YELLOW-BELLIED MARMOTS DEPRESS METABOLISM TO ENTER TORPOR

СНИЖЕНИЕ МЕТАБОЛИЗМА У ЖЕЛТОБРЮХИХ СУРКОВ ВО ВРЕМЯ НАЧАЛА ОЦЕПЕНЕНИЯ

LES MARMOTTES À VENTRE JAUNE RÉDUISENT LEUR MÉTABOLISME POUR ENTRER EN TORPEUR

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Abstract

When entering torpor, oxygen consumption decreased prior to the decline in body temperature for all 15 marmots used in this study. Most mean Q_{10} values were greater than 3.0, which supports metabolic inhibition rather than passive decline of metabolism because of the drop in body temperature. Changes in conductance were minimal and could not account for the changes in metabolism.

Key-words: *Torpor, metabolic depression, oxygen consumption, Q_{10}, conductance.*

Резюме

При входе в оцепенение потребление кислорода уменьшилось до снижения температуры тела у всех 15 сурков, охваченных данным исследованием. Большинство средних значений Q_{10} было большее чем 3.0, что скорее й поддерживает подавление метаболизма, чем его пассивное снижение из-за падения температуры тела. Изменения проводимости были минимальны и не могли влиять на изменения в метаболизме.

Ключевые слова: *оцепенение, снижение метаболизма,, потребление кислорода, Q_{10}, проводимость.*

Résumé

Chez les 15 marmottes utilisées dans cette étude, lors de leur entrée en torpeur, leur consommation d'oxygène décroît avant que leur température corporelle décline. La plupart des valeurs moyennes de Q_{10} étaient supérieures à 3,0, ce qui supporte l'hypothèse d'une inhibition du métabolisme plutôt que celle d'un déclin passif du métabolisme du fait d'une chute de la température. Les changements de conductance étaient minimaux et ne pourraient pas expliquer les variation du métabolisme.

Mots-clés : *Torpeur, dépression métabolique, consommation d'oxygène, Q_{10}, conductance.*

Introduction

Hibernating mammals reduce their energy metabolism to a fraction of their euthermic metabolic rate (VO_2). This reduction in metabolic heat production (M) represents the primary step for entering torpor. However, an animal's ability to reduce M and its relationship with body temperature (T_B) regulation remains unclear (Snyder & Nestler 1990; Heldmaier & Ruf 1992). The reduction of VO_2 can be explained by two different mechanisms. Reduction of energy metabolism could be a physical effect of temperature (Q_{10}) (Geiser 1993) or an active inhibition of metabolism (Heldmaier *et al* 1993*b*).

Metabolism may be reduced if T_B decreases and VO_2 follows passively. Thus, low Q_{10} values suggest that VO_2 declines as a consequence of a decline in T_B (Kayser 1964, Geiser 1988). T_B declines because cold-induced thermogenesis is inhibited which in turn reduces VO_2 followed by a thermal effect on tissue metabolism (i.e., Q_{10}) that causes further cooling; Q_{10} ranges from 2.0 to 2.8 in several species (Snapp & Heller 1981). In contrast, the high Q_{10} observed in several species (Kayser 1961, Wang & Hudson 1971) suggests that metabolism is reduced by a combination of lowered T_B and metabolic depression (Geiser 1988, Storey & Storey 1990, Malan 1993) or solely as the result of active metabolic inhibition (Heldmaier & Ruf 1992). It has been further argued that much of the confusion regarding metabolic depression and Q_{10} effects is a result of changes in conductance (Snyder & Nestler 1990).

In this paper we demonstrate that during entry into torpor VO_2 clearly declines and the decrease in T_B follows. We further examined the role of Q_{10} and conductance in the reduction of VO_2.

Materials and methods

The capture, transportation, housing, and procedures for measuring VO_2 and T_B of the 15 yellow-bellied marmots (*Marmota flaviventris*) used in this study are described elsewhere (Woods *et al* 1998). T_B and VO_2 were measured through one entire torpor bout for each animal or a group of three young; in a few instances a second bout was recorded. Additional measurements were made at ambient temperatures lower than the hibernating temperature. VO_2, T_B and ambient temperature (T_A) during normothermy and torpor were used to calculate Q_{10} and conductance for each animal for each bout of torpor. Q_{10} was calculated from the following formula:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_{B2} - T_{B1}}},$$

where R_1 is the VO_2 at T_{B1} and R_2 is VO_2 at T_{B2}.

Conductance was calculated as:

$$C = \frac{VO_2}{(T_B - T_A)}$$

where C = conductance

Results and discussion

Entering Torpor

When entering torpor, VO_2 decreased prior to the decline in T_B in all marmots. For example, in YF2275, VO_2 reached its minimal value in seven hours, whereas T_B required 28 hours to reach its minimum value (Fig. 1). We observed a short burst of VO_2 prior to the decline in oxygen consumption which then fell to almost zero before rising to a minimal stready-state. This pattern, which allows T_B to be lowered passively according to predictions of cooling curves, is similar to that observed in *Spermophilus lateralis* (Heldmaier *et al* 1993*b*).

