[Frontiers in Bioscience 8, s258-264, May 1, 2003]

THERMAL CHRONOBIOLOGY OF DOMESTIC ANIMALS

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1. ABSTRACT

This article reviews the literature on the circadian and estrous rhythms of body temperature in farm animals. Although most research in this area has lacked the methodological sophistication of research conducted on laboratory animals, the experimental results are consistent with the general principles of thermal chronobiology derived from laboratory studies and, at the same time, provide specific information about the peculiarities of livestock species. Detailed knowledge of the normal parameters of the body temperature rhythms is important for the advancement of diagnostic procedures in veterinary medicine and for the optimization of farm yield in the dairy and meat industry.

2. INTRODUCTION

Biological rhythms have been extensively studied in plants and animals. Two classes of rhythms that have received considerable attention in animal research are those related to the nycthemeron (circadian rhythmicity) and those related to the reproductive cycle (estrous rhythmicity). Circadian and estrous rhythmicities have been demonstrated in a variety of physiological and behavioral variables in a variety of species (1,2). Rhythmicity in core body temperature has been extensively studied in humans and laboratory animals but much less in farm animals (3,4). The purpose of this article is to review the sparse but growing literature on the thermal chronobiology of livestock and to highlight the importance of further research in this field.

Body temperature is an important variable to be studied for many reasons (5). First, the homeostatic regulation of body temperature is a fundamental physiological process that ensures the stability of the internal milieu in birds and mammals. Second, the thermoregulatory system is an encompassing system that utilizes behavioral and autonomic processes in integration with other physiological systems, such as the respiratory system (for panting in several species of birds and mammals), the digestive system (for salivary discharge and grooming in rodents), the cardiovascular system (for control of heat loss through peripheral vasodilation and vasoconstriction), and the motor system (for thermogenesis through shivering in striated muscles). Third, the regulation of body temperature is an essential component of the process of fever, which plays an important role in an organism's response to infection and disease. Fourth, manipulation of body temperature is a standard procedure in various surgical and therapeutic procedures (such as hyperthermia in the treatment of cancer or hypothermia during organ transplant).

More specifically, the rhythmicity of body temperature is an important process to be studied not only to advance knowledge on the temporal variability of thermal homeostasis but also as a means to facilitate the study of biological rhythmicity in general. Because of the relative ease of monitoring body temperature (as compared to monitoring gaseous exchange or blood hormone levels), and because of the robustness of the rhythm of body temperature, the rhythmicity of body temperature has been widely used as an indicator of the rhythmicity of the biological clock (6,7). Future advances in the study of thermal chronobiology in livestock will not only provide greater understanding of general chronobiological processes in birds and mammals but will also generate essential knowledge for the enhancement of veterinary medicine and optimization of the dairy and meat industry.

3. DAILY RHYTHMICITY

Daily or circadian rhythmicity of body temperature in animals maintained under a synchronizing light-dark cycle is characterized by four parameters (8,9): the mean level around which body temperature oscillates,

Table 1. Values of the parameters of the core body temperature rhythm in the published literature

Species	Mean Level (°C)	Range of Excursion (°C)	Acrophase (hours after sunrise)	Source
Goat	38.6	0.6	10	12
	38.7	1.9	12	11
	38.9	0.7	14	10
	38.9	1.0	9	53
	39.0	0.4	16	23
Sheep	39.0	0.9	12	54
	39.3	0.3	14	23
	39.3	0.6		14
	39.4	1.2	10	15
	39.6	0.8		55
	40.4	0.8	9	16
Pig	37.6	0.9	12	24
	38.8	0.4		25
	39.4	0.4	12	56
	39.7			57
	39.8			58
	40.1			59
Horse	37.7			60
	38.0			61
	38.0	0.4	15	62
	38.3	1.0	14	26
	38.4			63
Cattle	38.6	1.8	10	55
	38.8	0.8	16	64
	38.9			65
	38.9	1.0		27
	39.1	1.2	10	66
	39.2			67
Chicken	39.8	1.0	9	68
	40.2	1.4	6	51
	40.8	0.9	11	50
	41.0	0.7		29
	41.0	0.7	11	28
	41.0	1.3	10	40
Turkey	40.2	1.0	12	34
	40.8			39
	41.0			69

the range of excursion of the oscillation, the phase of the oscillation in relation to the light-dark cycle (with the time of the daily peak being referred to as the acrophase), and the detailed profile of the oscillation (the wave form). The latter parameter (wave form) has not been systematically studied in laboratory animals, much less in farm animals, and will not be discussed here. A compilation of data on the other three parameters is presented in table 1.

