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The circadian rhythm of body temperature

Roberto Refinetti[1]

[1] *Circadian Rhythm Laboratory, University of South Carolina, 807 Hampton Street, Walterboro, SC 29488, USA*

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1. ABSTRACT

This article reviews the literature on the circadian rhythm of body temperature. It starts with a description of the typical pattern of oscillation under standard laboratory conditions, with consideration being given to intra- and interspecies differences. It then addresses the influence of environmental factors (principally ambient temperature and food availability) and biological factors (including locomotor activity, maturation and aging, body size, and reproductive state). A discussion of the interplay of rhythmicity and homeostasis (including both regulatory and heat-exchange processes) is followed by concluding remarks.

2. INTRODUCTION

Repeated measurements of body temperature over time -- allowing the study of 24-hour rhythmicity -- have been conducted in animals and human subjects since at least the mid-1800s (1-6). A few literature reviews, often with limited scopes, have been published occasionally in the last quarter of a century (7-10). The topic is important for at least two reasons: 1) the body temperature rhythm is a convenient marker of the circadian clock for studies on biological rhythms and sleep, and 2) the rhythm reflects a constant conflict between homeostasis and circadian rhythmicity in the control of core temperature in mammals and birds.

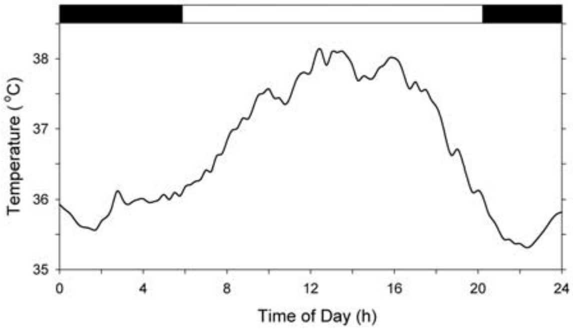

Figure 1. Mean pattern of daily oscillation of intra-abdominal temperature of an Anatolian ground squirrel obtained by averaging data from 10 consecutive days in 15-min intervals. The animal was housed in an individual cage in the laboratory with food freely available. The horizontal rectangles denote the dark and light phases of the prevailing light-dark cycle. Data from Gur, Refinetti, and Gur, 2008 (18).

This review will start with the description of daily rhythmicity of body temperature in organisms kept under standard laboratory conditions, which usually include: 1) a daily light-dark cycle with 12 hours of light and 12 hours of darkness, 2) constant, neutral ambient temperature, and 3) food and water freely available at all times. Attention will be given to similarities and differences between species and between individuals of the same species.

The influence of non-cyclic environmental factors on the CRT will be discussed next. The discussion will include variations in ambient temperature and in food availability. The influence of cyclic environmental factors, which can synchronize circadian rhythms including the CRT, will not be discussed here because most studies in this area use outputs of the circadian system other than the CRT.

Afterwards, the influence of biological factors will be discussed. Biological factors include variations in the organism's locomotor activity, natural maturation and aging, variations in body size, and changes in reproductive state. These particular biological factors were selected for discussion primarily because much research has been conducted on them, but also because age, body size, and reproductive state are fundamental properties of organisms.

Next, the relationship between the circadian and homeostatic components of body temperature regulation will be discussed with emphasis on both regulatory and heat-exchange processes. The CRT is the result of an interplay of mechanisms of heat production and heat loss controlled by the circadian system.

A final section will summarize the issues previously discussed and will put them all in perspective.

3. RHYTHMICITY UNDER STANDARD CONDITIONS

The expression "circadian rhythm of body temperature" (CRT) will be used throughout this article, but it is important to point out that the expression lacks technical precision. First, the word "circadian" is used in the non-technical sense equivalent to "cycling every 24 hours." In contrast, those who study circadian rhythms reserve the term "circadian" to a rhythm that has been shown to free-run with a period (cycle length) of 18 to 30 hours in the absence of environmental cycles and to be capable of synchronization by environmental cycles with 24-hour periods (11). Of course, once a species has been shown to exhibit a CRT, it is reasonable to assume the existence of a CRT in all members of the species studied thereafter. It is not that clear, however, whether the demonstration of a CRT in one mouse species, for example, justifies the use of the expression in other mouse species. Most researchers would say that this generalization is not justified. What about different breeds, or different age cohorts, of the same species? Such cases remain debatable, and they highlight the problem at hand. Careful researchers will, of course, always avoid unjustified assumptions.

The second imprecision in the expression "circadian rhythm of body temperature" has to do with the phrase "body temperature." It is traditional usage in thermal physiology to reserve the phrase "body temperature" to an abstract temperature computed as the weighed mean of the temperatures of various parts of the body (12). Yet, most studies of the CRT rely on measurements at a single part of the body, usually the intra-abdominal cavity. This measurement of body "core" temperature is most commonly obtained by means of probes inserted into the intestines through the anus or by means of temperature-sensitive radio-transmitters or digital data loggers surgically implanted in the peritoneal space. In small animals, the stress of handling involved in manual measurement of core temperature can significantly affect the animal's temperature, so that the use of radio transmitters or data loggers is a necessity (13-15).

3.1. Pattern of oscillation

Figure 1 shows a typical, averaged body temperature rhythm. The data were obtained with a digital data logger surgically implanted in the intra-abdominal cavity of an Anatolian ground squirrel (*Spermophilus xanthoprymnus*) prior to the annual hibernation season. In this diurnal animal, temperature is clearly low at night, rises during the day, and falls again at night. The curve is quite smooth because it depicts the average of 10 consecutive days, so that small irregular fluctuations are averaged out.

To the extent that the CRT is a reproducible pattern of oscillation, it can be characterized by parameters that describe "pure" oscillatory phenomena such as sine or cosine functions. As shown in Figure 2, a regular oscillatory process can be characterized by its mesor (mean level), its amplitude (which is approximately half the full range of oscillation), its period (i.e., the duration of the cycle), and its phase (often reported as the position of the peak of the wave, called the acrophase, in relation to an external reference point) (16). Because the CRT is not a pure mathematical function, two other parameters are needed to fully characterize it. One of them is the wave form, which often differs considerably from a sine or

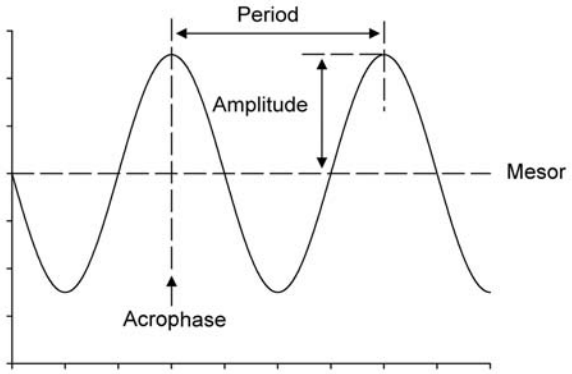

Figure 2. Diagram of an oscillatory process identifying four parameters of the oscillation: mesor, period, amplitude, and acrophase. Wave form and robustness are not explicitly depicted.

