

Body temperature profiles of the Korean field mouse *Apodemus peninsulae* during winter aggregation

Mika Masaki¹, Chihiro Koshimoto², Kimiyuki Tsuchiya³, Aya Nishiwaki⁴ and Tetsuo Morita^{1,*}

¹ Laboratory of Physiological Ecology, Faculty of Agriculture, University of Miyazaki, Miyazaki, Miyazaki 889-2192, Japan

² Department of Bio-resources, Division of Biotechnology, Frontier Science Research Center, University of Miyazaki, Kiyotake, Miyazaki 889-1692, Japan

³ Laboratory of Wild Animals, Faculty of Agriculture, Tokyo University of Agriculture, Atsugi, Kanagawa 243-0034, Japan

⁴ Laboratory of Restoration Ecology, Faculty of Agriculture, University of Miyazaki, Miyazaki, Miyazaki 889-2192, Japan

Abstract. Factors affecting body temperature (Tb) fluctuations in winter were examined in Korean field mice *Apodemus peninsulae*. Animals were maintained under the following three conditions to mimic autumn followed by winter, plus two modes of behaviour, solitary and grouped, in winter: 1) short day (8 Light:16 Dark) at $25 \pm 2^\circ\text{C}$ and solitary, for 12 weeks towards the end of which their Tb was recorded; 2) constant darkness (DD) at $4 \pm 2^\circ\text{C}$ and solitary, for a week; and 3) DD at $4 \pm 2^\circ\text{C}$ and in groups (two or three animals in a cage), for about 10 days. Using implanted data loggers Tb was monitored in 13 mice that were exposed to these three conditions in sequence. When the animals' body temperature was below 30°C , it was assumed that they were torpid according to the bimodal pattern of minimum daily Tb. The maximum period of daily torpor was 390 min/day, and torpor was exhibited by seven of the thirteen animals exposed to conditions-2) and -3). Since torpor was found in one mouse even under condition-1), without any environmental stressors, it is suggested that this species is prone to spontaneous daily torpor. Cohabitation tended to synchronize Tb fluctuations irrespective of the state of the animals, torpid or not. Thus, this species may aggregate and synchronize torpor and/or Tb fluctuations to reduce heat loss during winter.

Key words: *Apodemus peninsulae*, body temperature fluctuation, daily torpor, huddling, synchronization.

Some species of small mammals are known to form social groups or aggregations in winter, even when they have exclusive territories in other seasons (Madison 1984). The most often cited explanation for this is that group members may reduce their body surface, when exposed to low ambient temperatures, by huddling and thereby conserve body heat (West and Dublin 1984). In fact, in the deer mouse *Peromyscus leucopus*, the survival rate at low temperatures was generally higher when individuals were housed in groups and allowed to huddle than when they were housed individually (Sealander 1952). Some of the animals employing this strategy of winter aggregation become torpid and save even more energy. Morris (1968) reported his field observation that three torpid wood mice *Apodemus sylvaticus* were aggre-

gated in the same nest in winter and Morton (1978) found that fat-tailed dunnarts *Sminthopsis crassicaudata* and house mice *Mus musculus* shared one nest and some of the nest mates were torpid at the same time. In social hibernation of alpine marmots *Marmota marmota*, synchronization of torpor within groups has also been observed (Arnold 1988). These findings suggest that winter aggregation, in conjunction with synchronized torpor, occurs in many species of small mammals living in cool/cold localities.

Synchronized torpor is also suggested by a report showing that during daily torpor, the minimum metabolic rates per animal were similar in torpid animals housed in groups and individually, although the former had higher minimum body temperatures (Tb) during

*To whom correspondence should be addressed. E-mail: morita@cc.miyazaki-u.ac.jp

torpor than the latter (Walton and Andrews 1981a). Furthermore, from the point of view of energy efficiency, synchronized daily torpor seems to have greater benefit than the torpor displayed randomly in each cage mate. However, synchronized torpor or reduction of Tb has not yet been demonstrated, for simultaneous recording of Tb of individual animals in the same cage has been difficult using ordinary methods such as radio telemetry because of signal interference. Using a temperature-sensitive data logger implanted into each subject, we attempted to examine the synchronization of Tb fluctuations during winter aggregation in the Korean field mouse *Apodemus peninsulae*.

