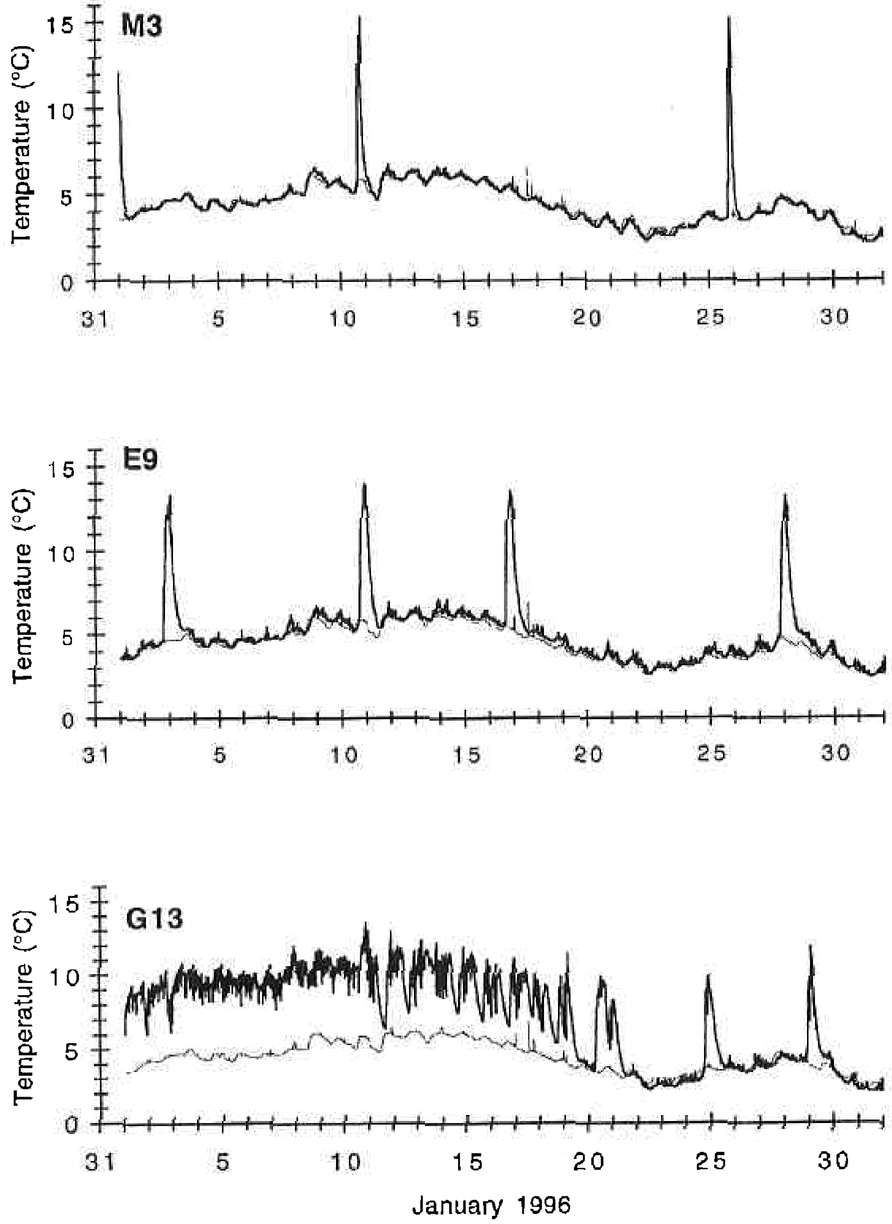

Fig. 2. Nest temperature pattern in January of a *Muscardinus* (M3), an *Eliomys* (E9) and a *Myoxus* (G13). The fine bottom line in G13 is the control temperature in an empty nest box. In M3 are three, in E9 are four bouts of euthermia, in G13 daily torpor bouts are observed between January 11 and Janurary 20, followed by 10 days of hibernation with short arousals.

