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Aboveground activity rhythm in Arctic black-capped marmot (*Marmota camtschatica bungei* Katschenko 1901) under polar day conditions

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Abstract – Daily aboveground activity of wild black-capped marmots of Yakutia (*Marmota camtschatica bungei*) was recorded under 'polar day' conditions at 71°57' N and 127°19' E (north of the Polar Circle). From the beginning of May until the end of August, the sun was permanently above or close to the horizon. However under this condition of continuous lighting, the aboveground activity of these arctic hibernating mammals was periodic. Onset and end of activity showed marked changes throughout the seasons. Activity time increased strongly from hibernation emergence until the end of July and then decreased slowly until onset of hibernation. Below daily mean temperatures of 5 °C, activity started when the sun was 35° above the horizon, and ended when it dropped below 28°. When daily mean temperatures were above 5 °C, activity onset was synchronised with a solar altitude around 17–18° and activity ended at 10°. Activity onset was more precise relative to the solar altitude than the end of activity. This may be explained by late feeding bouts, following a midday thermal stress. In absence of rapid natural light-dark (LD) transitions that occur at civil twilight, our results suggest that the activity pattern of black-capped marmots may be synchronised by the light cycle through the solar altitude and ambient temperature. © 2001 Éditions scientifiques et médicales Elsevier SAS

Arctic / black-capped marmot / daily activity / foraging / solar altitude / synchroniser / temperature

1. INTRODUCTION

Black-capped marmots (*Marmota camtschatica bungei* Katsch. 1901) live permanently on the High Arctic sides of the Lena River (71° N, 127° E, Yakutia, Russia) and are exposed to extreme conditions throughout the year. From September to mid-May, they hibernate. They emerge from hibernation at the end of May with the beginning of the continuous 'polar day', when the sun always remains above the horizon. At lower latitudes, in most animals, the daily light-dark (LD) cycle is the principal synchroniser of the circadian activity rhythm [7, 8, 15, 20, 37]. Particularly, in more temperate conditions, the aboveground activity rhythm of marmots was entrained by the solar day (*M. baibacina* [12]; *M. monax* [19]; *M. flaviventris* [31]; *M. menzbieri* [29]; *M. marmota* [34]). Other periodic factors, such as temperature [6, 16, 17], food accessibility [7, 32, 43] or even azimuth position of the sun [26, 38], could modulate daily activity patterns of animal species. However, in the High Arctic during the polar day, two important components of the solar day, sunrise and sunset, are absent. So the question arises as to how circadian mechanisms function in marmots under such conditions.

In the High Arctic, despite the lack of sunrise and sunset, a daily rhythm was shown in different mammal and bird species for which light-dark (LD) cycles were known to be synchronisers of circadian rhythms [15, 26, 27, 38, 44]. Later, differences in responses to light of the onset and the end of circadian activity were described in many animal species [15, 38] and a

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two-oscillator model of activity rhythms of animals was proposed [35, 36].

Our objective in this study was to present for the first time field data on the activity rhythm of family groups of the black-capped marmot under continuous polar day conditions. In particular, we wanted to determine what seasonal changes occur in their activity pattern in relation to the following ecological factors: solar altitude and ambient temperature. This will allow us to discuss the function of their responses in the light of the two-circadian oscillator models proposed by Pittendrigh [35, 36].

2. MATERIALS AND METHODS

2.1. Study area

This work was realised in the Lena River Delta Nature Reserve (North Yakutia, 71°56' N, 127°19' E, Russia), on the banks of the Lena river in a mountain-tundra environment, altitude 300 m.

2.2. Biological model

Black-capped marmots are diurnal and sedentary mammals, occurring in mountain-tundra and in alpine stages of the Verkhoyansk Mountain Chain, from 20 to 1 500 m altitude [25]. The environment is characterised by permafrost and low ambient temperature. Presence of permafrost constrains digging shallow shelters only from 0.25 to 0.6 m below the surface [24, 46]. Black-capped marmots hibernate for 8 months (between mid-September and mid-May) and reproduce once a year. Mating occurs inside the burrows in April before the emergence from hibernation [23, 46]. The female gives birth to five to six siblings. Marmots live in family groups, consisting of a reproductive pair and their offspring [24]. In its specific habitat of Northern Yakutia, the population dramatically lost two-thirds of its size during the last 40 years [28, 41]. Thus the subspecies *Marmota camtschatica bungei* is one of the most vulnerable species of the genus *Marmota* [11].