The decline in VO_2 followed by a decrease in T_B supports an active inhibiton of metabolic rate (Lyman 1982). This sequence of a rapid decrease in VO_2 followed by a slow decline in T_B also occurred in *M. marmota* (Heldmaier *et al* 1993*a*), *M. monax* (Lyman 1958), and *S. richardsonii* (Wang 1979). The same pattern was present in the entrance into daily torpor in *Peromyscus maniculatus* (Nestler 1990). The mechanisms that induce metabolic depression were not examined in this study, but clearly the marked reduction of VO_2 prior to the decline in T_B demonstrates that entering torpor is not caused by Q_{10} effects.

Q_{10}

Q_{10} was calculated from differences between VO_2 and T_B of normothermic animals in their thermalneutral zone and VO_2 and T_B of torpid animals (Geiser 1988). Q_{10} values were similar to those of enzyme and tissue metabolism that have Q_{10}'s of 2 to 3 (O'Connor & McKeever 1950), which suggests that the reduction of VO_2 can be explained by the biochemical effects of Q_{10} (Kayser 1964, Snapp & Heller 1981). We measured mean Q_{10} values between 1.7 and 35.89; most mean values exceeded 3.0 (Table 1). Values greater than 3.0 indicate that the reduction in VO_2 cannot be explained by Q_{10} alone because the rate of decline in VO_2 is greater than that predicted from the biochemical effects of Q_{10}.

Q_{10} values for animals at a T_A of 10^0C were higher during the initial phases of entering torpor when T_B was between 35^0 and 25^0C than when T_B was lower (Table 1). In contrast, animals at a T_A of 6^0C exhibited higher values of Q_{10} when T_B varied from 25^0 to 15^0C (Table 1). However, the overall Q_{10} from 35^0 to 15^0C was similar in both groups of animals. Possibly T_A may affect the pattern of metabolic suppression, but more study is needed.

Table 1.

Q_{10} values at different temperature ranges for marmots at 6^0C and 10^0C T_A (T_A = ambient temperature).

T_A (^{0}C)	Temperature Range (^{0}C)	Q_{10}		N
		Mean	SD	
10	35-15	3.51	1.03	5
6	35-15	3.74	0.94	10
10	35-30	4.93	1.55	5
10	30-25	35.89	67.36	5
10	25-20	2.47	1.69	5
10	20-15	1.70	1.27	5
6	35-30	4.14	2.10	10
6	30-25	4.94	4.39	10
6	25-20	13.39	22.82	10
6	20-15	5.97	10.48	10

Conductance (C)

Endotherms regulate T_B by balancing heat production and heat loss. The rate of heat loss, expressed as conductance (C), can be affected by regulating either heat production or heat loss. T_B is regulated rather than the converse relationship of T_B regulating heat production. Therefore, Q_{10} may not be a valid measure of metabolic control in endotherms. Thus, the reduction in VO_2 during entrance into torpor may occur through the regulation of C (Snyder & Nestler 1990).

Conductance remained low during torpor, increased rapidly during arousal, and declined precipitously during entry into torpor (Fig. 2). This decrease in conductance during entry into torpor contrasts with the increased conductance reported previously (Snapp & Heller 1981, Lyman 1982). Increased C during entrance into torpor could facilitate the reduction of T_B and the decrease of C during arousal could permit greater heat gain (Snapp & Heller 1981). Thus, changes in C enable the animal to maintain a higher T_B than T_A under conditions of low VO_2 (Snyder & Nestler 1990). The high conductance that we measured during arousal apparently was transitory as conductance rapidly decreased while T_B increased (Fig. 2). This transitory increase in C possibly occurred because of the rapid increase in VO_2, which would initially increase C. The rapid decrease in C from its peak value would facilitate the increase in T_B, as postulated by Snapp & Heller (1982).

However, yellow-bellied marmots by changing C did not significantly regulate changes in T_B. The only effective way to increase total conductance is to increase the evaporation of water because changes in dry conductance would not provide sufficient heat loss in the short time period of arousal and re-entry. Marmots probably rely on metabolic water to meet their water needs during hibernation (Armitage *et al* 1990). The use of water to cool during re-entry would exceed the amounts of water available from metabolism. The pattern of conductance during a torpor bout (Fig. 2) suggests that conductance is maintained at a minimal level to conserve energy and that heat is lost passively. There is a short time period of higher C that corresponds with the initial phase of re-entry into torpor, which suggests that C has a minor role in facilitating heat loss.