3.3 Length of torpor bouts in *Muscardinus* and *Eliomys*

During the period of hibernation without perturbation (December to end of February), torpor bouts lasted from 2 to 30.8 days. Taking into account the longest period as did FRENCH (1985), it lasted 21.0 6.7 days (range 15.7–30.8 d) in *Muscardi-*

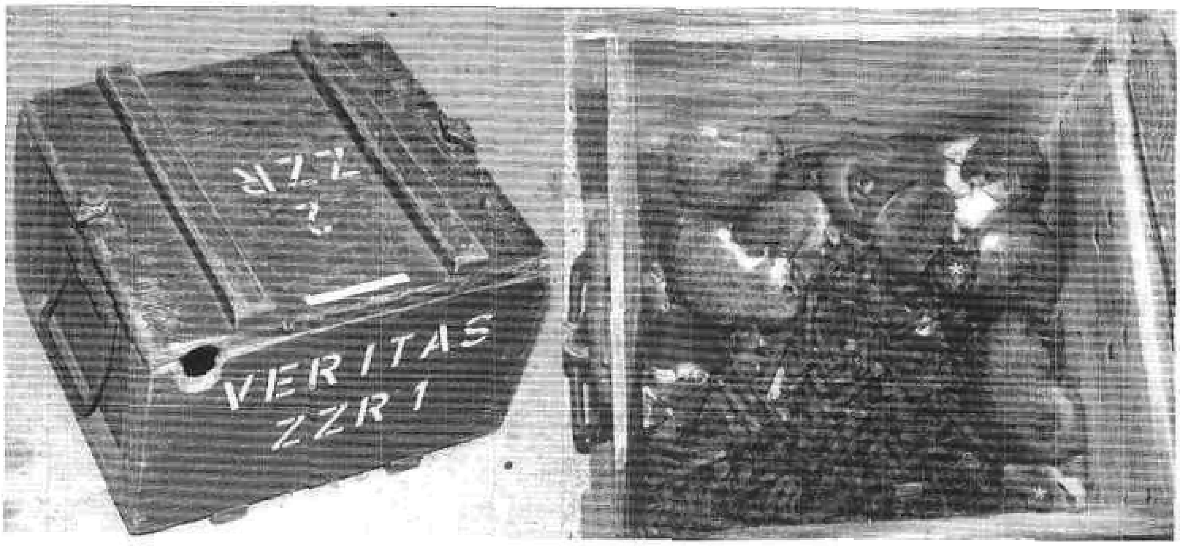

Fig. 3. Wooden screw container chosen by 11 *Myoxus* as hibernaculum in a military depot. Table 1. List of experimental animals (*Muscardinus* M1–M5, *Eliomys* E6–E10, *Myoxus* G11–G15), capture localities, date of capture, mass at capture and mass at onset of hibernation.

nus and 13.9 1.9 days (range 12.4–17.2 d) in *Eliomys*. The difference is close to significance level ($P = 0.051$). The correlation between the log of period (T), and the log of body mass (log T = 3.082–0.275* log M, r = 0.75, $P = 0.030$) is significant with 50 % of the variance explained by the body mass. For the mean of the five longest torpor bouts, the difference is still obviously a trend ($P = 0.07$). The general mean was 10.6 days in *Muscardinus* and 8.2 days in *Eliomys*.

4. DISCUSSION

4.1 Prehibernation behaviour

Freshly captured animals from nature probably show a behaviour more comparable to the normal than animals habituated for a long period. On the other hand, the stress and the limited possibilities may alter behaviour because natural clues are no longer available. These possibilities must be kept in mind when discussing controversial observations on captive animals.

Food preference

A rough comparison between the three species shows clearly that *E. quercinus* is mainly insectivorous, fruits and seeds being only moderately consumed, whereas *M. avellanarius* in our conditions preferred seeds (hazel nuts, sunflower seeds), while *Myoxus* prefered apples, followed by walnuts. However, this latter species did not eat Spanish nuts or sunflower seed which were reported by VIETINGHOFF-RIESCH (1960) and KOENIG (1960) to be very attractive. These items were only consumed when no other food was present. In general, our data confirm the main conclusions of STORCH (1978) who analysed the literature of food consumption. One obvious difference concerns the important carnivorous/insectivorous components in the food composition of *Myoxus*. According to VIETINGHOFF-RIESCH (1960) the fat dormouse is a destroyer of eggs and birds, a statement not confirmed by SCHULZE (1970). In our animals, insects were not eaten and in a new experiment (P. VOGEL, unpublished) quail eggs were not touched in autumn. Only once, in spring, were two of the five animals from the military depot observed eating small amounts of *Tenebrio*. This was perhaps a compensation for a restitution of body proteins after starvation, or, less probably, a seasonal switch in the regime approaching the season of reproduction.