Material and methods

The experimental procedures of this study were examined and approved by the Animal Experimentation Committee of the University of Miyazaki (Permission No. 2002-068).

Animals and maintenance

Five males and eight females *A. peninsulae* were used in this study. They were 6 to 8 month-old adults weighing 26.3 ± 1.4 g (mean \pm SE). The mice, which originated from the Khasan area of southern Primorsky Krai, Russia, had been bred and maintained as a laboratory colony at the Experimental Animal Center in Miyazaki Medical University, housed individually in transparent plastic cages (20 \times 30 \times 13 cm), with wood chips for bedding under a light-dark cycle (16L : 8D) at $25 \pm 2^\circ\text{C}$ of ambient temperature (T_a). Commercial rodent diets (MF, Oriental Yeast, Co. Ltd., Tokyo) and water were provided *ad lib* throughout the study.

Experimental treatment

Prior to the experiments, all animals were housed individually and acclimated to short days with a 8L : 16D photoperiod (lights on at 0800 h; lights off at 1600 h) at $25 \pm 2^\circ\text{C}$ of T_a for 12 weeks, during which the data loggers were implanted in their body cavities as described below. Then, in order to mimic the circumstances of overwintering in subterranean nests of *Apodemus* (Kondo 1980; Marchand 1984), the environmental conditions were shifted to $4 \pm 2^\circ\text{C}$ T_a and constant darkness (DD), at 1500 h on the first day. One week after this shift, they were housed in groups consisting of two or three animals. One male and two females were allocated to each of groups A, C and D, and one male and one female to

each of groups B and E.

The measurement of body temperature

Temperature-sensitive data loggers (Thermochron iButton™ DS1921L-F51, Dallas Semiconductor Co., Dallas) were used. The devices were coated with thin layers of a paraffin-Evaflex mixture. The Evaflex vinyl resin (ethylene-vinyl acetate copolymers and terpolymers, Du Pont Mitsui Polychemical Co., Tokyo) was mixed with paraffin in a ratio of 5 parts paraffin to 1 part Evaflex to give the paraffin the plasticity needed when subjected to temperatures near 0°C . The coated data loggers weighed approximately 3.7 g and became 20 mm in diameter and 8 mm in thickness. A data logger was surgically implanted into the abdominal cavity of each animal under pentobarbital (Nembutal, Dainippon Pharmaceutical Co., Ltd., Osaka) anesthesia to monitor Tb, in the 11th week of the acclimation period. Prior to implantation, the data loggers were programmed to record Tb to the nearest 0.5°C every 15 minutes for 21 days. The animals were allowed to recover from the surgery for seven days at the end of which recording was started.

Tb was monitored under the following conditions: 1) short day (8L : 16D) at $25 \pm 2^\circ\text{C}$ and solitary, for 3 days and 15 hrs; 2) constant darkness (DD) at $4 \pm 2^\circ\text{C}$ and solitary, for 7 days; and 3) DD at $4 \pm 2^\circ\text{C}$ and in groups, for ca. 10 days. The data loggers were then removed and the data were retrieved to a personal computer using an adapter (DS1402D-DR8, Dallas Semiconductor Co., Dallas). The loggers were calibrated by placing them in a water bath of known temperature determined by a thermistor thermometer (BXA-33, Technol Seven, Tokyo) both before implantation and after removal. Data in the loggers were significantly correlated with the temperature ($P < 0.001$).

An appropriate criterion for the occurrence of torpor had first to be established because the data loggers have an accuracy of less than $\pm 1^\circ\text{C}$. The critical temperature based on telemetry with an accuracy of $\pm 0.1^\circ\text{C}$ varied from 30 to 32°C (Vogt and Lynch 1982; Ruf and Heldmaier 1992; Bartels et al. 1998). Following the procedures of Ruf et al. (1991), and Lovegrove and Raman (1998), we determined our criterion from the bimodal frequency distribution of minimum daily Tb (Fig. 1) as less than 30°C .

The torpor data obtained only under the condition of DD and at 4°C were used for statistical comparisons. ANOVA and Fisher's exact test were applied to Tb and to duration and incidence of torpor, respectively.

