the observation of Y chromosomes intermediate between the X and normal Y, suggest that we may be observing an early stage in the evolution of heteromorphic sex chromosomes.

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Hibernation and Body Weight in Dormice: A New Type of Endogenous Cycle

Abstract. *Under conditions unfavorable to hibernation (22°C), the body-weight cycles of dormice are only a few weeks long, but under conditions in which dormice hibernate (5°C), the cycles can last many months; the more the animals hibernate, the longer are the cycles. Such cycles contrast with the relative independence from torpor of the period of circannual cycles in other hibernating rodents and with the temperature compensation of circannual and circadian cycles in general.*

Circannual cycles in animals maintained in a constant environment for long periods occur in a variety of species, but the underlying mechanisms are poorly understood (*1*). Given the well-developed state of knowledge on circadian rhythms, it has been natural to apply concepts that have been useful in research on circadian rhythms to circannual rhythms (*2, 3*). In this context, one must, when developing theories of circannual rhythms, be aware of cycles that are different in their properties from circadian cycles. One such cycle, with properties different from circadian rhythms and from other circannual cycles so far described, is the body-weight cycle in dormice, *Glis glis*. I now report that the period of these cycles is dependent on whether the animal lowers its body temperature and hibernates, whereas the period of circadian cycles is generally compensated for changes in temperature (*4*).

Body-weight cycles with a period of approximately 6 weeks occur in dormice kept at about 25°C (*5*). Two observations suggested that these cycles might be temperature dependent. (i) A few animals with longer cycles than most tended to be lethargic and cool when weighed, even though they were in a warm room (*6*). (ii) When dormice are kept in a cold room (0° ± 2°C), cycles of torpor in those animals that hibernate average 6.1 months (*7*). However, in the first case there was no systematic assessment of torpor, and in the second, only torpor was recorded; it was thus impossible to compare cycle lengths in animals that hibernated with those that did not. I therefore studied weight cycles in matched groups of dormice maintained at different temperatures.

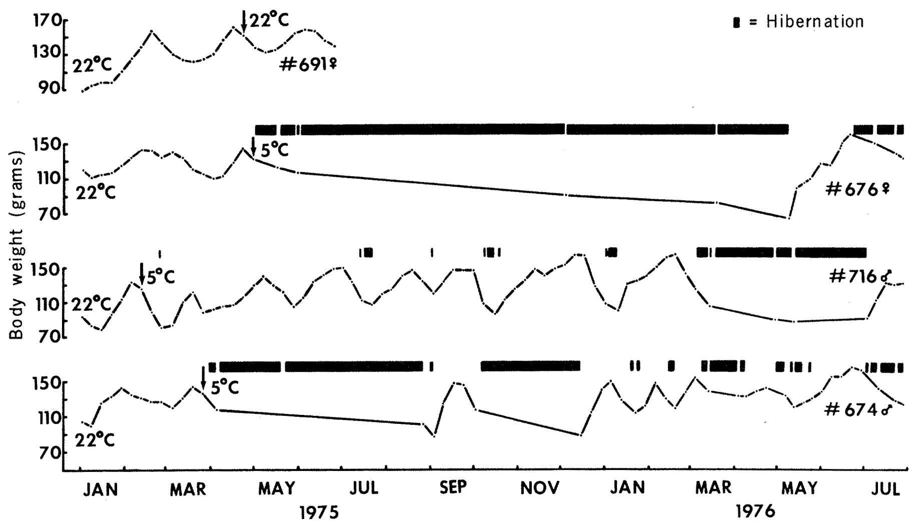
Fifty dormice were obtained in November 1974 from a dealer (Stacel) in France. They were housed under standard conditions in a holding room at 22° ± 2.5°C with 12 hours of light in 24 hours (LD 12 : 12) (*8*). The first 27 animals showing clear cycles of weight were selected for the experiment. One week after the weight of an individual animal had reached a peak the animal was transferred to either a cold room (5° ± 3°C) or another warm room (22° ± 3°C). Two animals were transferred to the cold room for every one to the warm room. Assignment to the rooms was made on the basis of a prearranged schedule, with the first animal that showed cycles going to the cold room, the second to the warm room, and the third to the cold room; this sequence was repeated for the next three animals as they reached and passed a peak weight, and so on. Three animals died in hibernation, leaving 15 animals in the cold room and 9 in the warm room.

Both cold and warm rooms were on an LD 12 : 12 hour cycle. The animals were weighed to the nearest gram once a week; for hibernating animals, weighing was postponed until they became active. Animals were inspected daily, and hibernation was monitored by the sawdust technique (*9*). After the main experiment was completed, direct measures of rectal temperature with a telethermometer (3-cm immersion) confirmed that animals judged to be hibernating were within 1°C of ambient temperature.