Cannibalism during starvation is not exceptional. Similar reports are cited by VIETINGHOFF-RIESCH (1960). This possibility did not prevent the death of other animals by starvation in the presence of carcasses and may indicate that flesh is not an adequate food.

Another problem is the question about the necessity of food consumption during hibernation. At some arousals, *Eliomys* left the nest and consumed meal worms. In the Jura mountains, one garden dormouse was observed foraging in sunshine in February 1996 (H. BRACK, pers. comm.). PAJUNEN (1970) hibernated this species without any food and water. This is also possible for *Muscardinus*. But this species too occasionally leaves the nest and forages during winter time as shown by VOGEL & FREY (1995) in free-ranging animals.

Body mass

All three species are true hibernators, characterized as such by not accumulating a stock of winter food and the capability of increasing their body weight to about 100 % of lean mass (FRENCH 1988), independent of body size.

Muscardinus with only 55 % weight increase does not fit into that general statement. Specimens from the same population sampled in October/November by CATZEFLIS (1983) had a mean weight of only 18.0 g (n = 36). Within his samples he observed 13 clearly adipose individuals with a mean weight of 27.8 g (25–32 g) which had increased their weight by 62 % compared to spring weights taken at the same place. The difference of 7 % can be explained by the fact that at capture our animals were not at the lowest level. In *Zapus princeps*, weight increase starts only four weeks before hibernation (CRANFORD 1978). In *Muscardinus* the situation seems similar and would explain the low weights found by CATZEFLIS (1983).

The largest weight increase was shown by *Eliomys* with a mean of 109 % and a maximum of 173 %. GABE et al. cited by PAJUNEN (1970) had an animal in which the prehibernation weight increased by 118 % compared to spring weight. The prehibernation weight of Finnish garden dormice was 180.2 g (n = 6), 88 % higher than spring weight (PAJUNEN 1970) and in French dormice only 103.1 g (n = 39) equivalent to 76 % above the spring weight (PAJUNEN 1974).

In *Myoxus*, according to KOENIG (1960), the summer weight was between 70 and 110 g and can roughly double before winter. More precise data are given by VIETINGHOFF-RIESCH (1960) for 4 animals. Their lowest mean weight was 74.6 g and the prehibernation weight 108.1 g, an increase of only 45 %. Our fat dormice with a mass increase of 61 % reveal a normal potential for fattening. This can be done in a very short time as shown by the increase of 63 % in 9 days equivalent to a mean increase of 5.8 g by day.

Winter nest

The construction of the winter nest is obviously hampered in captivity. *Muscardinus*, which hibernates normally in a spherical nest constructed from leaves on the surface of the soil (WALDHOVD & JENSEN 1976, VOGEL & FREY 1995), accepted the nest box without modification. The situation is quite different in *Eliomys* which hibernates, according to BUSSY (1965), in a large nest of moss and fine minced vegetable material placed in a natural or artificial cavity. In our captivity conditions, filling up the nest box with minced material was the rule.

In *Myoxus* however, the nest in the box was not modified which may be explained by the fact that in nature *Myoxus* hibernates generally in the soil at a depth of 40 to 60 cm without any nest material. Many reports on this situation are reviewed by VIETINGHOFF-RIESCH (1960) and confirmed from England by MORRIS & HOODLESS (1992). According to these reports, several animals may be grouped together. In buildings, the hibernation places are very variable. The hibernaculum in the military depot is however a particular situation: the dormice gnawed a hole in the wall of the box, in order to sleep on iron screws without a soft soil, 11 of them together in a very small area. This shows at least the flexibility of this species.

4.2 Hibernation in captivity

The late onset of hibernation in *Muscardinus* is in agreement with the situation in free-ranging common dormice (CATZEFLIS 1983, VOGEL & FREY 1995). As arousal takes place in March or April, hibernation lasts only 4 to 5 months in this species. This could explain the fact, that in this species the weight gain was lowest compared to the other species. Under experimental conditions, this species enters hibernation also in disturbed conditions and even at room temperatures of 19 °C (P. VOGEL, pers. observations).

Eliomys started hibernation early in October. This may be explained by the origin of the animals from the Jura mountains (locality at 1383 m). Hibernation lasts here at least 8 months, generally from mid September to June. It may be longer in the Alps where I captured this species at 2200 m. The long hibernation period may also explain the fact that it was in this species that the highest weight gain in prehibernation body mass was recorded. In captivity, *Eliomys* hibernates without any problem. In the experimental conditions of PAJUNEN (1970) this species would hibernate on sawdust without any nest.