At least five studies of the core body temperature rhythm of the goat (*Capra hircus*) have been conducted. A sample of data from one of these studies is shown in figure 1. Visual inspection reveals a robust daily rhythm with an ascent phase during the day and a descent phase during the night. In this study (10), the daily peak of the rhythm (acrophase) was consistently reached in the early evening (2 h after sunset, or 14 h after sunrise). As shown in table 1, however, different acrophase values were obtained in other studies, ranging from 9 to 16 h after sunrise. This discrepancy can be partially, though not fully, explained by the fact that different studies employed different photoperiods (i.e., different durations of the light phase of the light-dark cycle), which affects the timing of the acrophase. The average mean level of the temperature rhythm ranged from 38.6 to 39.0 °C in the five studies. This spread of 0.4 °C is surprisingly narrow in view of the fact that in none of the studies was ambient temperature thermostatically controlled. The fact that the mean level of body temperature varied only 0.4 °C in studies conducted under different ambient temperatures, in some cases with large diurnal oscillations, attests to the accuracy of the thermoregulatory system of the goat. Finally, the average daily range of excursion of the temperature rhythm varied from 0.4 to 1.9 °C in the five studies. This relatively large inter-study variability can be attributed mostly to the variability in ambient temperature. Thus, the largest range of excursion (1.9 °C) was obtained in a study where ambient temperature varied more than 20 °C between day and night (11). As a matter of fact, one of the studies found a range of excursion of 0.4 °C when the animals were tested outdoors in the (mild) winter and of 1.1 °C when the animals were tested in the (hot) summer (12). While the use of natural photoperiods and natural variations in ambient temperature may provide a naturalistic research environment, it also prevents the rigorous study of rhythmic parameters that can be achieved in controlled laboratory experiments (13).

Six studies of the body temperature rhythm of the sheep (*Ovis aries*) are included in table 1. Not all studies detected robust rhythmicity, and this is indicated by the absence of acrophase values. In one of the studies, ambient temperature was maintained constant but the animals were fed only once a day (in the morning), and the increased thermogenesis associated with feeding seemed to account for most of the daily variation in body temperature (14). In another study, where ambient temperature oscillated from 10 to 30 °C daily, the oscillation in body temperature seemed to follow the oscillation in ambient temperature (15). However, a relatively robust rhythm of body temperature was observed in the remaining studies, where ambient temperature underwent small diurnal fluctuations. The average mean level of the temperature rhythm ranged from 39.0 to 40.4 °C in the six studies. The highest value in this range may be due to the fact that young lambs, rather than adult sheep, were used as subjects (16). If this value is excluded, the spread of values of the mean level of the temperature rhythm in the remaining five studies is 0.6 °C, which is only slightly larger than the 0.4 °C spread obtained in the studies on goats. The average daily range of excursion in the studies on sheep varied from 0.3 to 1.2 °C. This highest value (1.2 °C) was obtained in the study where ambient temperature oscillated 20 °C daily (15). Finally, the average acrophase ranged from 9 to 14 h after sunrise, even though the duration of the photoperiod was 12 h in all but one study.

