










Rest and cold: different circadian responses to natural cold in five species of predatory mammals

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Abstract Aiming to answer the question of how the rest-activity cycle and subcutaneous temperature change with a decrease in ambient temperature, we studied the following species of predatory mammals: domestic cats (*Felis catus*, $n = 4$), Far Eastern forest (Amur) cats (*Prionailurus bengalensis euptilura*, $n = 3$), Eurasian lynxes (*Lynx lynx*, $n = 3$), sables (*Martes zibellina*, $n = 3$), and forest ferrets/furo (*Mustela putorius*, $n = 3$). All subjects were studied in spacious forested area enclosures. Subcutaneous temperatures in the interscapular region of the back as well as locomotor activity were recorded during 70 days using miniature data loggers in the autumn–winter period (air temperature fluctuated from 12 to -20 °C). The results show different responses to natural cold: (1) a circadian rise in subcutaneous temperature which is not associated with an increase in locomotor activity (Amur cats); (2) a circadian rise in subcutaneous temperature which correlates with an increase in locomotor activity (lynxes, domestic cats); (3) rises in subcutaneous temperature which correlate with increases in locomotor activity, but are not circadian (sables, ferrets). The results demonstrate different strategies for adapting to natural cold in various predatory mammals in conditions of captivity.

1 Introduction

Modern experimental physiology is based mainly on results obtained on very limited amount of experimental animal species in laboratory conditions. The ecophysiological characteristics of wild animals in natural or semi-natural surrounding remained poorly studied until the recent development of miniature autonomous loggers. The appearance of these low-power devices made it possible to carry out long-term recordings of various physiological indicators: locomotor activity, body and brain temperature, EEG, EKG, EMG, EOG, etc., in conditions of free behavior of animals. However, the problem in such studies is the need to access the objects under study after the end of the recording to take readings, that is, download information from the internal memory of the devices. This problem is solved in different ways. In particular, when studying the behavior of feral domestic cats in Australia, Hilmer et al. [1–3] took advantage of the government’s campaign to bait feral cats. However, in many other cases it is necessary to use enclosure conditions for keeping wild animals. Such captive surrounding cannot be called completely natural, since predators do not have to hunt and they do not experience real hunger, receiving a regular optimal dose of food. Their territories and contacts with other individuals of their own and other species are limited. But still, even such an environment is incomparably preferable to laboratory conditions for ecophysiological research, since the object animal is completely under the influence of natural surrounding: weather, humidity, noises and smells, climatic and light factors. Such conditions are suitable, among other things, for studying the hitherto unknown natural circadian rhythm and its seasonal dynamics in wild predatory mammals. The purpose of this work was to partially fill this gap.

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2 Methods

We studied the following species of predatory mammals: 4 adult male domestic cats (*Felis catus*, age 2–3 years, 3.2–3.5 kg b.w.); 3 adult male Far Eastern forest (Amur) cats (*Prionailurus bengalensis euptilura*, age 2–3 years, 5.3–6.3 kg b.w.); 3 adult female Eurasian lynxes (*Lynx lynx*, age 18 months, 15–17 kg b.w.); 3 adult sables (*Martes zibellina*, 2♂, age 3 and 7 years, about 1.5 kg b.w. each, and 1♀ age 8 years, about 1 kg b.w.); and 3 adult forest ferrets/furo (*Mustela putorius*, age about 1 year each, 1♂, about 1.5 kg b.w., and 2♀ about 0.8 kg b.w.). All animals from the moment of birth are constantly kept in spacious enclosures in a forest area at the Joint Usage Center “Live collection of wild species of mammals” at A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences at the territory of the biological station “Tchernogolovka” (Moscow region). Each enclosure has a small shelter house with hay bedding. The enclosures are in natural light, there is no artificial illumination either in the enclosures themselves or in the adjacent territory. All predators receive minced chicken (~ 200 g) as a basic rationed feed once a day 6 days a week, except for lynxes which receive 1 whole chicken per head/per day (~ 800 g), also 6 days a week. Under general anesthesia (Zoletil + Medetomidin or Xylazin, i.m.) each animal was implanted through a small incision at the wither with an ecologger TMDL-4.0 (a miniature autonomous temperature sensor equipped with an accelerometer, manufactured by EMBI Research LLC, Novosibirsk, Russia [4]) between the muscles of the interscapular region of the back, to a depth of 2–3 cm from the surface of the body. The incision was sutured; the animals were injected with an antibiotic and placed back to their enclosures.

Subcutaneous body temperature (ST) was measured in centigrade (°C), and locomotor activity (MA) was measured in conventional units dG (fractions of the free acceleration $G = 1$, where dG is the resulting acceleration in three dimensions). The temperature and motion sensors take measurements every minute, average them over a period set by the user, and store them on the internal memory. In this study, the average period was taken of 10 min. In this mode, the power of each ecologger’s battery retains for 9–10 weeks. Registration lasted in the autumn–winter period from the end of October till the beginning of January, total about 70 days. During this period, air temperature fluctuated between 12 and – 20 °C. At the end of the experiment, the animals were again anesthetized in the same way, the loggers removed, the incision sutured, the animals injected with an antibiotic, and they placed back to their enclosures.

The data from ecologgers’ information storages were read by a special device and represented in both table and graphical forms as Excel files. Typical 6–10 days fragments of the autumn and winter periods of every pair of ST and MA recording were extracted and processed by the Excel program separately with the determination of mean values and standard error of means ($M \pm S.E.M.$). In addition, the warmest and the coldest days’ ST and MA were analyzed hour by hour, and Pearson’s correlation coefficient calculated for each pair of ST and MA curves.