Compared to these species, the results regarding *Myoxus* are very intriguing. In the offered captivity conditions no hibernation occurred, and only food restriction led to daily torpor bouts. Obviously, cage conditions result in stress and in a total inhibition of hibernation. Several persons (F. CATZEFLIS, J. HESS, pers. comm.) confirmed this observation and KOENIG (1960) reported that freshly captured fat dormice never hibernate. This is in agreement with the findings of STEIGER (1992) who reported that of two fat dormice, only one showed hibernation of just three days. WILZ & HELDMAIER (1995) monitored one fat dormouse that spent 104 days in daily torpor and only 14 days in hibernation. This pattern clearly is not representative of what happens in nature, where the fat dormouse may enter hibernation as early as August (MORRIS 1997) and return to activity only in May or June (BIEBER 1995). The sensitivity of this species was also shown by KÖNIG (1960) who tested experimental conditions with a low feeding rate leading to the death of 3 animals. In contrast to many other hibernators, *Myoxus* in disturbed situations needs food and water. As shown by the animals of the military depot, two months of starvation led to over 50 % mortality. As a consequence, this species should be studied either in nature or in hand raised animals showing no sign of stress. In fact, KÖNIG (1960) hibernated well adapted animals without problem and could handle them at 8 °C without waking them up.

The maximum length of torpor bouts in *Muscardinus* was 30.8 days. This is comparable of one record in nature to 27 days (VOGEL & FREY 1995). In *Eliomys*, the longest bout was 17.2 days, a value situated between the recorded maximum of 14.6 days in Finnish and 22 days in French garden dormice kept by PAJUNEN (1970, 1974) in similar conditions. The failure in *Myoxus* clearly shows the influence of the experimental conditions: even identical conditions do not ensure identical quality of results. Data from older literature (e.g. VIETINGHOFF-RIESCH 1960) on torpor bout length are not reliable because many authors reporting long torpor duration were not aware of intermittent euthermia without any activity.

The comparison of maximal length of torpor bouts, tested for *Muscardinus* and *Eliomys* only, was significantly inversely related to body mass as reported by FRENCH (1985). The idea that larger mass should give greater autonomy, as also advanced by GEISER et al. (1990), is not confirmed by the results. Some data collected by FRENCH (1985) tend to show that the lowest metabolic rate in torpor is independent of body weight. If this is the case, then torpor bout length should also be independent of body weight. What may then explain the reverse relationship? FRENCH (1985) concluded that »large species are slightly less tolerant of the proposed metabolic imbalance than small species«, an explanation which is at the moment not possible to test. GEISER & RUF (1995) presented an impressive body of physiological data of mammalian hibernators and did not find any correlation between maximum torpor length and body weight. But this is perhaps due to the fact that they did not distinguish between hibernators relying on fat only or on stored food. In any case, more data are needed, and hopefully one day it will be possible to compare torpor bout length using a larger range of body sizes, including *Myomimus*, *Dryomys*, *Glirulus* and reliable data for *Myoxus*.

SCHULZE, W., 1970: Beiträge zum Vorkommen und zur Biologie der Haselmaus (*Muscardinus avellanarius* L.) und des Siebenschläfers (*Glis glis* L.) im Südharz. Hercynia (N.F.) 7, 355–375.

STEIGER, R., 1992: Energiehaushalt im Winterschlaft vom Goldmantelziesel (*Spermophilus lateralis*) und vom Siebenschläfer (*Glis glis*). Diploma thesis, University of Marburg.

STORCH, G., 1978: Familie Gliridae Thomas, 1897 – Schläfer. In: Niethammer, J. & F. Krapp: Handbuch der Säugetiere Europas. Vol. 1. Akad. Verlagsgesellschaft, Wiesbaden, pp. 201–279.

TRACHSEL, L., TOBLER, I. & HELLER, 1991: Are ground squirrels sleep deprived during hibernation? Am. J. Physiol. **260**, 1123–1129.

VIETINGHOFF-RIESCH, A. von, 1960: Der Siebenschläfer (*Glis glis* L.). Monographie der Wildsäugetiere, vol. XIV, G. Fischer Verlag Jena. pp. 196.