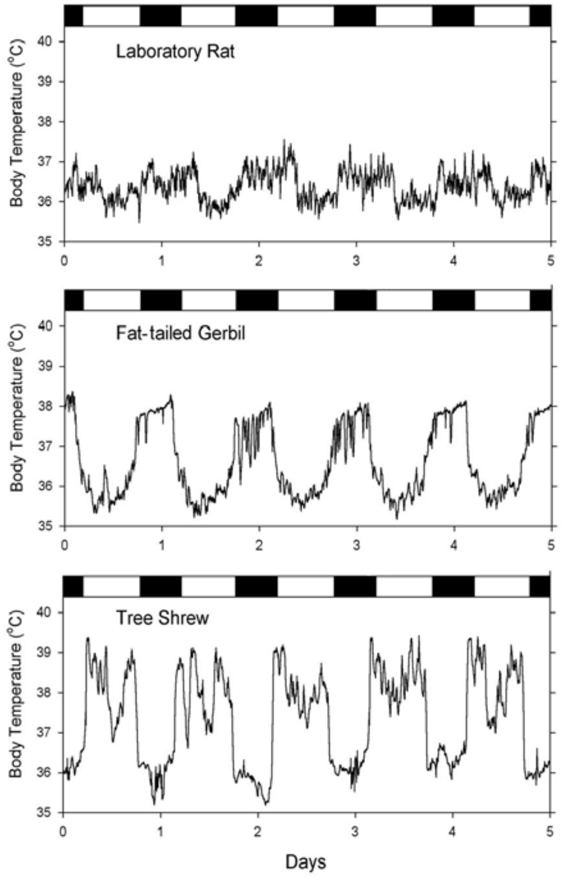

Figure 3. Five-day segments (with 6-minute resolution) of the records of body core temperature of representative individuals of three mammalian species: laboratory rat (*Rattus norvegicus*), fat-tailed gerbil (*Pachyuromys duprasi*), and tree shrew (*Tupaia belangeri*). The data were collected by telemetry in the laboratory. The white and dark horizontal bars at the top indicate the duration of the light and dark phases of the prevailing light-dark cycle. Figure adapted from Refinetti, 1999 (363).

cosine wave and sometimes approximates a square wave. Variations in wave form, which are often affected by but are not solely the result of random variability ("biological noise"), invariably affect the strength and reproducibility of the CRT. The magnitude of this reproducibility (or the degree of "stationarity" of the time series) is the sixth parameter of the CRT, often called the robustness of the rhythm (17).

Although a clear oscillatory pattern is often evident by visual inspection of data plots, sometimes computational tools are necessary for the identification of rhythmicity, particularly when the signal-to-noise ratio is low. Numerical analysis is also needed as a means of securing an objective index of rhythmicity and of characterizing the parameters of the oscillation. Various numerical procedures suitable for the analysis of circadian rhythms have been recently reviewed and compared (16). Analysis of the data in Figure 1 reveals that the oscillation has a mean level of 36.8 ^{O}C, amplitude of 1.2 ^{O}C (range of oscillation of 2.5 ^{O}C), acrophase at 13:05 h, a relatively sinusoidal wave form, and robustness of 60% (18).

3.2. Intra- and interspecies differences

Daily rhythmicity of body temperature has been extensively documented in a variety of species. The laboratory rat (*Rattus norvegicus*) is the species on which the greatest number of studies has been conducted (19-68), but many studies were also conducted on domestic mice (69-86), golden hamsters (87-96), and many other rodent species (97-129). A large number of studies has also been conducted on primates (130-145), including humans (146-184), as well as in dogs (185-188), cats (189-191), goats (192-196), sheep (197-203), horses (203-208), cattle (209-213), other mammals (214-234), and many species of birds (235-252). Although only mammals and birds are true endotherms and have the ability to generate body temperature rhythms in homogeneous thermal environments, other animals are capable of generating body temperature rhythms by selecting different ambient temperatures at different times of the day. Consistent daily variation in the selection of ambient temperature along a temperature gradient has been documented in crustaceans (253-256), fishes (257-261), and reptiles (262-275). At least one reptile -- the green iguana (*Iguana iguana*) -- is capable of generating a small-amplitude rhythm of body temperature even when housed in a homogeneous thermal environment (276, 277). Honey bee colonies, which function as endothermic pseudo-organisms, also exhibit daily rhythmicity of "body" temperature (278).

Figure 3 facilitates the comparison of the CRTs of three rodent species. This figure shows raw data collected every 6 minutes, so that so-called ultradian oscillations can be seen as high-frequency oscillations superimposed on the 24-hour oscillatory pattern. Inspection of Figure 3 clearly indicates that the rhythms of the nocturnal animals (laboratory rat and fat-tailed gerbil) are characterized by higher temperatures during the night, whereas the rhythm of the diurnal animal (tree shrew) is characterized by higher temperatures during the day. Also evident are differences in wave form: square for the rat, rectangular for the gerbil, and bimodal for the tree shrew. In addition, the amplitudes of the rhythms differ among the species: the daily range of oscillation of the temperature rhythm is less than 2 ^{O}C for the rat but more than 4 ^{O}C for the tree shrew. Table 1 lists the mean level, range of oscillation, and acrophase (peak time) of the body temperature rhythms of 67 species of mammals and birds. As will be discussed in detail in section 5.3, the mean level of the CRT tends to be higher by more than 1 ^{O}C in large-sized species than in small-sized ones, although there is considerable inter-species variability. Also, the body temperature of birds tends to be more than 3 ^{O}C higher than that of mammals (on average, 41 ^{O}C and 37.5 ^{O}C, respectively), and the temperature of marsupial mammals tends to be about 3 ^{O}C lower than that of placental mammals. The range of oscillation also varies with body size across species: the range is almost 2 ^{O}C narrower in large species than in small ones -- although, again, there is considerable inter-species variability. As for the acrophase, it usually occurs at night in nocturnal animals and during the day in diurnal animals, but it does not seem to be related to body size, except that few large mammals are nocturnal.

Very few studies have addressed directly the question of whether intraindividual differences (i.e., day-to-day differences in the rhythmic pattern exhibited by an individual of a given species) are comparable to interindividual differences (i.e., differences between the average rhythmic patterns of different individuals of the same species). To the best of the author's knowledge, only three studies have addressed the question, one for the rhythm of melatonin secretion (279), one for the rhythm of cortisol secretion (280), and one for the rhythm of body temperature (206). The results of these studies are consistent with the impression that one acquires by reading studies conducted on various individuals of various species, namely, that the variabilities differ in different parameters of the rhythm and in different species but that -- whenever there is a difference between interindividual variability and intraindividual variability -- the latter is always smaller than the former. That is, the day-to-day variability of an individual's rhythm does not exceed the variability between the rhythms of different individuals. Intraindividual variability is consistently smaller than interindividual variability.