2.3. Observations

Observations started on 12 May 1998, before the first marmot emergence from hibernation on 23 May, and continued until 1 September 1998.

At this latitude, the polar day extends from 12 May to 2 August.

In the fields, only the size of the juveniles of a given year can be easily distinguished from the other animal age classes. Thus all individuals, with the exception of juveniles of two family groups of black-capped marmots 1 km apart, were observed in their mountain-tundra environment (group 1: four individuals, altitude 300 m, southern exposure; group 2: two individuals, altitude 300 m, south-west exposure).

Family groups were observed with binoculars (8×40) and a Kowa telescope (22×66 lens) all the polar day long. Observations were made each day, alternately for one family group. Observations were cancelled when marmot activity was strongly disturbed by rain or snowfall, making the sampling schedule random. The timing of activity onset of the first animal emerging from the burrow and the timing of end of activity of the last aboveground animal in a family group (local time) were recorded during 36 d (18 d for each group). During those days, the number of aboveground animals and the number of foraging animals were noted once every 15 min (scan sampling; [2]).

2.4. Ecological factors

During the observation period, ambient temperature was measured under and outside of a shaded shelter with an electronic thermometer (± 0.2 °C) every quarter of an hour. All marmot home ranges faced South and marmots were almost permanently exposed to solar radiation. Therefore, only out-of-shelter temperatures 10 cm above the ground were used in the statistical analyses. Solar altitude (angle) was calculated in degrees for each quarter of an hour for each day using the Hour World 2.15f software (© 1994–1998 by Leighton Paul).

2.5. Statistical treatment

As sample sizes were small, we used median (M) and absolute deviation (AMD) as well as non-parametric statistics at a significance level of $P \leq 0.05$.

In order to compare the activity in marmot groups of different size, we calculated hourly the ratio between the median number of aboveground animals and the total number of animals per group. The number of aboveground marmots and foraging marmots were arranged in seven 5 °C range temperature classes and compared using the Kruskal-Wallis analysis of variance and the multiple comparison test [42]. In order to avoid dependent measures, only the value of an observed number was chosen at random each day for each temperature class.

Solar altitude at the onset and end of activity were analysed with the Mardia-Watson-Wheeler test [10]. Seasonal changes in onset and end of daily activity were tested through comparison of angle deviations of the solar altitude with the Mann-Whitney test [10, 42].

3. RESULTS

3.1. Climate and external factors

During the second half of May, snow cover was still abundant. Mean maximum solar altitude was 39.9° and mean temperature 0.3 °C. Maximum solar altitude reached 42.3° at the end of June then decreased until the end of our observations. Mean temperature increased to 12.8 °C at the end of July and then decreased slowly until the end of August, due to the inertia effect of the earth (*table I*). In spite of continuous daylight, the polar day has a 24-h rhythm in other factors. Animals for synchronising their activity rhythm (*figure 1*) could potentially use changes in periodic external factors (e.g. solar altitude, maximum temperature).

3.2. Seasonal activity

The first marmot emerging from hibernation was observed on 23 May, after the beginning of the polar day. Marmots entered hibernation at the beginning of September, so they were active for 70 d under polar day conditions and another month under short night conditions.

Aboveground activity was not continuous throughout the 24-h day. The remainder of the time, marmots stayed underground in their burrow where they may have been active.

Daily duration of aboveground activity was at a minimum at the end of May (group 1: median (M) = 1:00, absolute median deviation (AMD) = 1:39 h; group 2: 0:15, 1:05 h), and increased with temperature and solar altitude until June 22 (group 1: 14:10, 1:36 h; group 2: 13:00, 0:15 h). In July, although solar altitude decreased, temperature and length of daily activity reached their maximum (group 1: 16:10, 0:18 h; group 2: 15:00, 1:07 h). In August, temperature, solar altitude and length of daily activity decreased together (group 1: 11:21, 0:09 h; group 2: 10:45, 0:15 h; *figure 2*). Daily foraging activity duration followed the same pattern (May, group 1: 2:15, 2:00 h; group 2: 0 h / June, group 1: 10:30, 2:03 h; group 2: 11:30, 1:41 h / July, group 1: 15:30, 0:10 h; group 2: 14:15, 1:11 h / August, group 1: 11:00, 1:00 h; group 2: 8:37, 1:31 h). Marmots had longer aboveground and foraging activity times after the summer solstice than before.