VOGEL, P. & H. FREY, 1995: L'hibernation du muscardin *Muscardinus avellanarius* (Gliridae, Rodentia) en nature: nids, fréquence des réveils et température corporelle. Bull. Soc. Vaud. Sc. Nat. **83**, 217–230.

WILZ, M. & G. HELDMAIER, 1995: Winterschlaf, Sommerschlaf und Tagesschlaflethargie beim Siebenschläfer (*Myoxus glis*, L.). Verh. Deutsch. Zool. Ges. Abstract, p. 139.

SUMMARY

Hibernation of recently captured *Muscardinus*, *Eliomys* and *Myoxus*: a comparative study

P. Vogel

Prehibernation behaviour and hibernation pattern was investigated in three species of Gliridae, *Muscardinus avellanarius*, *Eliomys quercinus* and *Myoxus glis* in order to test the allometric relationship between torpor bout length and body weight. In specimens captured in September/October 1995, the preferred food was markedly different between species: *Myoxus* preferred fresh walnuts and large quantities of fruits (apples/pears), *Eliomys* meal worms (*Tenebrio molitor*), *Muscardinus* fresh hazelnuts and seeds of sunflower. Weight increase was 55 % in *Muscardinus* (final mass: 27.5±0.9 g), 109 % in *Eliomys* (112.1±10.2 g) and 61 % in *Myoxus* (166.0±21.7 g). Nest box temperature was monitored with a Grant Squirrel logger. *Eliomys* showed first daily torpor bouts at the end of September and hibernation in October and was not disturbed by moderate human activity. *Muscardinus* started hibernation only in November. *Myoxus* remained normothermic and very aggressive not only in the disturbed animal house, but also after transfer into a cellar of a house without human presence. Feed only once a month led after 10 days to daily torpor and then short hibernation bouts of 2–3 days. Six weeks after the food was not renewed, all experimental animals were found dead. Complementary observations of 11 *Myoxus* disturbed during hibernation and accidentally starved during two months in a military depot are reported. The mean of the longest torpor bouts in the two undisturbed hibernating species was 21.0±6.7 d in *Muscardinus*, and 13.9±1.9 d in *Eliomys*, and was significantly inversely correlated with body weight.

SAŽETAK

Hibernacija netom uhvaćenih *Muscardinus, Eliomys, Myoxus*: usporedbena studija

P. Vogel

Istraživano je prehibernacijasko ponašanje i hibernacija kod tri vrste porodice Gliridae, *Muscardinus avellanarius, Eliomys quercinus* i *Myoxus glis* da bi se testirao alometrijski odnos između duljine perioda torpora i tjelesne težine. Primjerci uhvaćeni u rujnu/listopadu 1995. uočljivo su preferirali različitu hranu: *Myoxus* svježe orahe i velike količine voća, *Eliomys* brašnare (*Tenebrio molitor*), *Muscardinus* svježe lješnjake i sjemenke suncokreta. Povećanje težine iznosilo je 55% kod *Muscardinus*-a (konačna težina: 27.5±0.9 g), 109% kod *Eliomys*-a (112.1±10.2 g) i 61% kod *Myoxus*-a (166.0±21.7g). Temperatura u kućicama mjerena je uređajem Grant Squirrel. Periodi torpora su prvo primijećeni kod vrtnog puha krajem rujna, a hibernacija u listopadu i nikako ga nije smetala umjerena ljudska aktivnost. *Muscardinus* je počeo s hibernacijom tek u studenom. *Myoxus* je ostao u normotermičkom stanju, vrlo agresivan ne samo kad je bio uznemiravan u kućici, nego i poslije premještaja u podrum nenaseljene kuće. Nakon hranjenja jednom mjesečno, životinje su poslije 10 dana prešle u stanje dnevnog torpora a nakon toga su slijedili kratki periodi hibernacije. Šest tjedana pošto hrana nije bila obnavljana, sve eksperimentalne životinje su pronađene mrtve. Objavljena su i usporedbena opažanja na 11 sivih puhova koji su bili uznemireni za vrijeme hibernacije i izgladnjeli tijekom dva mjeseca u vojnom skladištu. Aritmetička sredina najdužih perioda torpora kod dvije neuznemiravane hibernirajuće vrste bila je 21.0±6.7 dana za puha orašara i 13.9±1.9 dana za vrtnog puha, a bila je u znatnoj inverznoj korelaciji s tjelesnom težinom.