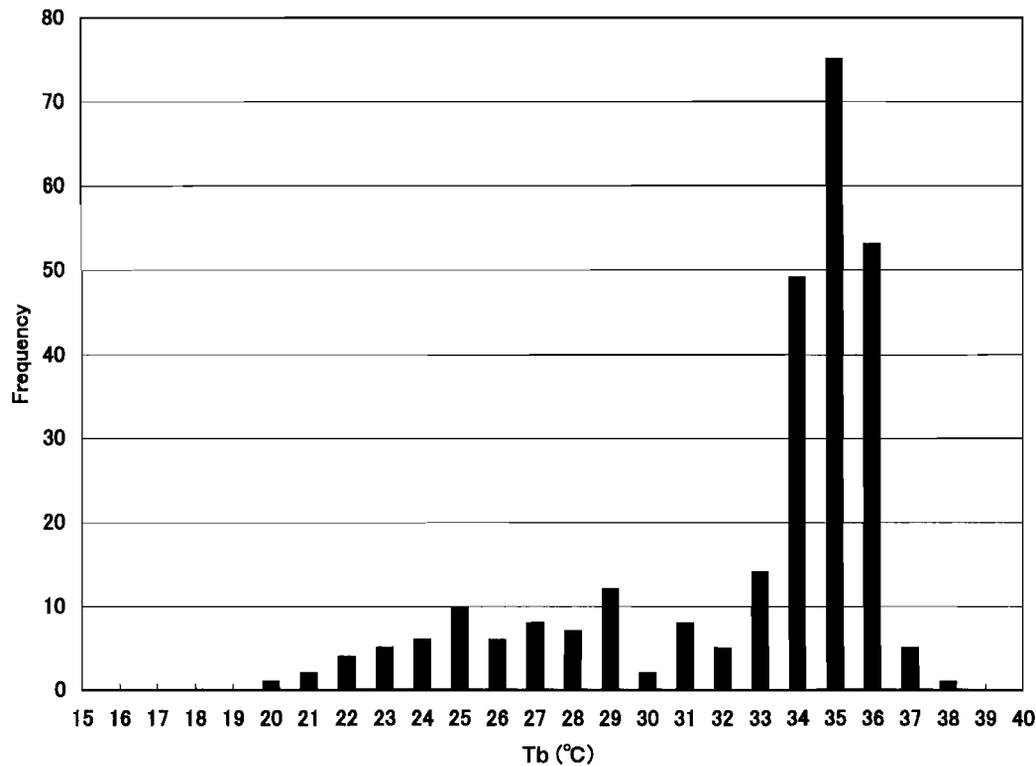


Fig. 1. Frequency distributions of the daily minimum body temperature (Tb) in thirteen Korean field mice *Apodemus peninsulae*.

Table 1. Statistics concerning parameters of torpor and euthermia in Korean field mice.

	Acclimation period		Experimental period			
	Single housing 8L:16D, 25°C (N = 13)	n	Single housing DD, 4°C (N = 13)	n	Group housing DD, 4°C (N = 13)	n
Mean daily Tb euthermia (°C)	36.7 ± 0.1	39	36.4 ± 0.1	91	36.2 ± 0.2	130
Mean Tb torpor (°C)	29.0 ± 0.2	3	26.7 ± 0.2	18	26.7 ± 0.1	64
Minimum Tb torpor (°C)	28.3 ± 0.4	3	25.7 ± 0.6	18	26.2 ± 0.3	64
Bout length range (min)	30–105		15–195		15–390	
Mean bout length (min)	70.0 ± 21.8	3	102.1 ± 11.6	18	125.9 ± 11.1	64
Torpor incidence	1/13		4/13		7/13	

Note: Torpor incidence is shown as the number of animals being torpid vs all animals. All values are shown as means ± SE except for bout length range. Mean Tb euthermia is calculated from Tb > 30°C. Mean Tb torpor is calculated from Tb ≤ 30°C. N refers to the number of animals and n to the number of observations. Statistical analysis was conducted using only the data from experimental period. ANOVA and Fisher's exact test were applied to the data on Tb parameters and bout length, and on torpor incidence, respectively but no significant effect of cohabitation.

Correlation coefficients were calculated between the body temperatures of all the animals and the extent of synchronization of Tb fluctuations was evaluated by cluster analysis applied to the correlation matrix of Tb.