A curious phenomenon associated with the body temperature rhythm of the sheep is the circadian modulation of starvation-induced hypothermia. It has long been known that prolonged food deprivation causes a fall in the core body temperature of homeotherms and that, in various species of small birds and mammals (body mass up to 2-3 kg), this hypothermia is modulated by the circadian

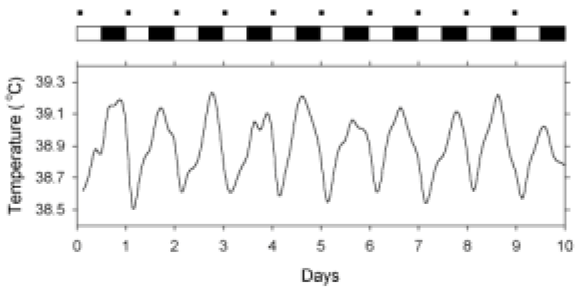

Figure 1. Records of body temperature of a goat maintained under a light-dark cycle for 10 days. The light and dark boxes at the top indicate the duration of the light and dark phases of the light-dark cycle. The small dark squares indicate the times of feeding. A robust daily rhythm can be seen.

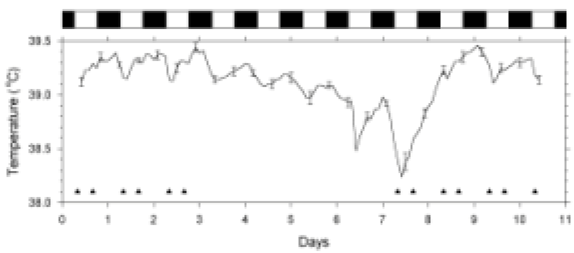

Figure 2. Mean body temperature of 5 sheep recorded over the course of 10 days. Means are plotted in 2-h intervals and connected by straight lines. To prevent cluttering of the figure, standard errors of the mean are plotted only in 10-h intervals. The light and dark boxes at the top indicate the duration of the light and dark phases of the light-dark cycle. The small dark triangles indicate the times of feeding. Starvation-induced hypothermia is evident from days 4 to 8 (with circadian modulation on days 7 and 8).

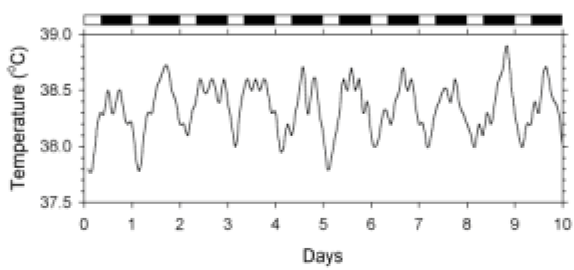

Figure 3. Records of body temperature of a horse maintained under a light-dark cycle for 10 days. The light and dark boxes at the top indicate the duration of the light and dark phases of the light-dark cycle. Food was provided at four equidistant intervals each day. A robust daily rhythm can be seen.

system, in the sense that hypothermia is observed primarily during the inactive phase of the daily activity cycle (i.e., during the night for diurnal animals and during the day for nocturnal animals), whereas relatively normal temperatures are recorded during the active phase (17-22). As shown in figure 2, this phenomenon is observed also in sheep (body mass 40 kg). Although body temperature fell both during the day and the night when food was withheld, a partial circadian modulation of the hypothermic response (indicated by an increase in the daily range of excursion) was observed. Thus, at sunset on the 7th experimental day, mean body temperature fell to 38.5 °C but subsequently rose to 39.0 °C before falling to 38.2 °C on the following morning. Feeding was resumed at this point, and body temperature rose continuously for the next 24 h, resuming the normal daily rhythm on the following day. It should be pointed out that circadian modulation of starvation-induced hypothermia was observed in sheep but not in goats subjected to the same protocol (23).

The third species represented in table 1 is the pig (*Sus scrofa*). We have located only three studies in which measurements of body temperature were conducted often enough to allow a characterization of the daily rhythm. Three other studies are listed in order to provide an estimate of the mean level of the body temperature rhythm (in these studies, body temperature was measured at a single time point during the day). The mean level in the six studies ranged from 37.6 to 40.1 °C. The higher values in the three non-circadian studies are probably due to the fact that temperature was measured only during the day, when higher values are expected than during the night (and, consequently, higher than the average for the full circadian cycle). However, the lowest value (37.6 °C) was obtained in animals of a miniature breed (Vietnamese potbellied) whose mean level of body temperature may not be comparable to that of larger breeds (24). This leaves us with only two studies, in which the mean level was found to be either 38.8 or 39.4 °C. Clearly, more studies in pigs are needed. This is especially true because one of the latter two studies found no evidence for the existence of a daily rhythm of body temperature except for a transient elevation in temperature due to feeding (25). In contrast, studies in humans and laboratory animals have provided strong evidence that the body temperature rhythm exists independently of rhythms in activity or food intake (3,4).