All experimental procedures performed in this study complied with the ethical standards approved by the legal acts of the Russian Federation and the principles of the Basel Declaration, and also were approved by the Regulatory Commission of Experimental Research (Bioethics Commission) of the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences.

3 Results

As can be seen from the fragments of records of Far Eastern forest (Amur) cats (Fig. 1A, upper graph; Table 1), there is no clear circadian rhythmicity in ST during the warm autumn period (mean air temperature 5 °C). ST shows random fluctuations around the “set point” of 36.2 °C. However, clear circadian rhythmicity in ST obviously appears in winter (Fig. 1A, bottom graph; mean air temperature – 11 °C; Table 1), with the acrophase during the daylight and the bathyphase during the dark period of the nycthemeron. At the same time, MA demonstrates tendency to increase during the dark circadian phase in autumn which disappears in winter. Daily averaging of the data (Fig. 1B, left side; Table 2) confirms that during the warmest autumn day no clear circadian rhythm of ST is observed. On the contrary, MA undergoes a circadian fluctuation with lower values during daylight hours. During the winter coldest day, the dynamics of ST change dramatically (Fig. 1B, right side; Table 2). At night, the ST dropped to 33.3 °C. Approximately from the midnight, a rapid increase in the ST begins, reaching its maximum at dawn and remaining as a plateau for 5 subsequent hours. Then its gradual decline starts, ending between midnight and 1AM. These circadian fluctuations of the ST occurred synchronously and in phase in all three animals. At the same time, the circadian daily decrease in MA smoothes, and the difference between the level of daytime and nighttime MA disappears. So MA does not increase and even decreases at the coldest day as compared to the warmest one without any circadian oscillation but despite, circadian ST demonstrates a high rise by 3 °C during the coldest day. Both curves, ST and MA, demonstrate a low Pearson’s correlation coefficient during the warmest autumn day and the lack of correlation during the coldest winter day.

In domestic cats living in semi-natural environment (Fig. 2A; Table 1), a similar though not identical circadian pattern of ST is observed: a strict daily rhythm which is not clearly seen during the warm autumn period appears