Free-running circadian rhythms of body temperature recorded in controlled environments without external temporal cues have been documented in birds (236, 238-242, 244, 246-248, 250, 281, 282), rodents (21, 32, 41, 50-52, 54, 59, 63, 68, 71, 83, 88, 96, 105, 116, 117, 124, 128, 283, 283-291), primates (130, 131, 134, 138, 139, 143-145, 292, 293), including humans (146, 159, 161, 162, 171, 294-300), and other mammals (189-191, 198, 205, 217, 230, 233, 301-303). While these studies provide sufficient evidence of the endogenous nature of the CRT, they do not necessarily demonstrate that the CRT is directly generated by the circadian clock. In principle, the CRT could be generated by another rhythmic process in the body, this other rhythmic process itself being generated by the circadian clock. The influence of biological factors on the CRT is discussed in section 5 below.

4. INFLUENCE OF ENVIRONMENTAL FACTORS

The environment in which an organism lives can affect its circadian rhythms in two major ways: through entrainment and through masking (304, 305). Entrainment is the synchronization of the endogenous clock by an environmental cycle, which is achieved through modulation of the period and phase of the circadian clock. Cyclic and non-cyclic variations in the environment can also mask a circadian rhythm by disturbing its wave form and thus altering the mesor and amplitude and mimicking alterations in period and phase.

Several decades of research on circadian rhythms have generated a large body of knowledge about entrainment mechanisms. The light-dark cycle is a potent entraining agent that has been thoroughly investigated (304, 306). Cycles of ambient temperature (307, 308) and food availability (309, 310) have also been shown to entrain circadian rhythms. Specific masking effects of ambient temperature and food availability on the CRT will be discussed here -- in sections 4.1 and 4.2, respectively.

4.1. Ambient temperature

Most studies of the CRT are conducted under constant temperature conditions in the laboratory or under uncontrolled conditions in the field, but several laboratory studies have used controlled changes in ambient temperature to address the issue of the effects of different ambient temperatures on the CRT.

Ambient temperatures constantly below or above thermoneutrality have not been found to affect the period or phase of the CRT -- and these negative findings are expected, as circadian period is "temperature compensated" even in ectothermic organisms (308, 311). However, exposure to lower temperatures down to 10 or 15 ^{O}C has been found to increase the amplitude of the CRT, and this increase in amplitude is often accompanied by a reduction in mesor. Greater CRT amplitude in the cold was observed in studies on squirrel monkeys (140), tree shrews (312), thirteen-lined ground squirrels (128), pigeons (238), mousebirds (313), sunbirds (314), and Australian frogmouth birds (315). On the other hand, no effect of ambient temperature on the amplitude of the CRT was found in rats (39, 66, 312), golden hamsters (312), or mouse lemurs (137). Genuine species differences, rather than differences in experimental methods, may be responsible for the conflicting results.

If the increase in the amplitude of the CRT in a cold environment results mostly from lower nadirs (without higher zeniths), it is often referred to as "torpor," a well-known mechanism of energy conservation analogous to seasonal hibernation (316, 317). Torpor may be induced by cold (or the short photoperiod that naturally accompanies the cold of winter) or simply by restricted food availability, as discussed in section 4.2. Daily torpor is controlled by the circadian system (317) and can, therefore, be thought of as

Table 1 Parameters of the CRT of 67 species of mammals and birds, as determined in 160 published studies

Species	**Mean (^{O}C)**	**Range (^{O}C)**	**Acrophase (HALO ^{a})**	**Source**
Acomys russatus	37.1	2.5	18	98
Aethomys namaquensis	36.8	3.9	18	102
Antechinus stuartii	36.5	3.1	19	214
Aotus trivirgatus	37.8	1.4	18	131
Apodemus flavicollis	37.4	1.7	17	103
Apodemus mystacinus	38.4	2.2	17	98
Arvicanthis ansorgei	38.6	3.0	6	68
Arvicanthis niloticus	37.5	2.2	6	105
Arvicanthis niloticus	37.6	1.7	5	106
Bettongia gaimardi	37.4	1.7	22	215
Bos taurus	38.2	0.9	18	211
Bos taurus	38.3	1.4	14	209
Bos taurus	38.7	0.8	10	212
Bos taurus	39.2	0.9	12	210
Bos taurus	39.8	1.0	19	213
Canis familiaris	38.7	0.7	11	188
Canis familiaris	39.1	0.5	11	187
Canis familiaris	39.2	0.4	12	387
Capra hircus	38.5	0.7	13	195
Capra hircus	38.8	1.0	10	192
Capra hircus	38.9	0.7	14	194
Capra hircus	39.0	0.4	16	202
Capra hircus	39.0	0.8	10	196
Cebus albifrons	37.2	2.7	6	132
Columba livia	40.0	2.1	6	235
Columba livia	40.3	2.7	6	338
Columba livia	41.5	1.5	6	236
Coturnix coturnix	41.0	1.3	15	240
Cynomys ludovicianus	37.4	2.5	7	216
Dasypus novemcinctus	35.5	2.6	18	217
Dasyurus viverrinus	36.5	3.6	18	227
Didelphis marsupialis	35.5	2.5	19	218
Didelphis virginiana	35.4	4.0	20	218
Equus caballus	37.4	1.0	12	208
Equus caballus	38.0	0.9	14	207
Equus caballus	38.3	1.0	14	205
Erinaceus europaeus	35.4	1.2	16	219
Eulemur fulvus	38.0	0.9	18	130
Felis catus	37.9	1.3	16	189
Felis catus	38.3	1.0	15	190
Felis catus	38.4	0.5	14	191
Gallus domesticus	40.2	1.1	12	249
Gallus domesticus	40.2	1.5	6	248
Gallus domesticus	40.7	2.2	8	242
Gallus domesticus	40.8	0.8	6	246
Glaucomys volans	37.1	2.1	17	108
Heterocephalus glaber	33.8	3.8	15	220
Homo sapiens	36.5	1.2	10	147
Homo sapiens	36.7	1.1	10	154
Homo sapiens	36.8	0.7	10	172
Homo sapiens	36.8	0.8	8	164
Homo sapiens	36.8	0.8	10	160
Homo sapiens	36.8	1.2	10	162
Homo sapiens	36.9	1.0	9	151
Homo sapiens	36.9	1.2	10	177
Homo sapiens	37.0	0.8	10	169
Homo sapiens	37.0	1.0	8	181
Homo sapiens	37.0	1.0	9	171
Homo sapiens	37.0	1.0	10	495
Homo sapiens	37.0	1.1	10	153
Homo sapiens	37.0	1.2	9	507
Homo sapiens	37.0	1.2	10	159
Homo sapiens	37.0	1.3	10	155
Homo sapiens	37.1	1.0	11	170
Homo sapiens	37.6	1.6	10	163
Isoodon macrouros	36.2	2.5	16	218
Isoodon obesulus	36.5	2.5	13	252