The next species represented in table 1 is the horse (*Equus caballus*). We have located only two studies in which measurements of body temperature were conducted often enough to allow a characterization of the daily rhythm. Three other studies are listed in order to provide an estimate of the mean level of the body temperature rhythm. The mean level in the five studies ranged from 37.7 to 38.4 °C, which is not too large of a spread, especially in view of the differences in recording procedures. The daily range of excursion was found to be 0.4 °C in one study and 1.0 °C in the other. A greater concordance was obtained regarding the acrophase, which was found to be reached at night in both studies (14 or 15 h after sunrise). A sample of data from one of the studies (26) is shown in figure 3.

Six studies on cattle (*Bos taurus*) are included in table 1, although only four of them attempted to determine the presence of daily rhythmicity. The values of the mean level of the rhythm are relatively consistent, ranging from 38.6 to 39.2 °C. The values of the daily range of oscillation go from 0.8 to 1.8 °C. In one of the studies, high frequency oscillations in body temperature were quite large and

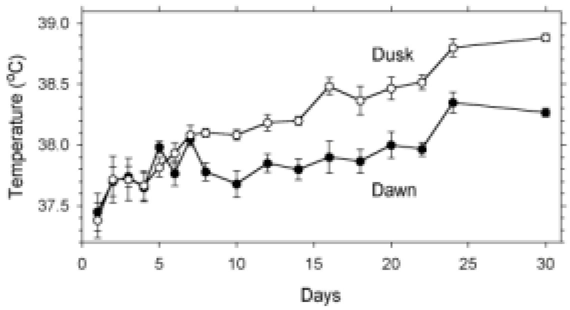

Figure 4. Mean (± SE) rectal temperature of 6 newborn foals recorded 1 h before dusk and 1 h before dawn for 30 days after birth (ambient temperature: 17 °C). The control of body temperature clearly changes during the first month of life.

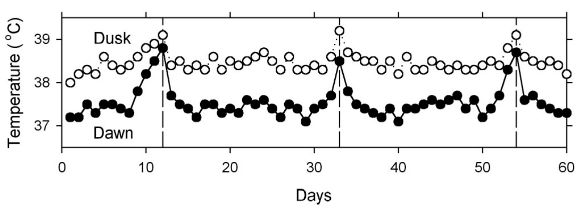

Figure 5. Records of body temperature of a cow as measured at dawn and dusk over two months. Vertical dashed lines indicate days of estrous as determined by vaginal mucous discharge. A clear elevation in body temperature during estrous is seen.

prevented the identification of a daily rhythm (27). Three of the studies found robust daily rhythms, although the acrophases varied from the late afternoon (10 h after sunrise) to the middle of the night (16 h after sunrise).

At least six studies of the core body temperature rhythm of the chicken (*Gallus domesticus*) have been conducted. In this species, daily rhythmicity is often confounded by estrous rhythmicity in females (see next section). In two studies, the elevation in body temperature that accompanies oviposition prevented the identification of circadian rhythmicity (28,29). In the other four studies, daily rhythmicity was observed, especially in males, and higher temperatures occurred during the day. A 7^{th} study not listed on table 1 also found robust daily rhythmicity, but the use of uncalibrated temperature sensors prevented the determination of absolute temperature values (30). In the six studies with calibrated sensors, the mean level of the temperature rhythm ranged from 39.8 to 41.0 °C. This wide spread cannot be consistently accounted for by differences in experimental procedures, and it should be pointed out that other studies using only one temperature measurement per day found values consistently higher than 41.0 °C (31-33). A wide spread was also obtained for the daily range of excursion, which ranged from 0.7 to 1.4 °C. Although the acrophase values also varied considerably (range: 6 to 11 h after sunrise), they were all restricted to the light phase of the light-dark cycle.