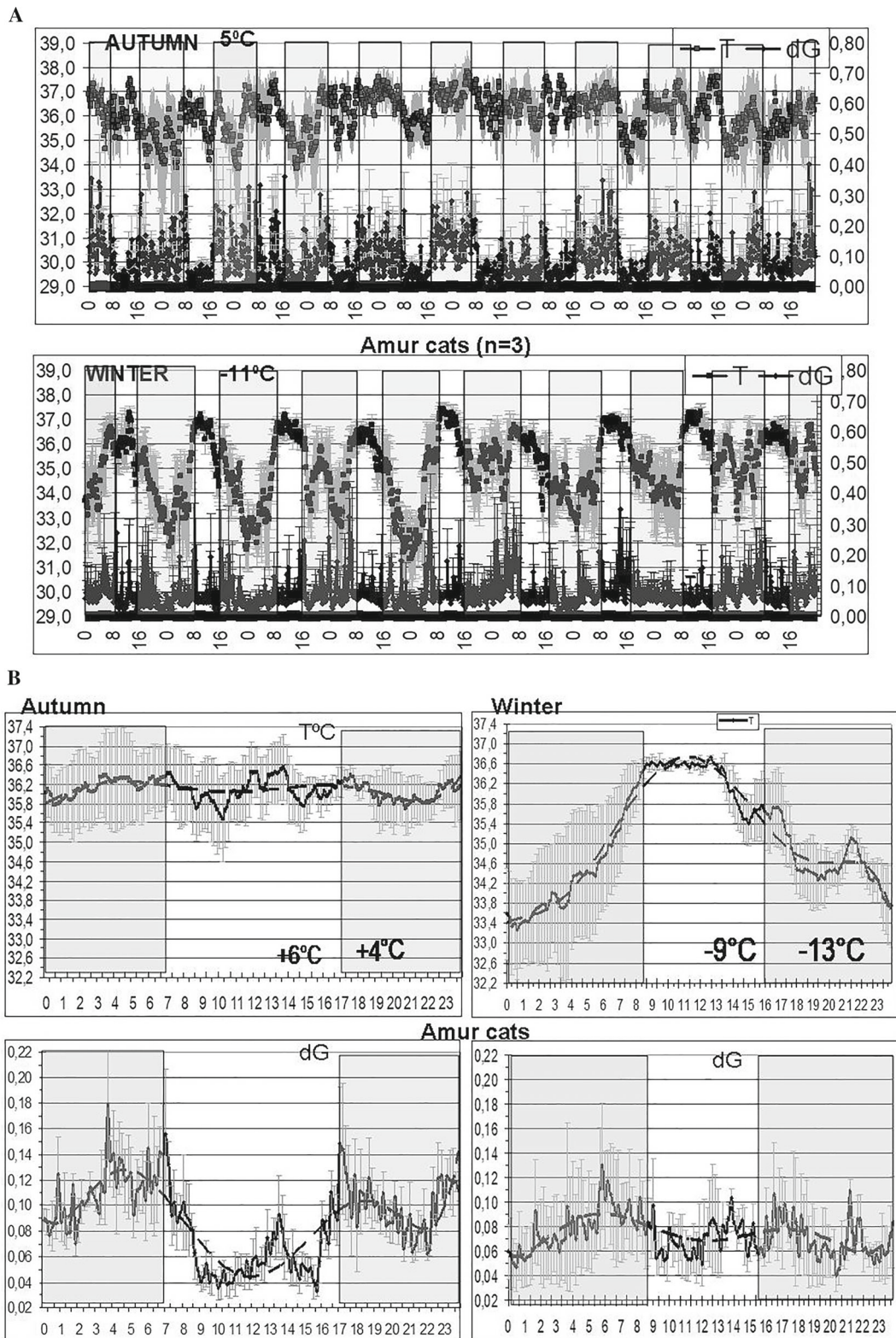


Fig. 1 **A** Far Eastern forest (Amur) cats ($M \pm S.E.M.$, $n = 3$). Fragments of 70-days recordings. Mean air temperatures are $+ 6\text{ }^{\circ}\text{C}$ during the day and $+ 4\text{ }^{\circ}\text{C}$ at night in the autumn period (top graph) and $- 9\text{ }^{\circ}\text{C}$ during the day and $- 13\text{ }^{\circ}\text{C}$ at night in the winter period (bottom graph). In each graph, upper curves: ST, lower curves: MA. Abscissa axis presents the time of day in hours. Left ordinate, ST ($10\text{ }^{\circ}\text{C}/\text{scale}$). Right ordinate, MA ($0.8\text{ dG}/\text{scale}$). Shaded areas, dark periods. **B** Circadian dynamics of ST (top graphs) and MA (bottom graph), in the fall warmest day (left graphs) and the winter coldest day (right graphs). Ordinate axes, top: ST ($5.2\text{ }^{\circ}\text{C}/\text{scale}$), bottom: MA ($0.2\text{ dG}/\text{scale}$). Shaded areas, dark periods. Abscissa axis, the time of day in hours. Dotted line, approximation to sinusoid. $M \pm S.E.M.$, $n = 3$

Table 1 The ST and MA values during autumn (daily air $T_{\text{mean}} = 5\text{ }^{\circ}\text{C}$) and winter ($T_{\text{mean}} = -11\text{ }^{\circ}\text{C}$) periods

Subject	Autumn ($5\text{ }^{\circ}\text{C}$)						Winter ($-11\text{ }^{\circ}\text{C}$)					
	ST ($^{\circ}\text{C}$)			MA (dG)			ST ($^{\circ}\text{C}$)			MA (dG)		
	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median
Amur cats (n = 3)	33.8	37.8	36.2	0.005	0.401	0.068	31.4	37.4	35.3	0.005	0.349	0.062
Domestic cats (n = 4)	34.2	38.7	37.0	0.012	0.242	0.059	32.8	38.9	35.7	0.004	0.379	0.067
Lynxes (n = 3)	34.4	38.7	36.6	0.000	0.599	0.057	33.1	37.5	35.8	0.011	0.552	0.109
Sables (n = 3)	34.6	39.2	36.6	0.005	0.885	0.229	31.9	37.3	34.4	0.005	0.906	0.208
Ferrets (n = 3)	35.0	38.5	36.6	0.016	0.531	0.089	32.5	37.4	35.1	0.016	0.635	0.088

during the cold winter period. Its acrophase is timed to the daylight, and the bathyphase—to the night dark periods. However, contrary to Amur cats, each rise of ST follows the correspondent increase in MA. Circadian fluctuation of ST is a moderate during the warm autumn period (air $T_{\text{mean}} = 5\text{ }^{\circ}\text{C}$). Hour-to-hour analysis of the warmest day (Fig. 2B, Table 2) reveals a circadian ST double rise. The ST fluctuates around the “set point” of $37\text{ }^{\circ}\text{C}$, decreases slightly at night reaching minimum by 5AM, and then rapidly rises reaching $37.5\text{ }^{\circ}\text{C}$ by dawn (6:30–7 AM). After dawn, ST drops sharply to $36.4\text{ }^{\circ}\text{C}$ and rises again to $38\text{ }^{\circ}\text{C}$ by 1PM (the noon local solar time). Then ST undergoes a gradual undulating decrease. Regarding the MA, it is noticeable that both rises in ST (at 6 AM and 1 PM) are coincided with increases in the dG values. The ST rise is a very high ($4\text{ }^{\circ}\text{C}$) during the winter coldest day with maximum at the daylight and minimum at the dark night periods. In winter, ST at night drops to $34.4\text{ }^{\circ}\text{C}$ (Fig. 2B, Table 2). From about 3 AM, it begins to rise, reaching the acrophase by 2 PM, after which there is a sharp decline, ending at about 7PM. From 7 PM to 3 AM, ST remains at a low level of $34.4\text{--}35\text{ }^{\circ}\text{C}$. As for MA, a pronounced circadian peak is noted, which maximum coincided with the acrophase of ST. The MA mean level increases in winter as compared to autumn (Table 1). All these oscillations occurred synchronously and in phase in all four cats. There are high Pearson's r both for the autumn warmest and the winter coldest days for two pairs of ST and MA curves ($r = 0.7$ and $r = 0.8$, correspondently, $p < 0.0001$, Table 2).