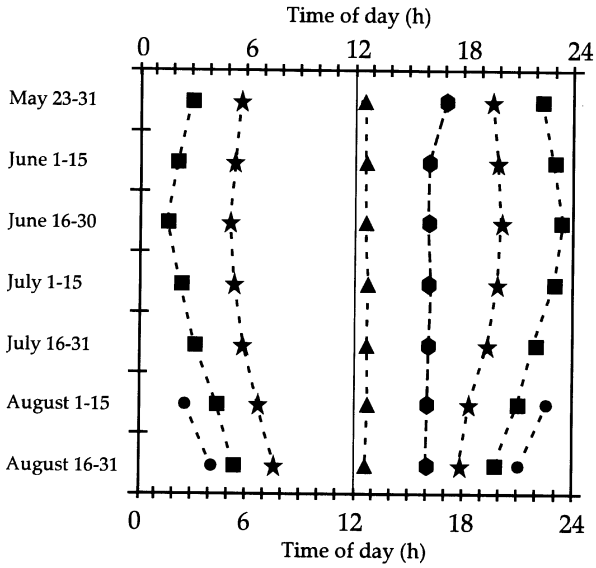

Figure 1. Periodic factors of the *Marmota camtschatica* environment in the Lena River Delta Nature Reserve. Circles, 0° solar altitude time; squares, 5° solar altitude time; stars, 15° solar altitude time; triangles, zenith time; hexagons, maximum temperature time. Solar altitudes were calculated on the 7th and on 21th of each month. The observation period was divided into seven half-months (23–31 May, 1–15 June, 16–30 June, etc.).

Table I. Temperatures and solar altitudes in the Lena River Delta Nature Reserve (23 May–1 September). Daily temperatures were recorded between 04:00 and 00:00, local time. Minimal and maximal daily solar altitude were calculated on 27 May, on 7 and 21 June and August, and on 15 July. Min., minimum temperature or daily solar altitude; Max., maximum temperature or daily solar altitude.

Time of year	Daily mean temperature under shelter (°C)						Daily solar altitude (°)	
	Group 1			Group 2				
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Max.
23–31 May	–1.9	0.3	1.8	–3.3	–1.3	0	2.1	39.9
1–15 June	0.4	1.6	3.6	–1.0	3.4	6.1	3.8	41.6
16–30 June	1.4	4.9	7.6	3.4	8.8	13.4	4.6	42.3
1–31 July	6.1	12.8	18.3	9.5	12.9	16.0	2.8	40.5
1–15 August	3.6	10.5	16.3	5.1	12.0	17.1	–2.25	35.4
16–31 August	2.3	5.3	8.2	2.0	5.8	8.3	–6.5	31.1

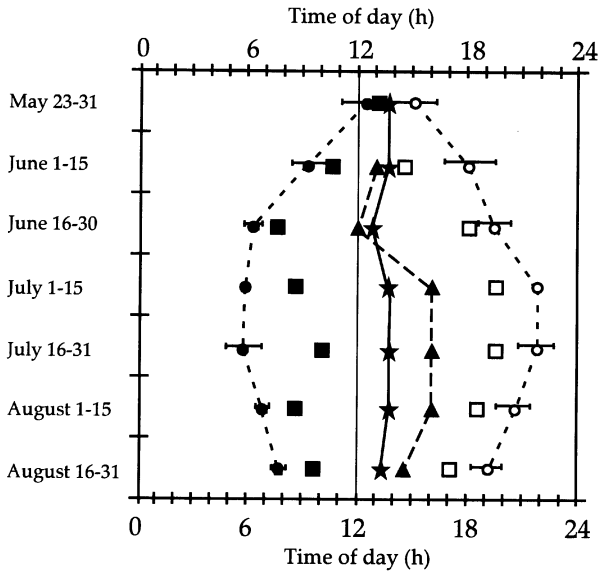

Figure 2. Main events in activity times of *Marmota camtschatica* in the Lena River Delta Nature Reserve. Black circles, aboveground activity onset; open circles, aboveground activity end; black squares, first activity peak; open squares, second activity peak; triangles, activity minima; stars, activity midpoint. The observation period was divided into seven half-months (23–31 May, 1–15 June, 16–30 June, etc.). Semi-monthly medians and absolute median deviations were calculated for the following parameters: onset of aboveground activity (local time); end of aboveground activity (local time); activity midpoint (1/2 [activity end minus previous onset], local time).