Results

Daily torpor was recorded in three of the five males and four of the eight females during the 21 days over which Tb was monitored. Animals that became torpid

underwent 3 and 21 bouts of torpor within the monitoring period and some of them entered torpor twice a day. Statistics of the parameters concerning torpor and euthermia in each of the environmental conditions are shown in Table 1. One animal displayed three bouts of torpor even at 25°C Ta under condition 1. No statistically significant effects were found within the parameters between animals housed individually or in groups under cold conditions and continual darkness (DD). The mean minimum Tb during torpor (±SE) was 28.3 ±

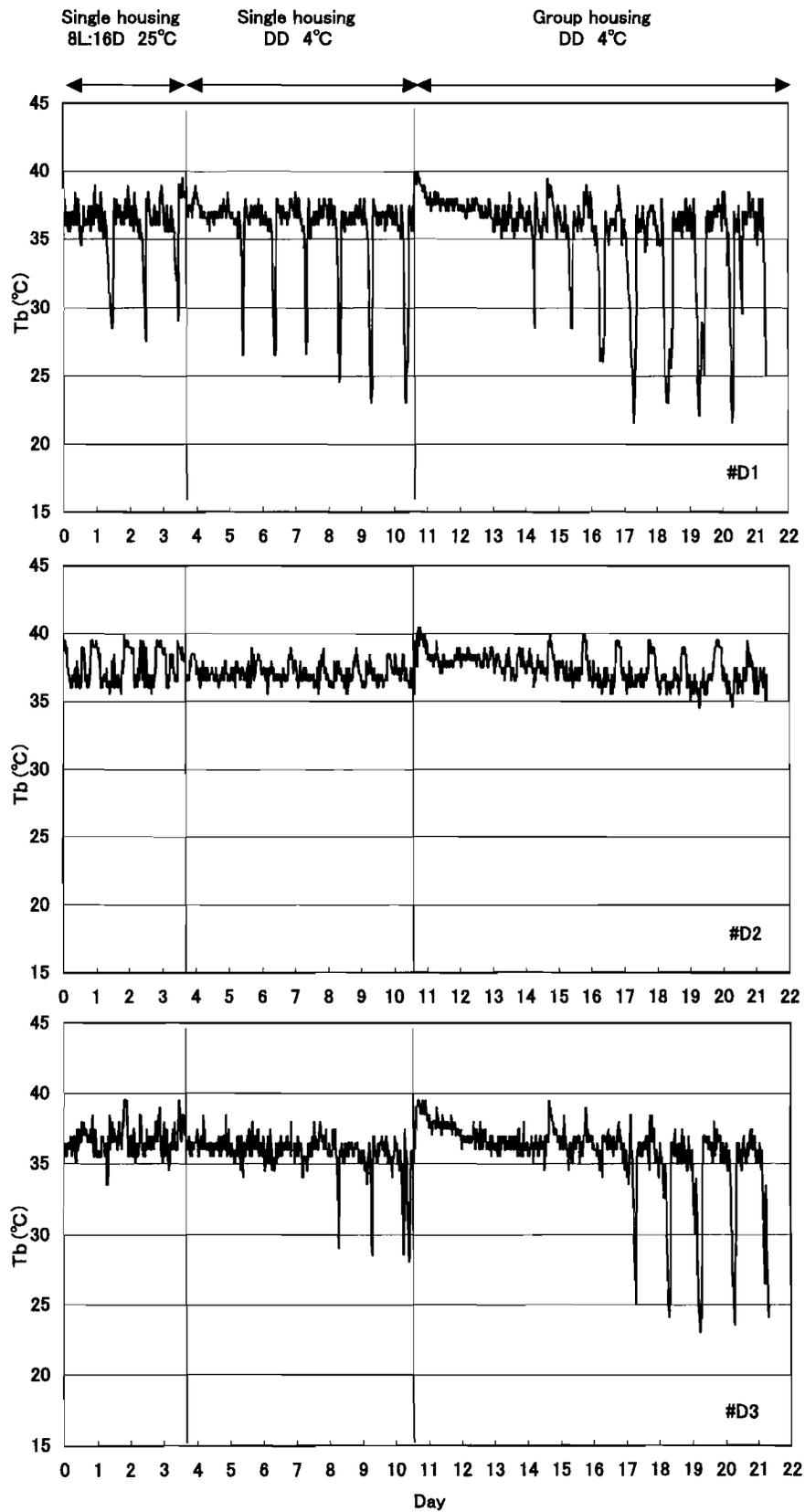


Fig. 2. Representative plots of T_b in three Korean field mice allocated to the same group (group D). #D1: male; #D2, #D3: female.