The last species listed on table 1 is the turkey (*Meleagris gallopavo*). We are aware of only one study that investigated the daily rhythm of body temperature in this species (34). It found the mean level to be 40.2 °C, the range of excursion to be 1.0 °C, and the acrophase to be 12 hours after sunrise.

Some additional information about the body temperature rhythm that is not shown in table 1 has to do with the development of rhythmicity in young animals. As shown in figure 4, the control of body temperature in foals improves during the first month of life (37). The mean level of body temperature is lower right after birth (37.4 °C), and no daily rhythmicity is observed (as indicated by the lack of difference between measurements taken at dusk and dawn). A dusk-dawn difference is noticeable at the beginning of the second week of life, although the mean level continues to ascend until the end of the third or fourth week.

In lambs, one study found that the adult mean level of body temperature (39.4 °C) is achieved already during the first week of life, although it is relatively labile until one or two months of age (38). Another study found that temperature at dawn is at the adult level right after birth but temperature at dusk does not achieve the adult level until the third week of life (37). In calves, daily rhythmicity of body temperature was observed as early as during the first or second week of life (39). In turkeys, the adult level of body temperature was observed during the first week of life (40).

4. ESTROUS RHYTHMICITY

Much is known about the oscillation in body temperature associated with the reproductive cycle in laboratory animals and humans. In humans, this knowledge is routinely used for contraceptive purposes and for the treatment of infertility (35,36). Several studies have been conducted on the estrous rhythm of body temperature in farm animals, mostly in cattle and chicken. A sample of data from our own study in cows is shown in figure 5. There is a clear elevation in body temperature (both at dawn and dusk) around the time of estrus.

In cows, the estrous cycle lasts 21 to 25 days and involves oscillations in both activity and body temperature (41,42). A rise in body temperature of 0.2 to 0.6 °C is observed on the day of estrous (41-46), although different studies describe this rise as lasting only a few hours (42,44,46) or through the whole luteal phase (41,43). The use of body temperature records to predict ovulation (as measured by ultrasonography or blood progesterone levels) has a detection rate of 80-87% and a false positive rate of 10-17% (42,44,46).

Chicken are peculiar in that the duration of their circadian cycle is very similar to the duration of their estrous cycle. In studies where the two rhythms could be distinguished, the estrous rhythm of body temperature was found be a few hours longer than the circadian rhythm of body temperature. That is, an elevation in body temperature associated with oviposition (with a period of 25 to 28 h) was superimposed on the circadian oscillation

(28,29,47). In one of these studies, the oviposition component was found to be responsible for temperature oscillation in the order of 0.8 °C, whereas the circadian component was responsible for oscillation in the order of 1.3 °C (47).

5. ENDOGENOUS AND EXOGENOUS DETERMINANTS

In laboratory animals, it is well established that circadian rhythms are generated by an endogenous pacemaker and modulated by environmental factors, principally the light-dark cycle (48,49). Presumably, this is also true for farm animals, although little research has been conducted on it. In order to provide reliable inferences about the functional characteristics of the circadian pacemaker, such as its free-running period, studies must be conducted under strict experimental conditions (50), which has rarely been done in farm animals. At a minimum, animals must be kept under a constant photic environment that does not provide temporal cues. Although constant light does not generate an external synchronizing signal, it does affect the expression of the endogenous period, which means that studies must be conducted in constant darkness. In addition, ambient temperature must not exhibit daily oscillation, and feeding must be equally spaced throughout the circadian cycle (or food be provided ad libitum). Also, long intervals of recording are necessary to ensure that the observed period of the rhythm differs significantly from 24.0 h (in principle, the endogenous period could be exactly 24.0 h but, in this case, the researcher would not be able to determine whether an unknown environmental factor is still synchronizing the internal clock).

We are not aware of a single study on the circadian rhythm of body temperature in farm animals that satisfies the requirements outlined above. However, there have been several studies conducted under constant light and under relatively stable conditions of ambient temperature and feeding. In chicken kept under constant light, a clear circadian rhythm of body temperature was observed (47,51,52). The closest estimate of the endogenous free-running period (23.5 h) is provided by a study in which roosters were maintained under dim constant light (52). In turkey hens, a period of 26.7 h was found, but the study was conducted under bright constant light (34). A study in lambs obtained evidence of endogenous rhythmicity in body temperature, although the experimental design did not allow computation of the free-running period (16). A period of 24.2 h was found for horses maintained under bright constant light with four equally-spaced feedings per day (26).