Regarding lynxes, Fig. 3A and B, and Table 1 show that ST both in fall season (when air temperature rises up to $12\text{ }^{\circ}\text{C}$) and in cold season (when it falls down to $-20\text{ }^{\circ}\text{C}$) undergoes clear rhythmic circadian oscillations with an amplitude about $1.5\text{--}3\text{ }^{\circ}\text{C}$. However, on the warmest autumn day this rhythm weakly correlates with a time-course of MA, though on the coldest winter day they correlate highly ($r = 0.77$, $p < 0.0001$, Table 2). On the warmest day, ST fluctuates around a “set point” of $36.8\text{ }^{\circ}\text{C}$, and in the coldest day—around $35.1\text{ }^{\circ}\text{C}$, $1.7\text{ }^{\circ}\text{C}$ lower. The average MA level is almost two times higher in the cold winter period than in the warm autumn period (Table 1). Maximum of both rhythms occur in the middle of the day, and minimum—in the middle of the night. Interestingly, during the coldest day there is a high inverse correlation between fluctuations in external and internal temperatures ($r = -0.73$, $p < 0.001$). That is, the lower ambient hourly temperature is, the higher is circadian ST response of the animals. The latter, in its turn, follows the circadian MA time-course (Table 2). All these oscillations occurred synchronously and in phase in all three lynxes.

As can be seen from Fig. 4A and B, and Tables 1 and 2, in sables ST fluctuates irregularly in the autumn period and in winter. At the same time, MA mean level does not increase in winter and even decreases. There is a high correlation between ST and MA curves, both in the warmest autumn and the coldest winter days ($0.7 < r < 0.8$, Table 2). Despite this, no clear circadian patterns were observed: bursts of MA and subsequent rises in ST could occur at any time of the day or the night. However, on the warmest day, most periods of MA rising were observed mainly at night and in the morning, and on the coldest day—immediately after sunset.

Ferrets do not demonstrate any circadian fluctuations in ST and MA (Fig. 5A and B, Tables 1 and 2). Their ST rises with every increase in MA independently of light–dark period and time of the day. In the autumn warmest day activity bursts mostly appear in the dark period, but in the winter coldest day this relation is absent. Both ST and MA curves correlate on the warmest autumn day ($r = 0.65$, $p < 0.0001$, Table 2) but this correlation disappeared on the coldest winter day.

Table 2 The ST and MA mean values during warmest ($T_{\max} = 12\text{ }^{\circ}\text{C}$) and coldest days ($T_{\min} = -20\text{ }^{\circ}\text{C}$)

Subject	The warmest day ($12\text{ }^{\circ}\text{C}$)						The coldest day ($-20\text{ }^{\circ}\text{C}$)								
	MA			r			ST			MA			r		
	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median
Amur cats	35.5	36.5	36.1	0.033	0.178	0.089	< 0.5	33.3	36.7	34.9	0.041	0.130	0.071	< 0.2	
Domestic cats	36.2	38.0	36.8	0.040	0.097	0.062	0.73*	34.4	38.2	35.0	0.042	0.155	0.067	0.83*	
Lynxes	35.5	38.0	36.7	0.016	0.307	0.094	< 0.5	33.2	36.7	35.1	0.026	0.271	0.120	0.77*	
Sables	34.6	38.4	36.7	0.026	0.688	0.188	0.78*	31.1	36.4	33.7	0.005	0.864	0.115	0.75*	
Ferrets	36.0	38.0	36.7	0.026	0.401	0.089	0.65*	33.0	36.5	34.8	0.016	0.287	0.088	< 0.3	