0.4°C, 25.7 ± 0.6°C, 26.2 ± 0.3°C for animals under conditions 1, 2 and 3, respectively. The duration of bouts of torpor ranged from 15 to 390 min. The minimum Tb recorded throughout the experiment was 20°C as shown in Fig. 1.

Representative plots of Tb for three animals in the same group throughout exposure to the three environmental conditions are shown in Fig. 2. Their Tb profiles differ considerably: one animal (#D2) never displayed torpor during the experiment, while the others (#D1 and #D3) frequently entered torpor, including the male mentioned above (#D1) who became torpid at 25°C of Ta.

As shown in Table 2, correlation coefficients of Tb within each group after cohabitation ranged from 0.40 to 0.66, which were higher than those before cohabitation

(range: 0.02–0.58), except in the case of group B with 0.14. When cluster analysis was applied to the correlation matrix, it showed that, in four of the five groups, cohabitation enhanced the synchronization of Tb fluctuations in animals kept under DD (Fig. 3).

Discussion

Small mammals often face difficulties in over-wintering and are considered to have developed physiological and behavioural adaptations to this problem, such as torpor (Hudson 1978), hibernation (Wang 1988), reduced body mass (Ure 1984) and aggregation (West and Dublin 1984). The wood mouse (*A. sylvaticus*) was found to use daily torpor when subjected to food restriction and cold

Table 2. Matrices of correlation coefficients of Tb in thirteen mice. Individuals identified by the same letter of the alphabet were those allocated to the same cage.

Single housing, DD, 4°C												
	#A2	#A3	#B1	#B2	#C1	#C2	#C3	#D1	#D2	#D3	#E1	#E2
#A1	0.35	0.29	0.25	0.07	0.35	0.32	0.36	0.56	0.13	0.35	0.50	0.39
#A2	1.00	0.29	0.22	-0.01	0.32	0.36	0.39	0.37	0.12	0.30	0.34	0.38
#A3		1.00	0.26	0.00	0.34	0.33	0.33	0.20	0.14	0.14	0.15	0.20
#B1			1.00	0.02	0.23	0.28	0.25	0.27	0.09	0.30	0.25	0.21
#B2				1.00	-0.03	0.01	0.02	-0.04	0.05	0.01	-0.04	-0.09
#C1					1.00	0.58	0.24	0.32	0.52	0.21	0.24	0.23
#C2						1.00	0.35	0.33	0.44	0.24	0.18	0.28
#C3							1.00	0.28	0.11	0.27	0.30	0.26
#D1								1.00	0.02	0.45	0.53	0.59
#D2									1.00	0.03	0.00	0.06
#D3										1.00	0.24	0.20
#E1											1.00	0.38

Group housing, DD, 4°C												
	#A2	#A3	#B1	#B2	#C1	#C2	#C3	#D1	#D2	#D3	#E1	#E2
#A1	0.58	0.40	0.23	0.22	0.16	0.27	0.25	0.11	0.15	0.21	0.35	0.32
#A2	1.00	0.49	0.33	0.20	0.24	0.28	0.31	0.23	0.33	0.37	0.36	0.31
#A3		1.00	0.31	0.16	0.24	0.30	0.37	0.35	0.36	0.39	0.40	0.37
#B1			1.00	0.14	0.21	0.29	0.25	0.31	0.32	0.39	0.32	0.24
#B2				1.00	0.17	0.19	0.13	0.16	0.24	0.21	0.20	0.22
#C1					1.00	0.61	0.58	0.39	0.40	0.24	0.25	0.39
#C2						1.00	0.54	0.35	0.42	0.28	0.29	0.36
#C3							1.00	0.42	0.41	0.35	0.41	0.43
#D1								1.00	0.57	0.66	0.42	0.55
#D2									1.00	0.53	0.29	0.40
#D3										1.00	0.48	0.50
#E1											1.00	0.62