3.3. Activity rhythm

The daily activity pattern, number of individuals aboveground, was bimodal with a morning and an evening peak. The activity mid-period occurred always 1 h (67 ± 9 min) after the sun was at its zenith. The activity minimum preceded the activity mid-period before the summer solstice and followed it after this date (*figure 2*).

3.3.1. Temperature effect

In both family groups, the number of aboveground marmots and foraging marmots varied with ambient temperature. When the temperature ranged between –5 and 0 °C, aboveground marmots were significantly less than when it was above 0 °C (*table II*). But marmot number also significantly decreased when the temperature was above 25 °C (*table II*), particularly in July and August (*figure 3*).

3.3.2. Solar altitude effect

3.3.2.1Activity onset

No activity onset was observed when solar altitude was below 11°. Onset of marmot activity of both family groups was concentrated around two solar altitudes (*figure 4*). From the end of May until mid-June, temperature was very low (cold period) and marmots emerged from their burrow only when the solar altitude was between 35 and 36°. During the other months (end of June–end of August, temperate period), onset of activity occurred when the solar altitude was between 17 and 18°. For each period, there was no significant difference between the two family groups, but solar altitude differed significantly between the angles of these two periods (Mardia-Watson-Wheeler test: group 1, $n = 17$, $B = 23.73$, $P < 0.01$; group 2, $n = 20$, $\chi^2 = 10.35$, $P < 0.01$).

Table II. Number of aboveground and foraging marmots in relation to ambient temperature outside shelter. *n*, Number of 15-min periods of observation; A, aboveground marmots; F, foraging marmots; Kruskal-Wallis one-way analysis of variances: H_a aboveground marmots, H_f foraging marmots. Multiple comparison test, at $P < 0.05$; significant differences: [a] with the 0–5 °C range, [b] with the 5–10 °C range, [c] with the 10–15 °C range, [d] with the 15–20 °C range, [e] with the 20–25 °C range.

	Group 1			Group 2		
		A	F		A	F
		$H_a = 24.2$ *	$H_f = 24.9$ *		$H_a = 20.7$ *	$H_f = 20.3$ *
Temperature	*n*	Mean rank	Mean rank	*n*	Mean rank	Mean rank
–5 to 0 °C	6	6.5[a, b, c, d, e]	11.0[b, c, d, e]	4	5.5[b, c, d, e]	11.0[b, c, d, e]
0 to 5 °C	13	26.6[c, d]	24.7[b, c, d]	9	18.8[b, c]	18.1[b, e]
5 to 10 °C	18	36.4	37.0	12	30.4	35.7[d]
10 to 15 °C	12	40.9	41.3	7	32.9	27.9
15 to 20 °C	6	45.4	39.7	7	30.1	23.9
20 to 25 °C	4	36.6	46.3	6	29.8	30.7
25 to 30 °C	4	16.5[b, c, d]	11.0[b, c, d, e]	4	12.3[b, c, d, e]	11.0[b, c, d, e]