Lasiorhinus latifrons	35.3	2.9	16	221
Macaca fuscata	37.0	2.4	9	133
Macaca mulatta	36.8	1.4	10	135
Macaca mulatta	37.2	1.0		292
Macaca mulatta	38.1	1.6	10	134
Macropus giganteus	34.6	2.8	19	222
Macropus rufus	36.3	1.7	17	222
Marmota monax	37.7	1.3	10	109
Meleagris gallopavo	40.2	1.2	12	250
Mephitis mephitis	36.4	1.3	12	87
Meriones unguiculatus	36.9	2.7	8	111
Meriones unguiculatus	37.4	2.7	14	19
Mesocricetus auratus	36.0	2.9	14	19
Mesocricetus auratus	36.8	1.7	18	94
Mesocricetus auratus	36.9	2.5	17	93
Mesocricetus auratus	38.0	1.3	17	89
Microcebus murinus	36.3	2.8	18	138
Microcebus murinus	36.5	2.5		137
Microcebus murinus	36.6	2.5	18	139
Microcebus murinus	36.8	2.0	16	136
Mus musculus	36.0	2.0	15	86
Mus musculus	36.2	2.4	17	508
Mus musculus	36.3	2.2	16	15
Mus musculus	36.5	1.8	21	84
Mus musculus	36.6	2.1	19	69
Mus musculus	36.6	2.2	18	77
Mus musculus	36.7	1.6	19	70
Mus musculus	36.8	1.7	18	74
Mus musculus	36.9	2.2	16	73
Mus musculus	37.0	2.0	17	20
Myrmecobius fasciatus	35.0	5.8	10	223
Nasua nasua	37.5	1.9	7	224
Octodon degus	36.5	2.0	5	117
Octodon degus	36.8	2.5	11	19
Octodon degus	37.0	1.7	5	113
Octodon degus	37.2	1.8	8	115
Octodon degus	37.3	2.0	6	114
Oryctolagus cuniculus	38.9	0.9	20	225
Oryctolagus cuniculus	39.8	0.8	12	87
Ovis aries	38.7	1.0	9	199
Ovis aries	39.3	0.3	14	202
Ovis aries	40.4	1.3	9	198
Pachyuromys duprasi	36.5	2.5	18	118
Petaurus breviceps	37.0	3.2	18	226
Procyon lotor	38.1	1.4	1	87
Rattus norvegicus	36.8	2.5	16	37
Rattus norvegicus	36.9	1.8	18	41
Rattus norvegicus	37.0	1.7	18	32
Rattus norvegicus	37.0	1.8	18	50
Rattus norvegicus	37.0	1.9	19	31
Rattus norvegicus	37.0	2.1	18	509
Rattus norvegicus	37.1	1.8	18	60
Rattus norvegicus	37.2	1.5	17	25
Rattus norvegicus	37.2	1.5	17	30
Rattus norvegicus	37.3	1.0	18	45
Rattus norvegicus	37.3	1.4	18	290
Rattus norvegicus	37.3	2.1	16	19
Rattus norvegicus	37.4	1.2		287
Rattus norvegicus	37.4	1.3	18	42
Rattus norvegicus	37.4	1.4	18	24
Rattus norvegicus	37.4	1.4	18	53
Rattus norvegicus	37.5	1.3	18	20
Rattus norvegicus	37.5	1.4	18	43
Rattus norvegicus	37.5	1.4	18	69
Rattus norvegicus	37.5	1.5	18	65
Rattus norvegicus	37.5	2.0	18	14
Rattus norvegicus	37.6	1.1	18	21
Rattus norvegicus	37.6	1.2	16	27
Rattus norvegicus	37.6	1.7	19	361
Rattus norvegicus	37.7	1.3	17	26

Rattus norvegicus	37.8	1.8	18	68
Saimiri sciureus	37.5	2.0	8	140
Saimiri sciureus	37.5	2.7	6	141
Saimiri sciureus	37.9	2.0		293
Sarcophilus harrisii	35.7	4.2	18	227
Sminthopsis macroura	36.2	5.5	18	318
Spalax ehrenbergi	36.4	1.5	5	124
Spermophilus beecheyi	36.4	2.4	5	125
Spermophilus lateralis	36.5	4.0	6	126
Spermophilus richardsonii	36.2	3.3	10	19
Spermophilus tridecemlineatus	36.4	5.0	7	128
Spermophilus tridecemlineatus	36.7	4.2	8	19
Spermophilus xanthoprymnus	37.0	4.0	7	18
Struthio camelus	39.1	1.8	9	251
Suncus murinus	35.0	6.0	14	228
Sus scrofa	39.0	1.4	14	230
Sus scrofa	39.6	0.5	9	229
Thallomys nigricauda	36.8	2.1	18	129
Thallomys paedulcus	36.6	2.9	18	102
Trichosurus vulpecula	37.4	2.9	16	218
Tupaia belangeri	37.4	4.2	6	108
Tupaia belangeri	38.0	5.0	5	233
Vombatus ursinus	34.7	1.4	18	234

[a] HALO = hours after lights on

a large-amplitude CRT. However, it is not currently known whether daily torpor involves a distinct physiological process or is simply an extension of the CRT in heterothermic species. A few studies investigating the ambient temperature selected by torpid animals seem to suggest that torpor is a natural extension of the CRT (318, 319).

4.2. Food availability

Because food ingestion is associated with an acute rise in body temperature in various species (197, 245, 320-322), and because animals and humans tend to eat mostly at certain times of the day (323, 324), it is conceivable that the CRT could be a mere side-effect of the circadian rhythm of food consumption. That is, in animals fed *ad libitum*, the concentration of feeding during the light phase or the dark phase of the light-dark cycle could possibly result in the chronic elevation of body temperature that characterizes the CRT. In reality, however, the CRT persists in the absence of daily oscillation in food consumption. Thus, humans and animals fed small meals at regular intervals throughout the day nonetheless exhibit clear CRTs (172, 180, 205, 325, 326). Furthermore, animals and humans fed no meal at all (that is, subjected to total food deprivation) still show daily rhythmicity in body temperature (24, 156, 188, 202, 219, 230, 237, 327-329). An example is provided in Figure 4. The rectal temperature of a goat was recorded at 3-hour intervals for several days. During the first three days, the animal received a single meal each day (indicated by the arrows). For the next three days, no food was provided. Food deprivation caused a small decline in body temperature, but rhythmicity was clearly preserved.

The fact that the CRT persists in the absence of daily oscillation in food consumption does not imply that disturbance of the usual pattern of feeding cannot affect the CRT. Numerous studies of "food anticipatory activity" in rodents have shown that food restriction can cause both entrainment and masking of the CRT (55, 330-333).