We conclude that the observed patterns of VO_2, T_B, and C during hibernation in the yellow-bellied marmot support that entry into torpor occurs as a result of the inhibition of metabolism with the decline of T_B following passively. This pattern is consistent with the view that marmots (and probably other hibernating ground-dwelling sciurids) are energy conservers that attempt to minimize energy costs during both the homeothermal and heterothermal phases of their annual cycle (Melcher *et al* 1989, Armitage *et al* 1990, Armitage & Salsbury 1992, 1993).

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FIGURES / *РИСУНКИ*

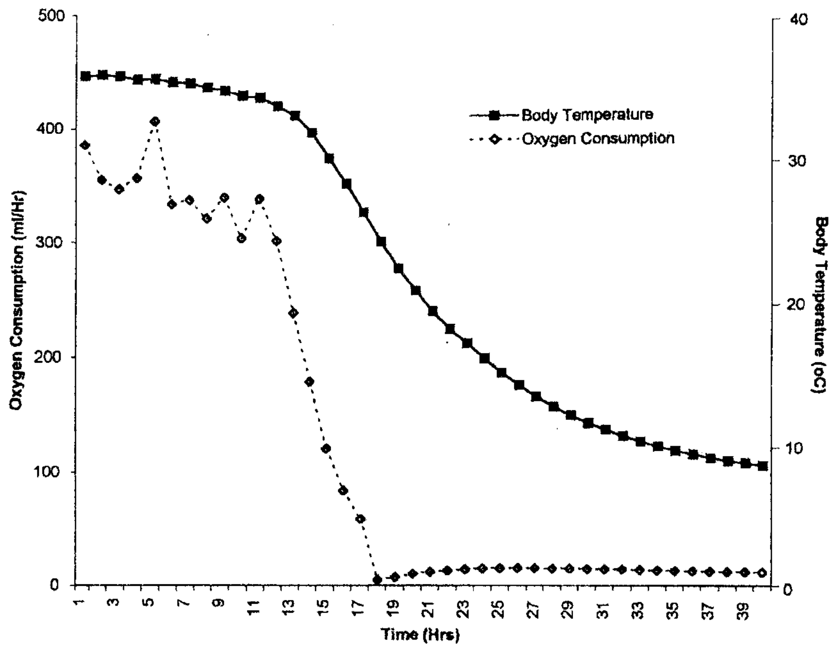

Fig. 1. Body temperature (T_B) and oxygen consumption (VO_2) during entry into torpor by young female 2275.

Рис. 1. *Температура тела (T_B) и потребление кислорода (VO_2) во время впадения в оцепенение у молодой самки 2275.*

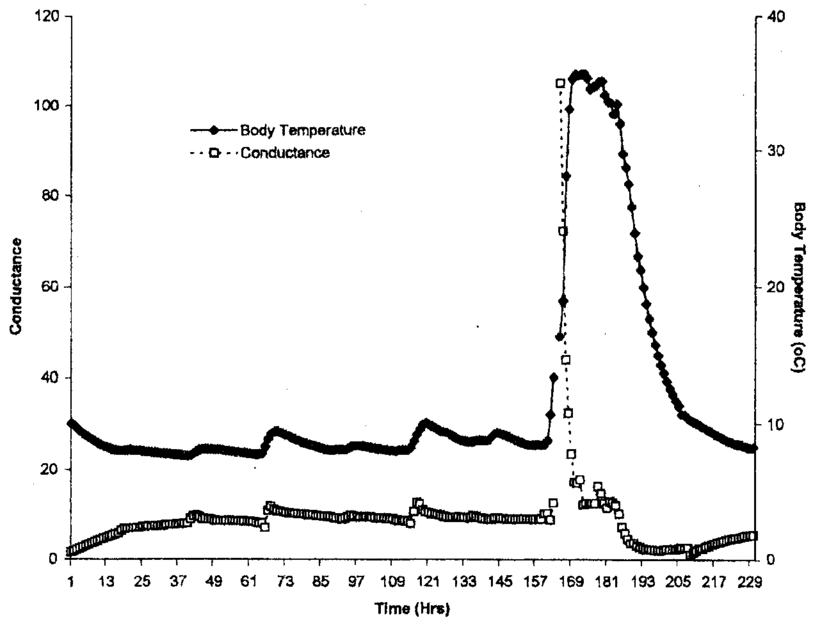

Fig. 2. Body temperature and conductance (C) during a bout of torpor by young male 2255. C = ml 0_2/hr/^{0}C.

Рис. 2. *Температура тела и проводимость (С) в течение баута оцепенения у молодого самца 2255. С = мл 0_2/час/^{0}С.*

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The results of researches on marmots carried out mainly during the 1990th in Russia and abroad are discussed: theoretical and practical problems of marmots' ecology and ethology, their protection and population management.

The book may be useful for wide range of zoologists, specialists on animals' protection and management, students of biology, etc.

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