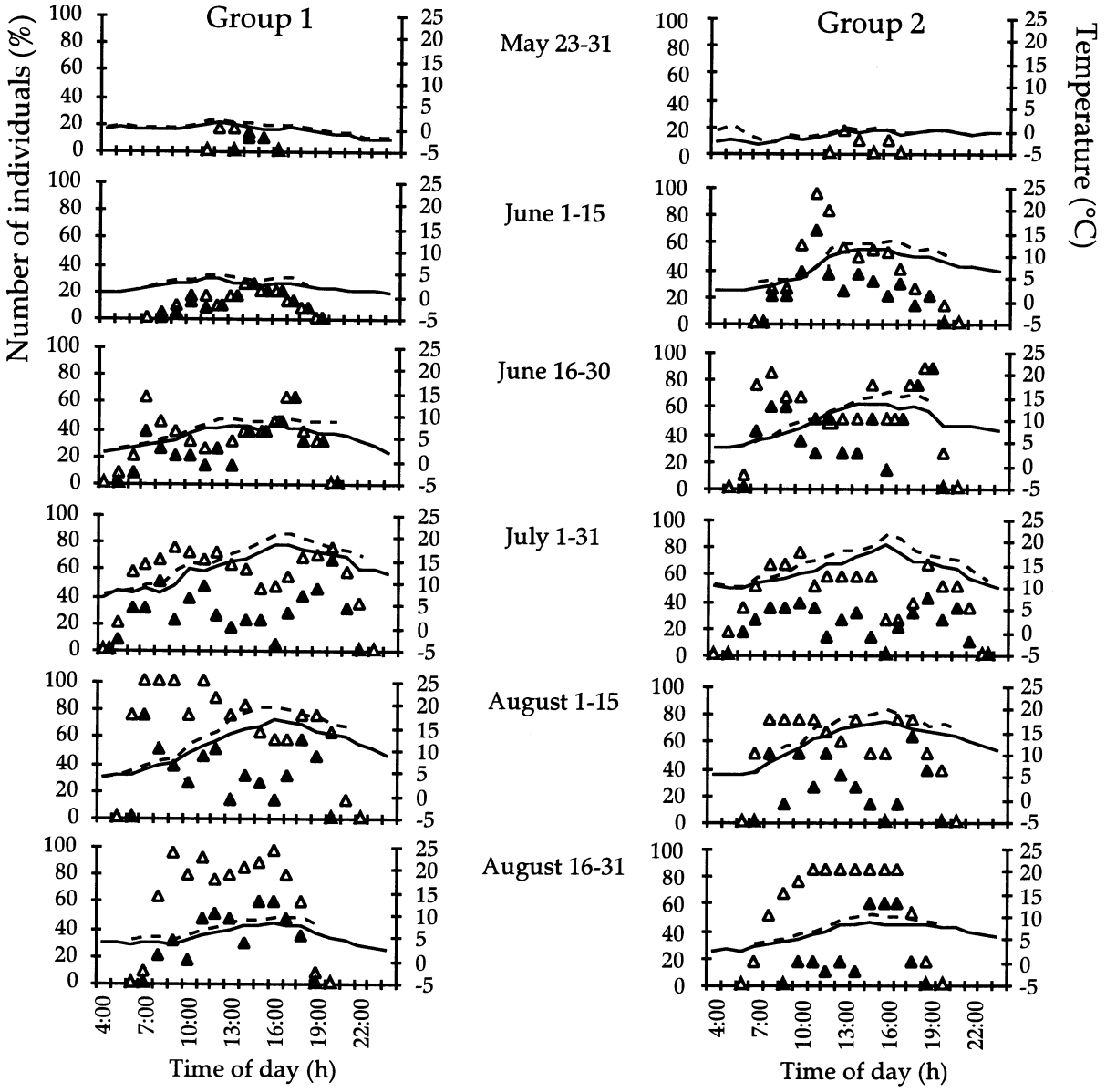

Figure 3. Semi-monthly medians of daily activity of black-capped marmots. Open triangles, hourly percentage of aboveground marmots; black triangles, hourly percentage of foraging marmots; solid lines, temperature under shelter; dashed lines, temperature outside shelter. The observation period was divided into seven half-months (23–31 May, 1–15 June, 16–30 June, etc.). Semi-monthly medians and absolute median deviations were calculated for the following parameters: onset of aboveground activity (local time); onset of foraging activity (local time); end of aboveground activity (local time); end of foraging activity (local time); aboveground activity time (activity end minus previous onset, in hours); foraging activity time (foraging end minus previous onset, in hours); activity midpoint (1/2 [activity end minus previous onset], local time).