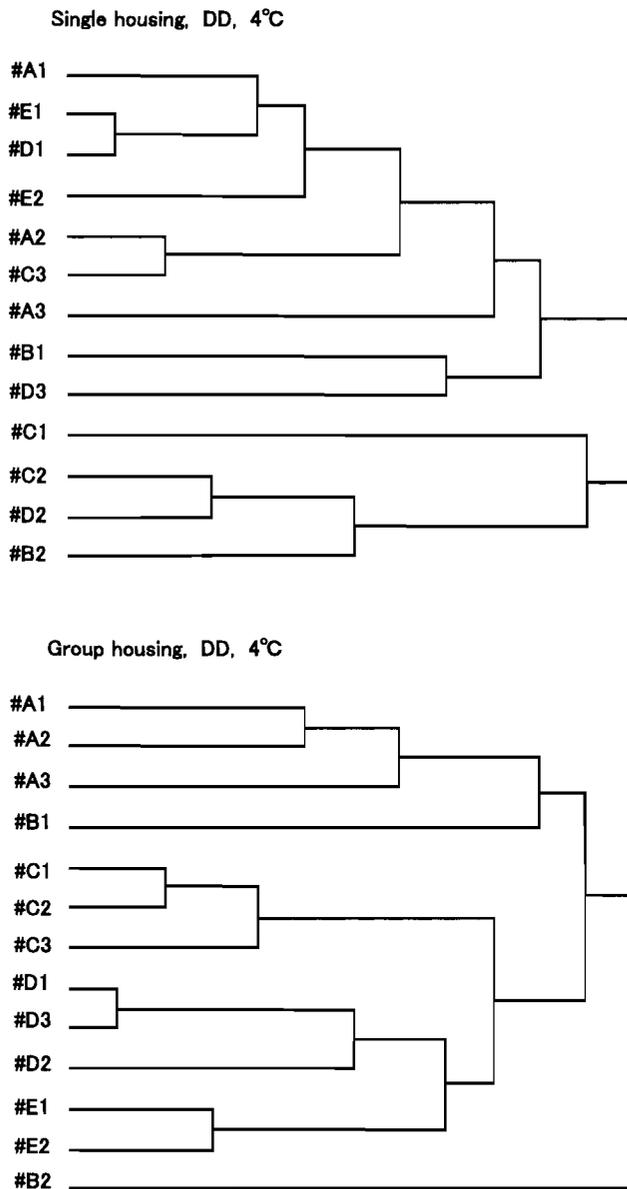


Fig. 3. A dendrogram calculated by cluster analysis using the correlation matrix of Tb profiles in all thirteen mice, which shows the effect of cohabitation. The individuals identified with the same letter of the alphabet were those allocated to the same cage.

(Walton and Andrews 1981a, 1981b), and winter aggregation (Zimmerman 1952). Thus, mice of the genus *Apodemus* appear to adopt daily torpor together with huddling for over-wintering and this study is the first to confirm these two adaptations in *A. peninsulae*.

The torpor elicited without any environmental stressors such as food shortage or cold is called spontaneous torpor (Hudson 1978; Heldmaier et al. 1989), which was shown by one of the thirteen mice in the present study (Table 1 and Fig. 2). Spontaneous torpor might function to conserve energy. Energy expenditure is elevated in

autumn by increased activity for food gathering and hoarding, as has frequently been found in species of *Apodemus* (Vander Wall 1990). Low incidence of spontaneous torpor in the present study may be explained either by individual differences in liability to enter torpor (Hudson 1978) or by the limited observation, for less than four days, in that part of the experiment. On the other hand, the relatively higher incidence of torpor under the conditions of DD and cold strongly suggests that most mice might employ torpor to over-winter in underground nests.

We found that the duration of torpor episodes, ranging from 15 to 390 min, never exceeded 24 h throughout the experiment as shown in Table 1. Therefore, Korean field mice can be classified as daily heterotherms that never display hibernation and exclusively undergo daily torpor, according to the criteria set out by Geiser and Ruf (1995). Thus, the Tb of these mice exhibits considerable daily fluctuations. It is well known that Tb and activity rhythms will free-run according to an intrinsic circadian clock when animals are subjected to a situation without any environmental cues, such as constant light (LL) or DD. The circadian rhythm begins to free-run immediately after the change of lighting schedule into either LL or DD, and each animal has its own free-running rhythm of specific duration (Ibuka 1990). Therefore, reduced synchrony in the Tb fluctuations of animals housed individually under DD (Fig. 3) appears to imply that the free-running circadian Tb rhythm in individuals allocated to the same group might desynchronize each other.