*p < 0.0001

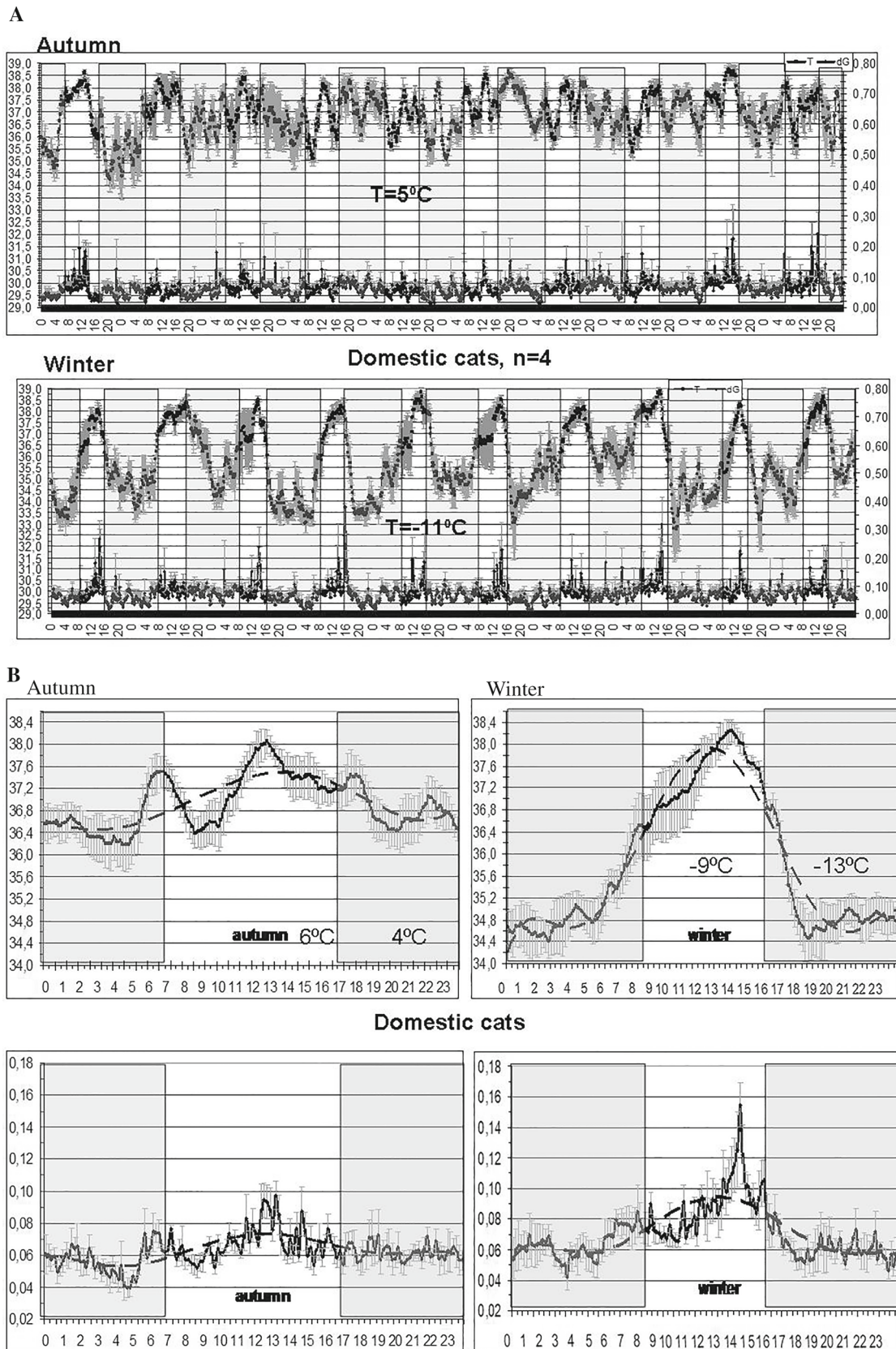


Fig. 2 **A** Domestic cats ($M \pm$ S.E.M., $n = 4$). Left ordinate, ST ($10\text{ }^\circ\text{C}/\text{scale}$). Right ordinate, MA ($0.8\text{ dG}/\text{scale}$). Other designations, as in Fig. 1A. **B** Ordinate axes, top: ST ($4.4\text{ }^\circ\text{C}/\text{scale}$), bottom: MA ($0.16\text{ dG}/\text{scale}$). $M \pm$ S.E.M., $n = 4$. Other designations, as in Fig. 1B

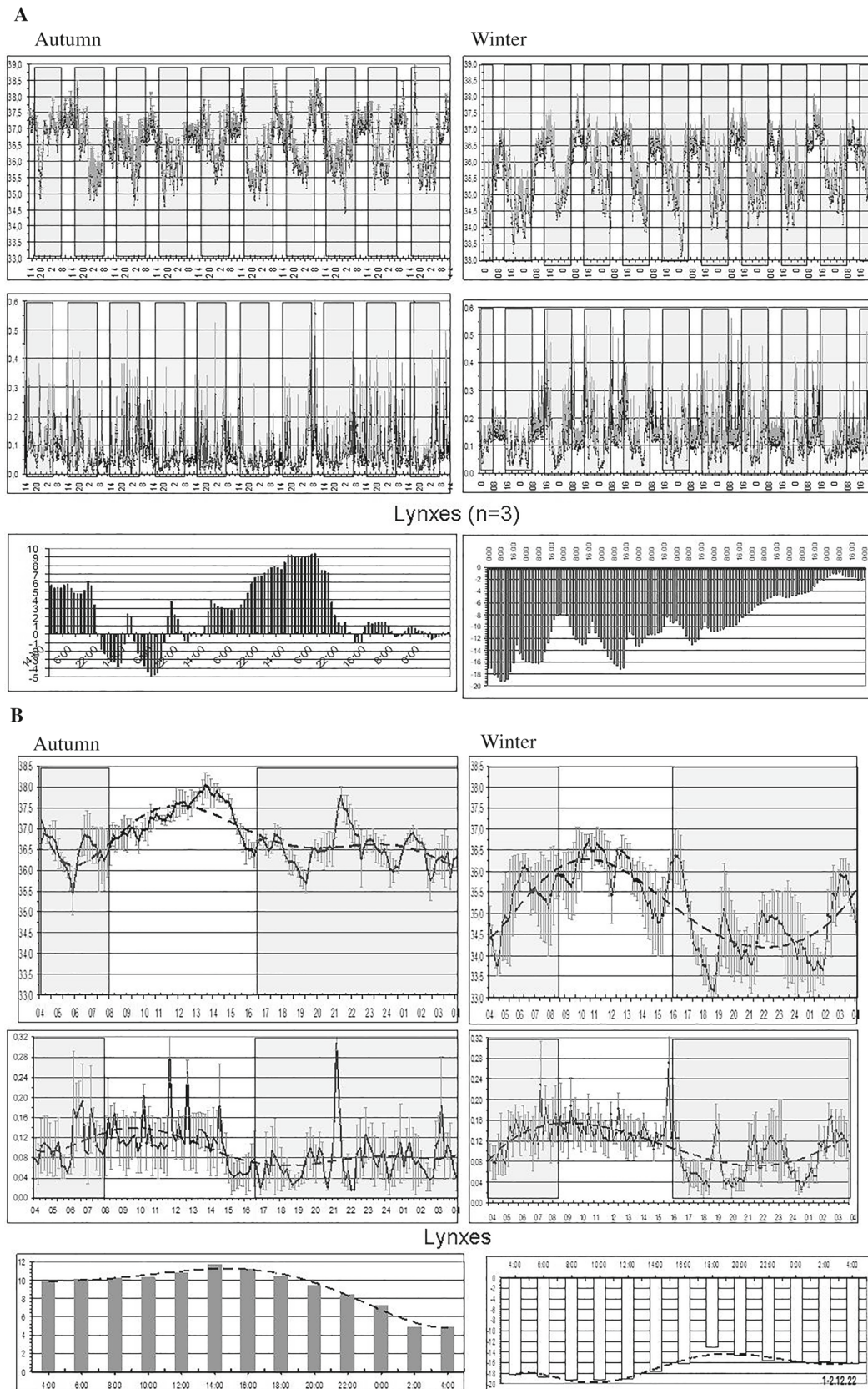


Fig. 3 **A** Lynxes ($M \pm S.E.M.$, $n = 3$). Top graph, ST (6° /scale); middle graph, MA (0.6 dG/scale); Bottom graph, air temperatures. Other designations, as in Fig. 1A. **B** Top graphs, ST (6.5° /scale); middle graphs, MA (0.32 dG/scale); bottom graphs, air temperatures. Other designations, as in Fig. 1B