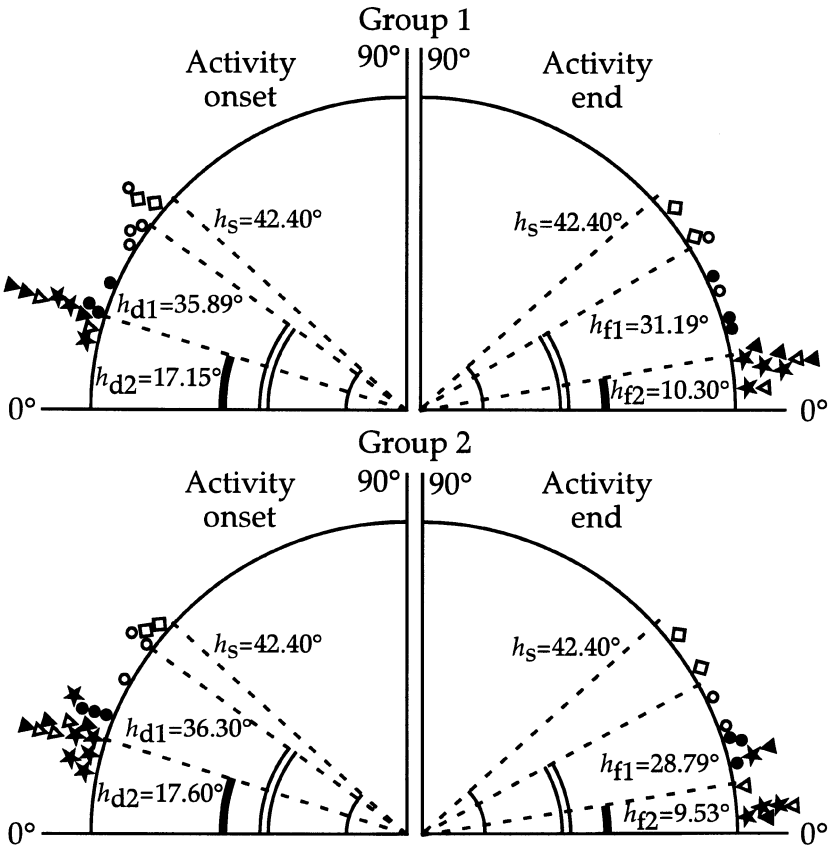

Figure 4. Onset and end of aboveground activity in relation to solar altitude. h_s solar angle during the summer solstice; h_{d1} mean solar angle of activity onset during the cold period; h_{d2} mean solar angle of activity onset during the temperate period; h_{f1} mean solar angle of activity end during the cold period; h_{f2} mean solar angle of activity end during the temperate period. Each symbol represents one observation. Open squares, 23–31 May; open circles, 1–15 June; black circles, 16–30 June; stars, 1–31 July; open triangles, 1–15 August; black triangles, 16–31 August.

During the temperate period, activity onset was more precisely related to a given solar altitude than activity end (*figure 4*).

3.3.2.2Activity end

No activity end was recorded when solar altitude was below 2.9°. The end of marmot activity was less precisely synchronised to a given solar altitude than activity onset (*figure 4*). Variation in angle of solar altitude for activity onset was significantly lower than that for solar altitude at activity end (Mann-Whitney test: group 1, $P < 0.05$; group 2, $P < 0.001$). The higher the temperature the later marmots retired as shown by the logarithmic regression of daily maximum temperature and solar altitude at the end of activity (*figure 5*).

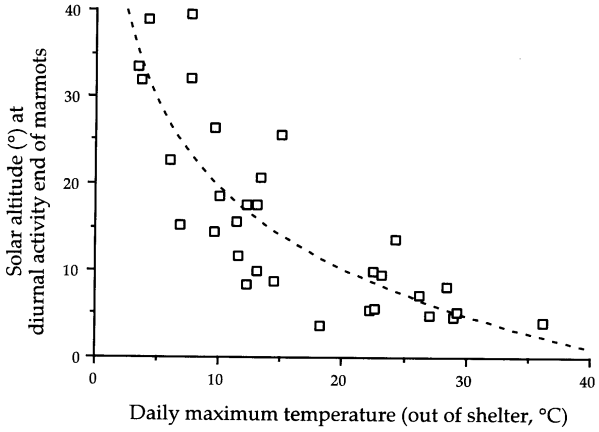

Figure 5. Correlation between daily maximum temperature and solar altitude at diurnal activity end. Each square represents one day of observations. Logarithmic fitting curve: $y = 48.2 - 30.1 \times \log(x)$; $R = 0.83$; $P < 0.001$. Kendall test: $n = 31$; $\tau = -0.64$; $P < 0.001$.

4. DISCUSSION

The circadian endogenous rhythm (biological clock) is considered as facilitating the adaptation of living