On the other hand, cohabitation under DD enhanced a synchronization of Tb rhythms irrespective of the state of individual mice, torpid or non-torpid (Fig. 3). Therefore, social contact facilitated by cohabitation seems to synchronize Tb rhythms in Korean field mice. Similar effects of social contact have been reported for the circadian activity rhythms in deer mice *Peromyscus maniculatus* (Crowley and Bovet 1980) and in palm squirrels *Funambulus pennanti* (Rajaratnam and Redman 1999). As physical contact is regarded as a potent zeitgeber in social synchronization of circadian rhythms (Rajaratnam and Redman 1999), strong physical contact through huddling may possibly play an important role in the synchronization of Tb rhythms found in this study.

We calculated correlation coefficients to determine the extent of similarity between animals in the Tb fluctuations but this method could underestimate the degree of synchronization of the Tb rhythm, when it is applied to a combination of animals with more regular and less

regular Tb amplitudes. However, as shown in Fig. 2 and Table 3, both in the case of animals (#D1 and #D2) with more regular Tb fluctuations, and animals (#D1 and #D3; #D2 and #D3) with more or less regular Tb fluctuations, we obtained a similar increase in the coefficients due to cohabitation, so the potential defect of under estimation by this method appears not to seriously affect the results.

Synchronization of Tb rhythms may contribute to energy saving, especially during arousal from torpor, as demonstrated by the synchronized re-warming from deep hibernation in alpine marmots (Arnold 1988). Animals consume considerable amounts of energy to increase their Tb from hypothermia to euthermia, and simultaneous re-warming by huddling may effectively reduce the energy consumption of each animal. Therefore, from the point of view of energy conservation, synchronization of Tb rhythms would be beneficial to animals that both aggregate and become torpid under cold conditions. Furthermore, huddling also reduces energy consumption during hypothermia in torpid individuals (Walton and Andrews 1981a). Thus, the combination of torpor, huddling and synchronization of Tb rhythms may conserve considerable energy during over-wintering in mice.

In contrast to hibernators, daily heterotherms are rarely able to drop Tb to the level of Ta in the nest and have to consume energy to some extent in order to maintain a thermal gradient between Tb and Ta, against the cold (Geiser and Ruf 1995). In the present study, the lowest critical Tb at which animals can maintain thermoregulation during torpor is considered to be 20°C (Fig. 1) and torpid animals were obliged to keep the thermal gradient at less than 18°C.

We found that not all the group members became torpid, which needs to be explained. If a euthermic animal joins the huddle, torpid animals can conserve energy to keep their Tb up through passive warming. On the other hand, the Tb of torpid individuals which is higher than Ta, would be favourable as heat insulation of euthermic animals. Thus, forming an overwintering group with torpid and euthermic animals may favour energy conservation each other. In fact, coexistence of torpid and non-torpid animals in a winter nest (Morton 1978) supports our hypothesis. However, further investigation of daily heterotherms is necessary in order to clarify the ecological significance of mixed huddles of euthermic and torpid animals.

Acknowledgments: We are grateful to David Gummer who suggested the new method for measuring Tb with ThermoChron data loggers.