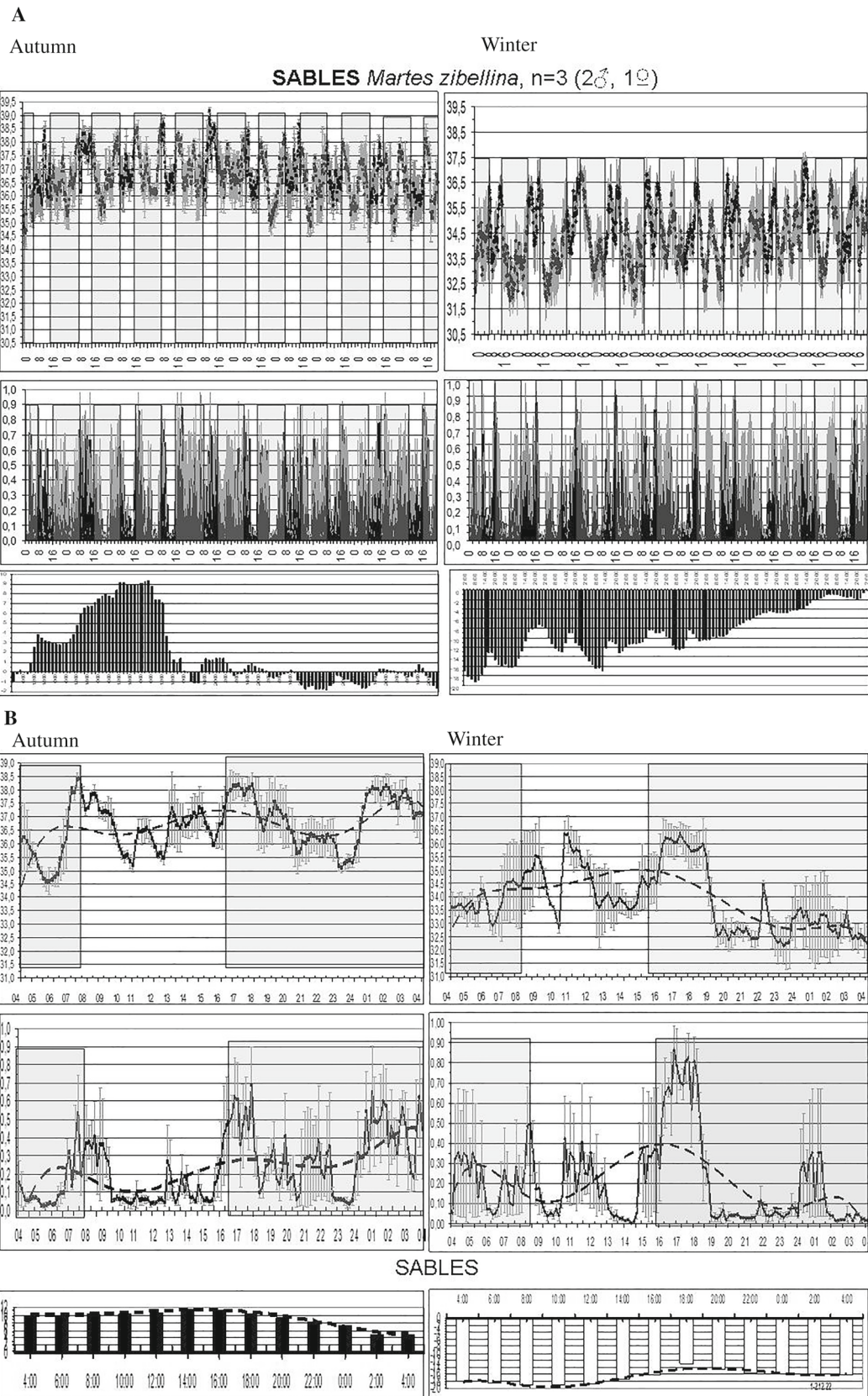


Fig. 4 **A** Sables ($M \pm S.E.M.$, $n = 3$). Top graph, ST (9° /scale); middle graph, MA (1 dG/scale); Bottom graph, air temperatures. Other designations, as in Fig. 1A. **B** Top graphs, ST (8° /scale); middle graphs, MA (1 dG/scale); Bottom graph, air temperatures. Other designations, as in Fig. 1B