In a number of species, moderate food deprivation induces a reduction in metabolic rate and a fall in body temperature (42, 237, 327, 329, 334-338). What is especially interesting about this phenomenon is its modulation by the circadian system. The hypothermia induced by food deprivation (or chronic food restriction) does not occur indiscriminately. Instead, it is restricted to the inactive phase of the circadian cycle. Although some animals have a natural disposition to exhibit daily torpor even when fed regularly (128, 223, 318, 339-349), various true homeotherms exhibit circadian-modulated starvation-induced hypothermia. This has been documented in doves (282), pigeons (235, 237, 338, 350, 351), quail (328), mousebirds (313, 352), finches (353), pygmy mice (354), deer mice (355), domestic mice (356), rats (42, 43, 329, 357, 358), lemurs (136, 138), sheep (202), and goats (194).

5. INFLUENCE OF BIOLOGICAL FACTORS

Over a century of research on circadian rhythms has produced extensive evidence that circadian rhythms are endogenously generated and that the period of a rhythm is genetically inherited, even if it can be partially and temporarily modulated by environmental factors (359, 360). The fact that the CRT is endogenously generated does not mean, however, that it is generated as an autonomous physiological process. In sections 5.1 through 5.4, I will consider (and reject) the possibility that the CRT is merely a side effect of the circadian rhythm of locomotor activity and will discuss how the CRT is affected by the developmental state of an organism, by its body size, and by its reproductive state.

5.1. Locomotor activity

The daily/circadian rhythms of locomotor activity and body temperature have been simultaneously monitored in many studies on various species (30, 31, 51, 74, 88, 95, 110, 130, 135, 159, 248, 285, 286, 361, 362). Generally, the temporal courses of the two rhythms are very similar. In diurnal animals, the activity and body temperature rhythms

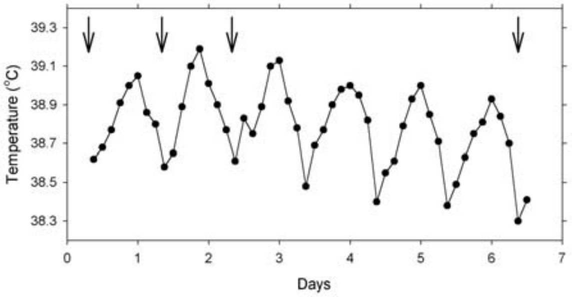

Figure 4. Seven-day segment of the records of rectal temperature of a goat (*Capra hircus*) maintained under a 24-hour light-dark cycle with and without daily meals (which are indicated by the vertical arrows). Figure adapted from Piccione, Caola, and Refinetti, 2003 (194).

exhibit high values during the day and low values during the night. Conversely, the activity and body temperature rhythms of nocturnal animals exhibit high values during the night and low values during the day. In both humans and rodents, body temperature starts to ascend slowly several hours before awakening and then rises abruptly (more so in rodents than in humans) at wake time (363).

Because the rhythms of body temperature and activity proceed closely together -- both under a light-dark cycle and in constant conditions -- it is natural to wonder whether the temperature rhythm is not simply a consequence of the activity rhythm. Indeed, it is well known that acute episodes of physical activity and exercise can elevate body temperature in humans (2, 176, 364-367) and other vertebrates (91, 134, 204, 220, 368-370), so that the daily elevation in body temperature associated with circadian rhythmicity might be a direct result of increased activity.

In order to investigate the potential causal link between the activity rhythm and the temperature rhythm, several researchers recorded the body temperature rhythm of human subjects maintained in continuous bed rest (156, 158, 371), or undergoing a "constant routine" protocol, which involves bed rest as well as sleep deprivation and the ingestion of frequent, equal-size meals (172, 180, 325, 326). Although the amplitude of the rhythm is reduced under this condition, robust rhythmicity persists. Thus, while the activity rhythm may alter the amplitude and shape of the body temperature rhythm, it does not cause it. Bed rest cannot be used with animals, but the autonomy of the CRT has been demonstrated by analysis of the day-night difference in the correlation between the rhythms of activity and temperature. Although nocturnal animals are generally more active at night than during the day, their body temperature is higher at night regardless of the actual activity level (51, 92, 95, 130, 372, 373). Conversely, the body temperature of diurnal animals is higher during the day regardless of the actual activity level (363). Thus, we may confidently say that the body temperature rhythm in animals, as in humans, is not caused by the activity rhythm.

The fact that the CRT is not caused by the activity rhythm does not imply that the CRT cannot be enhanced or disrupted (masked) by changes in activity. As a matter of fact, some researchers argue that the CRT is so strongly masked by changes in activity in free-living subjects that it should not be relied upon as a marker of the state of the circadian clock. Some argue that masking can be mathematically filtered out (374), whereas others recommend that the CRT be replaced by the rhythm of melatonin secretion as a reliable marker of the state of the clock (375). The advantages of the CRT include tradition, ease of measurement, and demonstrated autonomy from the activity rhythm, whereas the susceptibility to masking is a major disadvantage. The melatonin rhythm has the advantage of being resistant to masking caused by activity but has several disadvantages, including the need for frequent collection of blood (or saliva) samples and a high susceptibility to masking caused by environmental light during the night.

5.2. Maturation and aging

In rats, a rhythm of body temperature with a range of oscillation of 2-4 ^{O}C is observed on the day after birth, but it seems to vanish by 15-20 days of age (376-381). Weak rhythmicity appears again at 25 days of age and attains the adult range (1.6 ^{O}C) at 45 days of age (382). Because the early temperature rhythm vanishes in a few days and is observed only when the pups are kept at an ambient temperature below thermoneutrality, this rhythm is thought not to be a true precursor of the adult rhythm of body temperature but a form of cold-induced torpor (378, 383). In rabbits, temperature rhythmicity can be observed as early as 4 or 5 days after birth in pups allowed to remain with the doe (303, 384), but not in pups kept in isolation with continuous intra-esophageal feeding (379).

Newborn calves lack daily rhythmicity of body temperature. Daily rhythms comparable to those of adults are not observed until two months after birth (209). One research group reported the presence of rhythmicity two weeks after birth (385), but their calves were exposed to large daily fluctuations in ambient temperature (about 20 ^{O}C), which probably caused the fluctuation in body temperature. In calves maintained under constant ambient temperature, no difference between measurements taken at dawn and measurements taken at dusk was found for the first 10 days of life. Later on, measurements taken at dawn decreased gradually until a stable dusk-dawn difference of about 1 ^{O}C was achieved between 50 and 60 days after birth (209).