References

- Arnold, W. 1988. Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *Journal of Comparative Physiology B* 158: 151–156.
- Bartels, W., Law, B. S. and Geiser, F. 1998. Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). *Journal of Comparative Physiology B* 168: 233–239.
- Crowley, M. and Bovet, J. 1980. Social synchronization of circadian rhythms in deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 7: 99–105.
- Geiser, F. and Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* 68: 935–966.
- Heldmaier, G., Steinlechner, T., Ruf, T., Wiesinger, H. and Klingenspor, M. 1989. Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. *Journal of Biological Rhythms* 4: 251–265.
- Hudson, J. W. 1978. Shallow daily torpor: a thermoregulatory adaptation. In (C. H. Wang and J. W. Hudson, eds.) *Strategies in Cold: Natural Torpidity and Thermogenesis*. Pp. 67–108. Academic Press, New York.
- Ibuka, N. 1990. *Chronobiology of Behavior*. Asakura Shoten, Tokyo, 181 pp. (in Japanese).
- Kondo, N. 1980. Seasonal fluctuation of population size, activity and activity area of *Apodemus speciosus ainu* (Thomas) in a small stand. *Honyuudoubutsugaku Zasshi* 8: 129–138 (in Japanese).
- Lovegrove, B. G. and Raman, J. 1998. Torpor patterns in the pouched mouse (*Saccostomus campestris*; Rodentia): a model animal for unpredictable environments. *Journal of Comparative Physiology B* 168: 303–312.
- Madison, D. M. 1984. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. In (J. F. Merritt, ed.) *Winter Ecology of Small Mammals*. Pp. 267–274. Carnegie Museum of Natural History, Pittsburgh.
- Marchand, P. J. 1984. Light extinction under a changing snowcover. In (J. F. Merritt, ed.) *Winter Ecology of Small Mammals*. Pp. 33–37. Carnegie Museum of Natural History, Pittsburgh.
- Morris, P. A. 1968. Apparent hypothermia in the Wood mouse (*Apodemus sylvaticus*). *Journal of Zoology, London* 155: 235–236.
- Morton, S. R. 1978. Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy* 59: 569–575.
- Rajaratnam, S. M. W. and Redman, J. R. 1999. Social contact synchronizes free-running activity rhythms of diurnal palm squirrels. *Physiology and Behavior* 66: 21–26.
- Ruby, N. F., Ibuka, N., Barnes, B. M. and Zucker, I. 1989. Suprachiasmatic nuclei influence torpor and circadian temperature rhythms in hamsters. *American Journal of Physiology* 257: R210–R215.
- Ruf, T. and Heldmaier, G. 1992. The impact of daily torpor on energy requirements in the Djungarian hamster, *Phodopus sungorus*. *Physiological Zoology* 65: 994–1010.
- Ruf, T., Klingenspor, M., Preis, H. and Heldmaier, G. 1991. Daily torpor in the Djungarian hamster (*Phodopus sungorus*): interactions with food intake, activity, and social behaviour. *Journal of*

- Comparative Physiology B 160: 609–615.
- Sealander, J. A. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. *Ecology* 33: 63–71.
- Ure, D. C. 1984. Autumn mass dynamics of red-backed voles (*Clethrionomys gapperi*) in Colorado in relation to photoperiod cues and temperature. In (J. F. Merritt, ed.) *Winter Ecology of Small Mammals*. Pp. 193–200. Carnegie Museum of Natural History, Pittsburgh.
- Vander Wall, S. B. 1990. *Food Hoarding in Animals*. The University of Chicago Press, Chicago, 445 pp.
- Vogt, F. D. and Lynch, G. R. 1982. Influence of ambient temperature, nest availability, huddling, and daily torpor on energy expenditure in the white-footed mouse *Peromyscus leucopus*. *Physiological Zoology* 55: 56–63.
- Walton, J. B. and Andrews, J. F. 1981a. Torpor in single and huddled wood mice (*Apodemus sylvaticus* (L.)). *Acta Universitatis Carolinae-Biologica* 1979: 181–184.
- Walton, J. B. and Andrews, J. F. 1981b. Torpor induced by food deprivation in the Wood mouse *Apodemus sylvaticus*. *Journal of Zoology, London* 194: 260–263.
- Wang, L. C. H. 1988. Mammalian hibernation: An escape from the cold. In *Advances in Comparative & Environmental Physiology* 2. Pp. 1–45. Springer-Verlag, Berlin.
- West, S. D. and Dublin, H. T. 1984. Behavioral strategies of small mammals under winter conditions: solitary or social? In (J. F. Merritt, ed.) *Winter Ecology of Small Mammals*. Pp. 293–299. Carnegie Museum of Natural History, Pittsburgh.
- Zimmerman, K. 1952. Gattungstypische Verhaltensformen von Gelbhals-, Wald- and Brandmaus. *Der Zoologische Garten* 22: 162–171.

Received 23 July 2004. Accepted 13 April 2005.