The fact that animals of these various species exhibited rhythms synchronized (entrained) to the light-dark cycle before being placed under constant light indicates that light is a powerful entraining agent of circadian rhythms in farm animals, as it is in laboratory animals. Although feeding was found to mask the expression of the temperature rhythm in some studies in farm animals, only one study attempted to investigate the role of feeding as an entraining agent. Evidence was obtained that feeding time can entrain the body temperature rhythm of the goat, although the results were not fully conclusive (10).

The endogenous component of the estrous rhythm is assumed to be the maturation cycle of ovarian follicles. Consistent with this assumption, surgical removal of the post-ovulatory follicle eliminated the rise in body temperature in chicken, even though oviposition did occur (28).

6. SUMMARY AND PERSPECTIVE

Relatively little research has been conducted on the body temperature rhythms of farm animals. Based on the available data, it can be stated that, in a stable thermal environment, the daily rhythm of the goat has a mean level of 38.8 °C, a range of excursion of 0.7 °C, and an acrophase of 12 h after sunrise. The mean level of the daily rhythm of the sheep is significantly higher (39.5 °C), but its range of excursion (0.8 °C) and acrophase (11 h) are comparable. The parameters of the daily rhythm of the pig are very similar to those of the sheep (39.5 °C, 0.6 °C, and 12 h, respectively). In the horse, the mean level of the temperature rhythm is lower than in the other three species, the range of excursion is comparable, and the acrophase is slightly delayed (38.1 °C, 0.7 °C, and 14 h, respectively). In cattle, the mean level is similar to that of the goat (38.9 °C), the range of excursion is considerably wider (1.2 °C), and the acrophase is equivalent (12 h). The mean level of the temperature rhythm is significantly higher in chicken and turkey (40.6 °C) than in the mammalian species, whereas the range of excursion (1.0 °C) is comparable. The acrophase seems to be much earlier in chicken (9 h after sunrise) than in turkey (12 h). Although the development of the daily rhythm of body temperature during early life seems to proceed at different rates in different species, adult pattern are usually not attained until 3 to 4 weeks after birth. In some of the species, the endogenous origin of the rhythm in adults has been demonstrated.

Estrous rhythmicity in the body temperature rhythm of farm animals has been studied almost exclusively in cattle and chicken. An elevation in body temperature on or around the day of estrus (cycle period of 21-25 days) has been consistently observed. In chicken, a daily elevation in body temperature associated with oviposition (with a period of 25 to 28 h) is superimposed on the circadian oscillation (with period of 24 h under entrained conditions).

These results are consistent with the general principles of thermal chronobiology derived from the study of laboratory animals but also provide specific information about the peculiarities of livestock species. Awareness of the normal parameters of the body temperature rhythms is important in diagnostic procedures in veterinary medicine and in the optimization of growth rate in the dairy and meat industry. The potential applicability of this awareness is, of course, contingent on the acquisition of greater empirical knowledge to be attained through further research.

It is understandable that some research will continue to be conducted under natural conditions, which are representative of actual farming practices. However, greater understanding of fundamental processes in the thermal chronobiology of livestock will require controlled experiments similar to those conducted with laboratory animals. Refinements in reasearch procedures are important not as a mere academic exercise but as a source of improvement in farming practices. Although the study of physiological processes under current farming practices may have immediate applicability, it does not provide the advancement in knowledge of fundamental processes that is necessary for the development of new, more efficient practices. Thus, we feel that efforts in the immediate future should concentrate on rigorously-controlled studies, where ambient temperature, illumination, and feeding schedule are determined by research goals rather than by farming practices. Solid knowledge of basic physiological processes at the whole-organism level is essential if the industry is to benefit from the advances in genomics and proteomics that have been made in recent years and are certain to continue throughout the 21st century.

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Key Words: Body temperature, Circadian rhythm, Estrous cycle, Farm animal, Livestock, Review

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