Lambs (young sheep) and foals (young horses) also develop daily rhythms of body temperature during early life, although adult rhythms seem to be attained earlier than in calves, as a stable dusk-dawn difference is achieved about one month after birth (386). Evidently, different species develop the body temperature rhythm at different rates. In dogs, puppies of three different breeds failed to exhibit statistically significant daily rhythmicity for several days after birth. Regardless of breed or sex, rhythmicity matured over several weeks and attained a stable level by 6 weeks after birth (387). The reasons for the differences in timing among calves, dogs, lambs, and foals are not evident. Different species of domestic animals

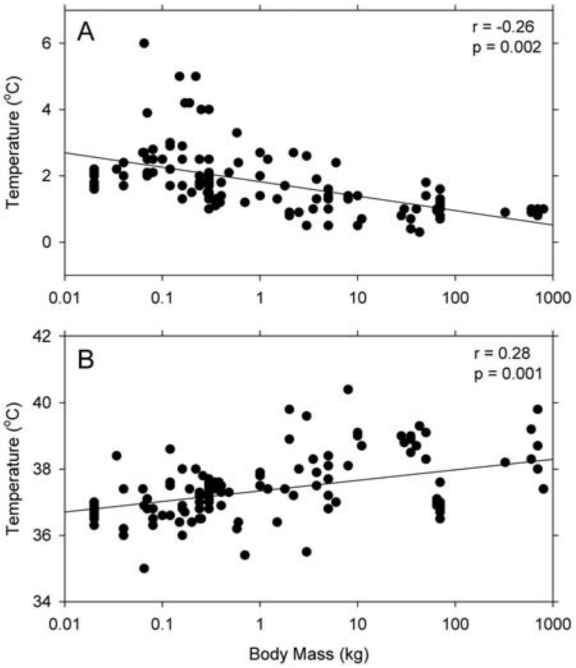

Figure 5. Relationship between the daily range of oscillation of the CRT and body size (A) and relationship between the mesor (mean level) of the CRT and body size (B), as reported in 135 published studies on 55 mammalian species. In both graphs, the abscissa is scaled logarithmically. The straight lines were fitted to the data by the method of the least squares (and the correlation coefficient and its associated probability under the null hypothesis are indicated). The data were obtained from the subset of mammalian studies listed in Table 1

exhibit different parameters of body temperature rhythmicity in adulthood (388), and it is to be expected that differences will also exist in the ontogenetic development of rhythmicity.

Newborn human babies do not have a rhythm of body temperature. The body temperature of a newborn oscillates randomly; a daily pattern is noticeable at 3 months of age; and a mature daily rhythm is not reached until a year or more after birth (389, 390).

Despite interspecies differences in the rate of maturation, the fact that the CRT is not present at birth seems to be a common finding. The absence of the CRT in early life may be due to immaturity of the circadian system, to immaturity of mechanisms of heat gain and heat loss, or to both. Immaturity of the circadian system is suggested by the fact that other bodily rhythms also undergo maturation. For instance, the rhythm of melatonin secretion is present immediately after birth in seals (391), but only two weeks after birth in hamsters and rats (392), and only three months after birth in humans (393, 394). However, the delay in the expression of rhythms is most likely due to the development of mechanisms downstream from the circadian pacemaker, because, at least in rats and sheep, the pacemaker itself is already oscillating before birth (395-399). Furthermore, the thermoregulatory system is known to undergo maturation in young mammals and birds, principally through the development of heat conservation mechanisms (400).

At the other end of the age spectrum, the CRT is affected by aging. By far the best characterized alteration in the circadian system related to aging is a reduction in the amplitude of circadian rhythms (401-403). Reduction in the amplitude of the body temperature rhythm in old age has been documented in humans (162, 163, 404, 405) as well as in various rodent species (53, 60, 61, 77, 119, 406-410).

Aging seems to also be associated with a change in the phase and period of circadian rhythms. A small advance in the phase angle of entrainment in old age has been documented in humans (163, 411-414) and rodents (61, 78, 407), although few of these studies monitored the CRT. Studies on golden hamsters have generally found that circadian period is shortened in old age (415-421), and shortening of circadian period was also observed in deer mice (415), and laboratory rats (422). However, lengthening of circadian period was observed in aging domestic mice (423, 424) and canaries (425). In humans, one study found no difference between the free-running periods of young and old subjects (426), whereas another found shorter periods in older subjects (162). Clearly, more studies are needed to clarify these apparently conflicting results.

5.3. Body size

Many years ago, Aschoff pointed out that the amplitude of the CRT is 3 to 6 times smaller in large animals than in small animals in the body weight range from 10 g to 1 kg (427). The data from 135 independent studies shown in Figure 5 (panel A) confirm that the amplitude is about 3 times smaller in large mammals than in small animals in the body mass range from 10 g to 1,000 kg. Presumably, large bodies buffer the effects of the oscillations in heat production and heat loss responsible for the CRT, although the effect is modest (as indicated by the relatively small correlation coefficient of -0.26). Curiously, body size has the opposite effect on the mean level of the CRT (Figure 5, panel B). Animals in the 1,000-kg range have, on average, body temperatures 0.6 ^{O}C higher than the body temperatures of animals in the 10-g range. Again, this is presumably due to the greater thermal inertia of large animals, and again caution should be exercised in the interpretation of this weak albeit statistically significant relationship. A recent literature survey based on 125 independent studies in mammals has also confirmed Aschoff's prediction (428). The amplitude of the body temperature rhythm was found to be smaller, and the mean level to be higher, in large animals than in small animals.

Interspecies studies of the relationship between body temperature and body size based on literature surveys have either failed to identify a significant correlation (429, 430) or identified a weak positive correlation (427, 428, 431). Curiously, intraspecies studies in dogs (387) and humans (432) identified a significant inverse correlation between body temperature and body mass. The data for

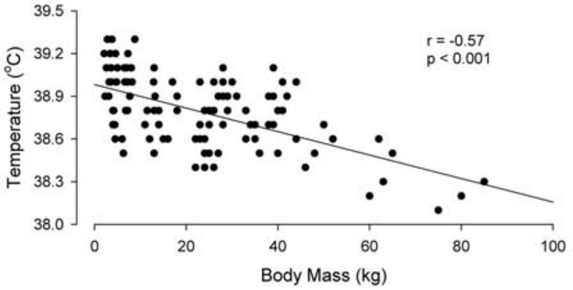

Figure 6. Rectal temperature as a function of body size for 115 dogs of 19 different breeds ranging from 2-kg Yorkshire Terriers to 85-kg Great Danes. The straight line was fitted to the data by the method of the least squares (and the correlation coefficient and its associated probability under the null hypothesis are indicated). Figure adapted from Piccione, Fazio, Giudice, and Refinetti, 2009 (387).

dogs are shown in Figure 6. The negative correlation between body temperature and body size has a coefficient of -0.57. Why interspecies coefficients should be positive and intraspecies coefficients be negative is not evident, but there must clearly be differences between species. As a matter of fact, a recent literature review identified no significant relationship between temperature and body mass in mammals overall but uncovered significant relationships for particular subgroups (433). For instance, a positive scaling relationship was found in bats, whereas a negative scaling relationship was found in artiodactyls. The finding that the scaling of body temperature is positive in some phylogenetic groups but negative in others implies that the causes of the scaling must be found in ecological factors that affected the evolution of different phylogenetic groups differently.