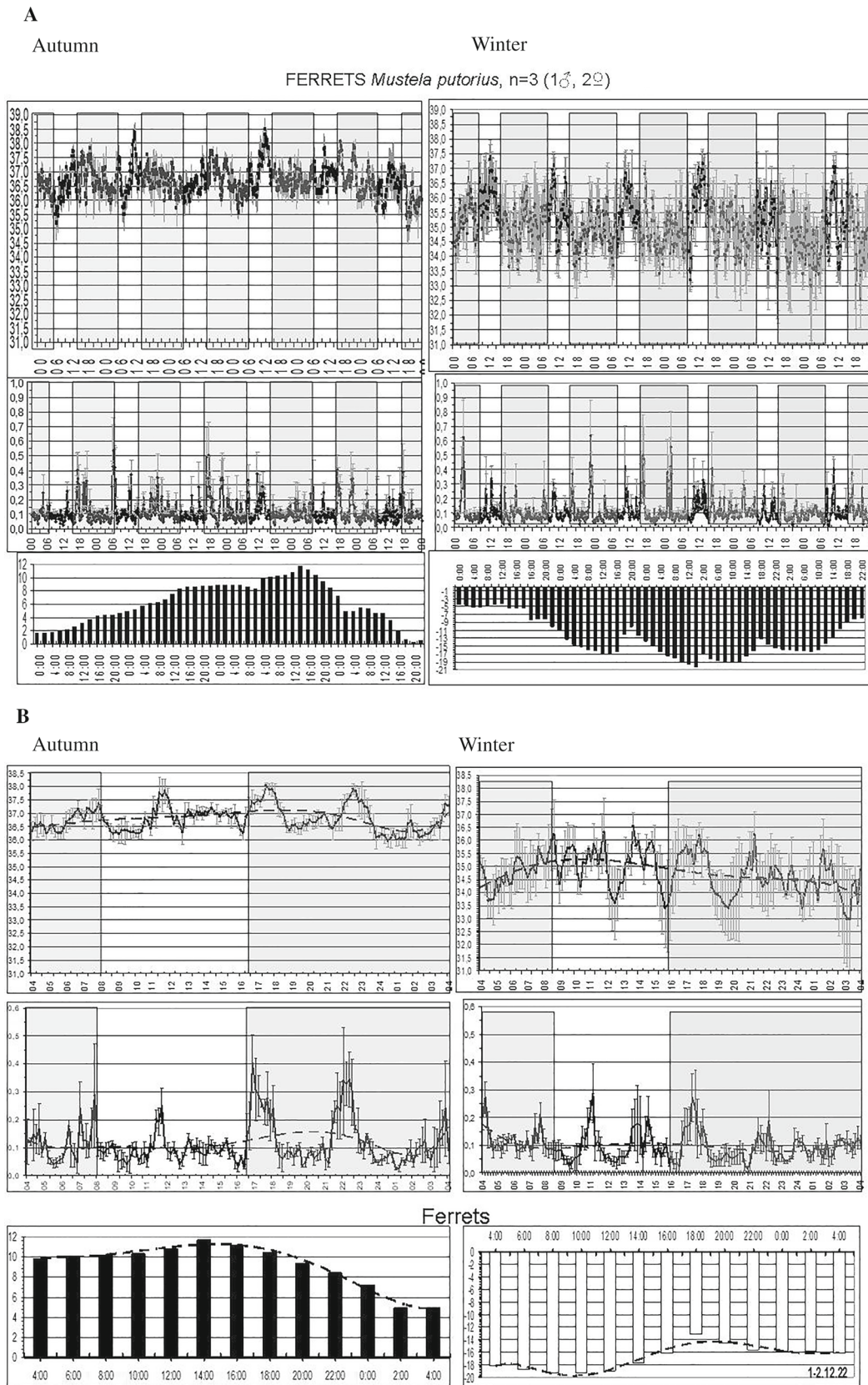


Fig. 5 **A** Ferrets ($M \pm S.E.M.$, $n = 3$). Top graph, ST ($8^\circ/\text{scale}$); middle graph, MA (1 dG/scale); Bottom graph, air temperatures. Other designations, as in Fig. 1A. **B** Top graphs, ST ($7.5^\circ/\text{scale}$); middle graphs, MA (0.6 dG/scale); bottom graphs, air temperatures. Other designations, as in Fig. 1B

4 Discussion

Circadian rhythms of activity and body temperature are influenced by several external factors, including ambient temperature and light [5, 6]. However, seasonal studies of rest-activity and body temperature rhythms were carried out only in representatives of several domestic and wild mammalian and avian species: in sheep [7], horse [8], the giant African rat [9], wolverine [10], oryx antelope [11], ostriches [12], cats [1–3, 13] and camels [14].

As can be seen from this study, carnivorous mammals, even closely related species (domestic and Amur cats), demonstrate different responses to winter cold. These differences are obviously related to differences in the ecology of the species studied. The Far Eastern forest (Amur) cat is a northern subspecies of the Bengal cat. This little-studied wild species has a number of interesting ecological and physiological adaptations that allow it to withstand long and frosty winters, although this animal does not have the ability to move through loose snow and cannot hunt during this season [15–18]. In Far Eastern forest (Amur) and domestic cats, circadian biorhythms MA and ST are not constant characteristics, but can appear, disappear and radically change with fluctuations in ambient temperature [13]. At positive ambient temperatures, the circadian rhythm of ST in Far Eastern cats is completely absent. However, at negative ambient temperatures, Amur cats experience rhythmic oscillations in ST. At the same time, the synchronicity and in-phase nature of the emerging biorhythms in all animals indicate that they are entrained by a certain external pacemaker(s). Judging by the data we received, such pacemakers are daily fluctuations of external temperature and alternation of day and night. It is obvious that with the onset of frosty weather, an animal living in an enclosure is forced to adapt, maintaining a relative constancy of the temperature of the “core” of the body. To do this, the animal extremely reduces heat dissipation, diminishing peripheral blood flow, which is reflected in the dynamics of ST. These cyclical oscillations, in turn, reflect the ambient air temperature shifts (maximum in the afternoon and minimum in early morning hours). As for physical activity, Far Eastern forest cats, which have accumulated a thick subcutaneous fat layer by winter, do not demonstrate any need for additional muscle warming. Their MA in general is not higher in winter, but even lower, than in autumn.