beings to their environment. This rhythm was observed in most animals maintained in experimental free-running conditions [4, 5]. In the natural environment, exogenous components adjust the circadian activity rhythm of animals to the daily 24-h periodicity. The day-night (LD) alternation is the main synchroniser [8]. However, another ecological factor, like ambient temperature, may also act as a synchroniser, in particular for poikilothermic animals. Homeothermic animals are less easily entrained by temperature. Eskin [16] had to use cycles with ranges of more than 30 °C to get entrainment in the house sparrow (*Passer domesticus*), whereas for the pig-tailed macaque (*Macaca nemestrina*) a range of only 16 °C was sufficient [6]. Ferron [17] showed a similar effect in two Sciurid species (*Glaucomys sabrinus* and *Tamiasciurus hudsonicus*): during temperate seasons, light was the main factor controlling their circadian activity distribution, but in winter the temperature effect became preponderant. In the Arctic, *Marmota camtschatica* lives in extreme climatic conditions and is subject to induced stress from cold. In *M. flaviventris*, monitoring of standard operative temperature (T_{es}; [9]) made it possible to show that marmot activity decreased with low temperature. The cost of thermoregulation could be reduced [30]. Indeed, oxygen consumption at 5 °C is twice what it is in the neutral thermal zone [3, 25]. Marmots have to respond to strong thermoregulation needs when they are active aboveground during the coldest hours of day.

Our results, in spite of the smallness of the sample size, suggest that solar altitude can play an important role in the daily activity pattern of family groups of black-capped marmots. Daily activity of black-capped marmots began later during the cold season (from May to beginning of June, solar altitude ≥ 30°). Foraging activity then was also low. During the temperate season (end of June–end of August), marmots began aboveground activity when the sun was about 17° above the horizon. During these 3 months, the onset of activity was tightly correlated with solar altitude. This was not the case for the end of daily aboveground activity. In the Arctic, a similar effect has been described for different mammal and bird species. The onset of circadian activity is usually stable throughout the annual cycle and presents less variation than at the end of daily activity [15, 38]. But, contrary to what these authors described, the onset of daily activity in black-capped marmots is more removed from civil twilight (sun 6° under the horizon) than the end of daily activity. This finding may relate to the intrinsic period of the circadian system which, in the case of the black-capped marmot, can be expected to be larger than 24 h [7]. A similar daily aboveground activity pattern has been described for alpine marmots (*M. marmota*) in field observations [40]. Although alpine marmots do not seal off their burrows and may perceive the twilight transitions, they emerged from their burrows at 16–17° solar altitude and ended their aboveground activity close to civil twilight at dusk. European ground squirrels (*Spermophilus citellus*), under natural conditions never seeing the twilight, emerge from their burrows hours after dawn and retire long before dusk [22].

Another aspect of thermal stress is related to high ambient temperatures. In an open environment, marmots are exposed to direct solar radiation when aboveground. With limited physiological abilities to discharge excess heat [33], marmots have to compensate by a behavioural thermoregulation. In an Alpine marmot population (*M. marmota*), animals were less and less active when T_{es} exceeded 25 °C [45]. In order to avoid an excessive increase of body temperature, marmots reduced foraging bouts. Heat was eliminated either by lying on rocks or by entering the burrow. The same reaction was observed for *M. flaviventris* [31]. This corroborates our observations that activity decreased when marmots were exposed to sun temperatures higher than 25 °C. Such a thermal constraint limits the aboveground period of activity and reduces the remaining foraging time in the early afternoon. Moreover, food access could act as a synchroniser for circadian activity in both mammals [8, 13, 32, 43] and birds [1, 20]. This synchroniser is usually less powerful than light [8, 20]. However, it becomes more important when food accessibility decreases [21, 32, 39] or after food starvation periods [13, 43].

This could explain the late foraging activity of marmots, on days when they have been submitted to a thermal stress in the middle of the day, reducing the access to food. This late period of food intake could be used by black-capped marmots to make up for an insufficient alimentation and to keep up their daily intake at a level sufficient to allow fat accumulation for an 8-month hibernation. This effect could explain the variability of end of activity relative to solar altitude.

Lasty, under natural conditions, social interactions and mutual training of animals living in the same family group could act to synchronise activity. This is known in birds [18] and mammals [14]. This type of synchronisation cannot be excluded in black-capped marmots, which is a strongly social species [24].

Our observations, performed in the Arctic's natural conditions, lead us to consider that several synchro-

nisers could act on the circadian activity of black-capped marmots. But the light cycle, in terms of solar altitude above the horizon, appears to be more important. However, marmots display different responses to light, in the morning and evening. This is in agreement with the two-oscillator model of circadian rhythm suggested by Pittendrigh [35, 36]. The onset activity oscillator (morning oscillator for diurnal animals and evening oscillator for night animals) is more determinant than the end activity oscillator. Nevertheless, extra observations will be necessary to supplement our understanding of circadian adaptive mechanisms of marmots to the peculiarities of their natural environment.

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