5.4. Reproductive state

Most female animals do not ovulate on demand, so that reproduction is possible only during the appropriate phase of an ovulatory cycle (434). The reproductive cycle involves not only timed ovulation but also estrous rhythmicity in hormonal secretions (250, 435-451), vaginal discharges (234, 444, 448, 449, 452-454), behavioral sexual receptivity (445, 446, 451, 453, 455-458), and locomotor activity (66, 114, 234, 435, 437, 452, 459-463). In addition, many species of mammals and birds exhibit estrous rhythmicity in body temperature (66, 114, 209, 234, 240, 242, 243, 250, 438, 442, 452, 461-470). All of these processes can mask the CRT in multiple ways. For this reason, most studies of daily and circadian rhythms of body temperature (or of locomotor activity, for that matter) are conducted on males.

6. RHYTHMICITY AND HOMEOSTASIS

The homeostatic control of body temperature has the goal of ensuring stability -- that is, of preventing deviations from an ideal set point. On the other hand, the circadian control of body temperature imposes a persistent oscillation in body temperature. Somehow, these two antithetic processes must be integrated. How this is accomplished in terms of physiological control will be discussed in section 6.1. How it is accomplished in terms of effector mechanisms will be discussed in section 6.2.

6.1. Regulatory process

Thermal physiologists have generally assumed that the CRT is primarily under homeostatic control and is secondarily modulated by the circadian system through an oscillation in the thermoregulatory set point (293, 471-473). According to this view, the circadian pacemaker acts on the thermoregulatory thermostat so that the set point is elevated during subjective day and lowered during subjective night in diurnal animals (or vice versa in nocturnal animals). An alternate arrangement, more logical from the viewpoint of circadian biologists, would be to have the circadian oscillation in body temperature primarily under circadian control, bypassing the thermoregulatory set point, and being secondarily modulated by the thermoregulatory system. Research conducted in the past 10 years or so strongly supports the alternate explanation.

The idea that the CRT might result from a daily oscillation of the thermoregulatory set point seemed to be supported by laboratory evidence that autonomic heat loss responses are activated during the circadian phase of low body temperature, and heat conservation responses are activated during the phase of high body temperature, in rats (474), pigeons (475, 476), and humans (148, 477-479). The reasoning was that, for instance, enhanced thermogenesis during the circadian phase when body temperature is high implies an elevation of the set point (because, presumably, the elevation in the set point was responsible for the enhanced heat production). The finding that injection of antipyretics could reduce the amplitude of the CRT of otherwise undisturbed rats (58) provided further support for the notion of circadian modulation of the set point.

What was wrong with the preceding reasoning was that the measurement of autonomic thermoregulatory responses at different times of the day does not really tell us anything about the state of the set point. It tells us only that heat production and heat loss mechanisms are being activated -- and it is a thermodynamic necessity that mechanisms of heat production or heat loss must be activated in order for body temperature to change (if ambient temperature is kept constant). In other words, the studies that allegedly supported the set-point explanation of the CRT failed to evaluate set point changes. In order to judge whether there is circadian modulation of the thermoregulatory set point, one must be able to monitor the set point. In order to measure the state of the set point, one needs a variable that is not normally required for the production of the body temperature rhythm but that, at the same time, does reflect the operation of the set point. It is known that autonomic and behavioral thermoregulatory responses can complement each other in the homeostatic control of body temperature (480-486), and it was pointed out above that the body temperature rhythm of endotherms does not require behavioral responses. Therefore, the use of behavioral responses can provide a reliable measure of the state of the set point.

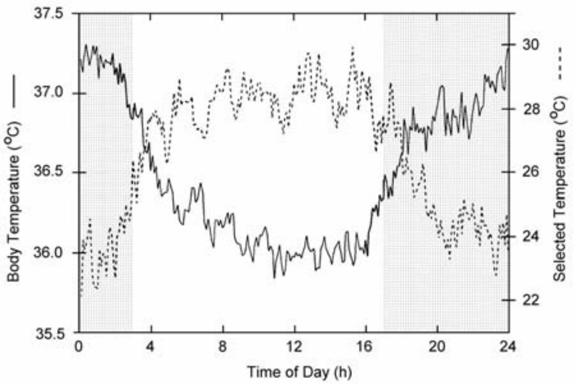

Figure 7. Relationship between the average rhythm of body temperature and the average rhythm of selected ambient temperature of fat-tailed gerbils (*Pachyuromys duprasi*) maintained in a temperature gradient under a 24-h light-dark cycle (as indicated by the shading). The average rhythms are derived from 5 gerbils, each studied over 10 consecutive days with 6-minute resolution. Figure adapted from Refinetti, 1998 (118).

The first investigator to directly address the issue was probably Hensel, in 1978, who studied the thermal sensation evoked by warming of the hand of human subjects at different times of the day and noticed that warm stimuli were perceived as more pleasant during the circadian phase of low body temperature than during the phase of high temperature (487). The following year, Carlisle noticed that rats exposed to the cold would press a lever for heat more vigorously during the phase of low body temperature than during the phase of high temperature (488). Research in many other laboratories over the years, using a variety of behavioral research techniques, has documented that higher ambient temperatures are preferred during the phase of low body temperature, and lower ambient temperatures are preferred during the phase of high body temperature, in rats (22, 45, 48, 329, 489-491), mice (492), golden hamsters (93, 490, 493), Siberian hamsters (319), fat-tailed gerbils (118), degus (115), stripe-faced dunnarts (318), tree shrews (108), flying squirrels (108), lemurs (494), and humans (495-498).

Figure 7 illustrates the phase opposition between the rhythms of body temperature and of preferred ambient temperature in fat-tailed gerbils (*Pachyuromys duprasi*) tested in a temperature gradient. As expected for a nocturnal animal, body temperature was high during the night and low during the day. The rhythm of behavioral temperature selection was, however, 180^{O} out of phase with the rhythm of body temperature. Clearly, higher environmental temperatures are selected when body temperature is low, and vice versa. Thus, the oscillation of the set point cannot possibly be responsible for the temperature rhythm. As a matter of fact, there is no reason to assume that the set point oscillates at all (499, 500). As *body temperature* oscillates, the animals behaviorally counteract the oscillation to defend the unaltered set point. The thermoregulatory system actually opposes the oscillation of body temperature imposed by the circadian system.