The rise of ST in the back is associated with the influx of hot blood from the depot due to local vasodilation [19]. This vasodilation reflects a decrease in sympathetic tone and is usually associated with blood inflow also to the extremities [20]. Since in the cold season MA of Amur cats does not increase, but even decreases, it can be assumed that circadian peripheral vasodilatation is associated with the release of thyroid hormones, which begins around midnight [21]. Such regime, with a daily single peripheral heating and subsequent passive cooling, apparently allows an animal, in conditions of inactivity, to maintain thermoregulation throughout the winter with minimal energy expenditure.

As for domestic cats living in the same conditions as wild Far Eastern cats, then, judging by our data, a powerful circadian rise in ST in the cold season is most likely associated with both factors: a small surge in the MA level and release of thyroid hormones. Domestic cats in winter do not need to hunt or look for a shelter: they always find food and shelter from humans.

It is interesting to compare the data we obtained in domestic cats living in forest enclosures with the results of studying Australian feral cats [1–3]. As Hilmer et al. have shown, these animals living in the wild surrounding demonstrate clear rhythms of behavioral activity and body temperature. Both rhythms demonstrate an acrophase in the middle of the night and a bathyphase in the middle of the day. However, after capture, as they stayed in enclosures, both rhythms gradually smoothed out within several months and changed to antiphase, with an acrophase in the middle of the day and a bathyphase in the middle of the night, which is more consistent with the data presented in this and our previous [13] reports. Thus, one can come to the conclusion that captivity conditions are the third factor (in addition to the day/night alternation and ambient temperature fluctuations) that can dramatically influence circadian rhythms of rest-activity and body temperature, at least in felids.

It is well known that Eurasian lynx is a wild cat with a special ecology and physiology [22]. In our lynxes living in captivity, the circadian rhythm of ST with a rise in the light and a decline in the dark periods of the day is clearly expressed in both autumn and winter. However, the detailed analysis shows that the fall and the winter rhythms are similar but not identical. The autumn “set point” is 36.6 °C, and the winter one is 35.8 °C. MA level in winter is almost 2 times higher than in autumn. ST reliably correlates with the correspondent fluctuations in MA only in the cold season ($r = 0.77$, $p < 0.0001$; Table 2). It is known that, in the wild, lynxes are not afraid of loose snow and hunt intensively all the winter [22]. Video recording of the behavior of lynxes, carried out by us, shows that they do not seem to “feel” the cold: at an air temperature of -20 °C they can lie in the snow outside the shelter house and, perhaps, even sleep. In nature environment, they are mostly active in crepuscular or dark periods of the nycthemeron [23, 24]. The high correlation of the MA and ST curves and the high inverse correlation of both curves with the dynamics of external temperature in winter indicate that in captivity the resistance of lynxes to cold is apparently associated mainly with an increase in behavioral activity.

In sables, both processes—ST and MA—are closely related to each other in both autumn and winter, but do not demonstrate a clear association either with the light–dark cycle or external temperature fluctuations. It is known that the behavior of the sable is not connected in any particular way with the alternation of seasons as well as light and dark periods of the day: the sable can be active and hunt at any season and any time [25, 26].

Under natural conditions, the forest ferret (*furo*) is considered a nocturnal animal [27]. However, in our studies, when kept in spacious forested area enclosures, only a slight predominance of nocturnal activity in the autumn period and crepuscular activity in the winter are noted. It was found in the ferret that ST is a good index of the core temperature [28, 29]. In ferrets, ST and MA also do not show a circadian relationship, but statistical analysis reveals a connection between both curves only in the warm autumn period. The weakly expressed nature of the circadian rhythm of rest-activity in the European ferret (*Mustela furo*), in contrast to the pronounced rhythm in the golden hamster (*Mesocricetus auratus*), was previously pointed out by other authors [30].

Our previous study of the dynamics of “core” body temperature (abdominal cavity) in combination with MA in these small predators—sables and ferrets—in the autumn also showed that their circadian rhythm is weakly expressed and less dependent on the light cycle [31]. In this series, the autumn circadian curves of ferrets show a slight predominance of nocturnal activity, while sables demonstrate more of an evening activity. There was practically no correlation between autumn core body temperature and MA native curves of sables and ferrets. However, a detailed analysis of the entire autumn recording period using the exponential smoothing method made it possible to identify the internal periodicity of circadian curves with the main acrophase at about 8PM. A high correlation of both pairs of smoothed circadian curves ($0.7 < r < 0.8$) was also revealed.

Thus, the present study demonstrates for the first time three types of responses to winter cold in five species of carnivores in captive surrounding: (1) a circadian rise in ST which is not associated with an increase in MA (Amur cats); (2) a circadian rise in ST which correlates with a correspondent increase in MA (lynxes, domestic cats); (3) rises in ST which correlate with increases in MA, but are not circadian (sables, ferrets).

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Author contribution

Conceptualization VMK, SVN, VVR; data curation MNE, GSA, KAV, ADK, VMK; formal analysis VMK, ADK; investigation MNE, KAV, ADK, SVN; methodology VMK, ADK; supervision VMK, SVN, VVR; writing—original draft VMK; writing—review and editing MNE, GSA, KAV, SVN, VVR.

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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