The thermoregulatory system's opposition to the circadian oscillation of body temperature is evidently not fully successful, as witnessed by the very existence of the rhythm. However, the amplitude of the temperature rhythm is effectively reduced by the action of the thermoregulatory system. This has been shown in two ways. One way was by comparing the amplitude of the rhythm in animals maintained in a constant-temperature environment with the amplitude in animals allowed to continually select their environmental temperature in a gradient. The amplitude of the body temperature rhythm was reduced in tree shrews and flying squirrels allowed to select their environmental temperature (108). The other way was by impairing the thermoregulatory system through surgical ablation of the main thermoregulatory center in the preoptic area of the brain. The amplitude of the body temperature rhythm was greatly enhanced in rats and golden hamsters with preoptic lesions (501-503), implying that ablation of the preoptic area releases the circadian oscillation of body temperature from inhibitory control. Thus, it can be inferred that the thermoregulatory center in the preoptic area of unlesioned animals restricts the oscillation of body temperature to an acceptable range. In other words, the *circadian* system generates an oscillatory signal that is communicated to the organs responsible for heat production and heat loss. At the same time, the *thermoregulatory* system generates a set point that, like most control systems, has a margin of hysteresis error. The integrated output of the two systems is an oscillation whose amplitude is restricted to the boundaries of hysteresis error.

6.2. Heat-exchange process

In order to produce a CRT, the body must produce an oscillation in the amount of metabolic heat produced and/or in the amount of heat lost to the environment. Aschoff reasoned early on that both heat production and heat loss needed to oscillate, and that the oscillation of heat loss needed to lag behind the oscillation of heat production (7). This has indeed been observed in rats (64, 287), squirrel monkeys (141, 293), and humans (172, 504). An example is shown in Figure 8. Cosine waves were fitted to the raw data of body temperature, heat production, and heat loss of a rat (top three graphs). The vertical dashed lines indicate the acrophases of the rhythms. Notice that heat production leads body temperature by 1.3 hours, whereas heat loss trails body temperature by 0.9 hour. If *heat balance* is calculated (bottom panel), a phase difference of 6 hours is found. That is, the heat-balance rhythm leads the temperature rhythm by 6 hours. This phase difference is presumably due to thermal inertia of the body and should be different in animals of different body sizes (427).

7. PERSPECTIVE

Daily oscillation in the body core temperature of mammals and birds has been documented in numerous studies on a large number of species. Body temperature is generally higher during the day in diurnal species and higher during the night in nocturnal species. The mean level of the oscillation is between 36 and 41 ^{O}C in most species, and the daily range of oscillation is between 1 and

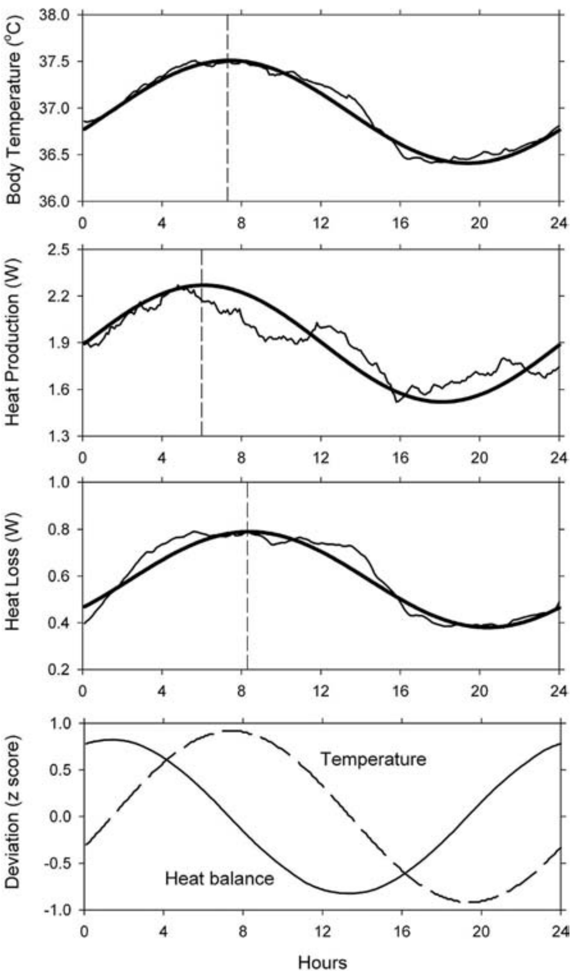

Figure 8. Relationships between body temperature, heat production, and heat loss of a laboratory rat maintained in constant darkness. Thin lines correspond to actual data collected at 6-minute intervals. Thick lines are cosine waves fit to the data. Dashed vertical lines indicate the acrophases of the rhythms. The last graph at the bottom compares the body temperature rhythm with the heat-balance rhythm (where heat balance is defined as the difference between the normalized values of heat production and heat loss). Figure adapted from Refinetti, 2003 (287).

5 ^{O}C. Under constant environmental conditions, the rhythm free-runs with a period shorter or longer than 24 hours, depending on the species.

The CRT is robust under constant, neutral environmental conditions, but its amplitude is enhanced in cold environments in some species. Enhanced amplitude can also be observed in animals with restricted access to food. Although the CRT persists in the absence of daily rhythmicity in activity, activity can greatly affect the CRT. Maturational stage, body size, and reproductive state can also affect the CRT.

The circadian oscillation in body temperature is primarily under circadian control, bypassing the thermoregulatory set point, and is secondarily modulated by the thermoregulatory system. The actual change in temperature is achieved by modulation of heat balance, with the oscillation of heat loss lagging behind the oscillation of heat production by a few hours.

Understanding the causes and properties of the CRT is important because homeothermic endothermy provides physiological and ecological benefits believed to be responsible for the adaptive success of birds and mammals in a wide range of aerial, aquatic, and terrestrial environments (505). Thus, the violation of homeothermy represented by the CRT must be seen as much more than just a curious deviation from an ideal pattern. Although it is generally assumed that hibernation and torpor are relatively recent specializations arising from homeothermic ancestors, it has been proposed that heterothermy may have actually preceded homeothermy in vertebrates (506). Thus, the CRT may very well be a mild recent form of an ancient process of daily torpidity. Interestingly, it has been extensively documented that extant ectothermic species, particularly reptiles (262-275), can generate CRTs if provided with the opportunity to select the temperature of their environment, which further supports the notion of an ancestral origin of daily/circadian rhythmicity. It is possible, therefore, that the evolutionarily "new" drive to maintain homeostasis in homeotherms conflicts with the "old" universal drive to oscillate body temperature -- and this may explain the opposition between the thermoregulatory system and the circadian system in the control of body temperature in contemporary homeotherms.

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Abbreviation: CRT: circadian rhythm of body temperature

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Send correspondence to: Prof. Roberto Refinetti, Circadian Rhythm Laboratory, University of South Carolina, 807 Hampton Street, Walterboro, SC 29488, USA, Tel: 843-549-6314, Fax: 843-549-6007, E-mail: refinetti@sc.edu

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