The experiment continued for each dormouse until its weight had reached at least one peak after the transfer to the cold or warm room. To be considered a peak in a cycle, the rise in weight had to be at least 20 g more than the lowest weight since the last peak, and it had to be followed by a drop of at least 20 g. This criterion corresponds well to intuitive judgments made by scanning graphs of body weight (Fig. 1).

The period of the first cycle completed after transfer to the cold room was much greater for those dormice that hibernated extensively than for those that did not (Figs. 1 and 2). Within the cold room the cycle lengths were positively correlated with the percentage of the cycle that was spent in hibernation (Spearman $\rho = .8$, $P < .01$). The mean cycle length in the 5°C room was 162 days (range, 28 to 425); in the 22°C room it was 53 days (range, 22 to 85). The difference stems mainly from the more frequent occurrence of cycles with a period of 3 months or more in the cold room ($P < .01$, Fisher exact probability test). Cycle lengths in animals that did not hibernate extensively, even though in the cold room, were similar to those of dormice in the warm room (Figs. 1 and 2).

When dormice hibernate in a cold room, the periodicity of their cycles is similar to the endogenous circannual cycles of other hibernating mammals (*2, 10*), although they can also be somewhat shorter (*7*). But when dormice are active, whether in a cold or a warm room, their



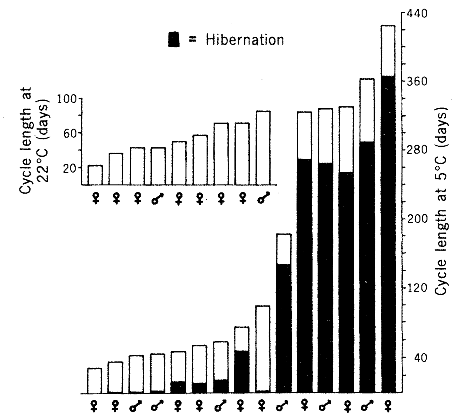


Fig. 1 (left). Body weight and hibernation of individual dormice, showing examples of animals that hibernated extensively (No. 676), hardly at all or never (Nos. 716 and 691), or for intermediate lengths (No. 674). Arrows show when animals were transferred to a different room, together with the temperature of that room. Only the first cycles completed after the transfer were used in the calculations and in Fig. 2. Periodic arousals with return to hibernation in a day are not shown. Fig. 2 (right). Length of body-weight cycle and days in hibernation within these cycles for dormice kept at 22° and 5°C.

cycles are very much shorter. This is not true of the circannual cycles of captive ground squirrels or woodchucks under constant conditions: in these species, if there is any shortening of the cycle in warm temperatures, it is relatively minor; moreover animals that do not hibernate, even though kept in a cold room, still have circannual cycles (*2, 9–11*). By contrast, the nonhibernating dormice have cycle lengths of only about 2 months.

Although the cycle in dormice is different from circannual cycles so far described in other hibernating rodents, it is nevertheless endogenous in that it persists in constant environmental conditions. With many endogenous cycles it has been convenient and profitable to think in terms of internal oscillators with characteristic frequencies. If the dormouse weight cycle is also going to be described in these terms, it must be emphasized that the temperature threshold for stopping or slowing down the oscillator is much higher than for circadian cycles of the same species, because Pohl (*12*) has demonstrated that circadian cycles in dormice persist at temperatures at least as low as 8.5°C. In various experiments in this laboratory dormice hibernating at temperatures as high as 13°C have exhibited a lengthening of the weight-loss phase of the cycle, similar to that described here. Moreover, if, in this case, an oscillator has been stopped or slowed in hibernation, the natural period must be assumed to be on the order of a few weeks; stopping or slowing the oscillator during extensive hibernation might then give a circannual cycle. A natural period of a few weeks would be different from the temperature-independent oscillator with periodicity of about a year that is presumed to underlie circannual cycles in other hibernators and birds (*2, 3*). It may also be asked, however, if in the case of dormice cycles it is appropriate to think in terms of oscillators at all. If there is an oscillator, the period is plastic, ranging from less than 4 weeks to more than a year.

An alternative interpretation is that temperature affects only the expression of cycles, with rhythms having characteristic frequencies of only a few weeks being expressed when dormice remain active and longer ones being expressed when they hibernate. In the second case, weight loss might be an obligatory consequence of hibernation if, for some reason, the animals were unable or unprepared to eat during their periodic arousals. Nevertheless, even if hibernation rather than weight is the important rhythm, its period differs from hibernation rhythms in many other species by being highly variable and often much shorter than a year (Fig. 1) (*7*). Moreover, an explanation in terms of temperature effects on expression is less economical in that it invokes two rhythmic processes to account for what appears to be continuum of periodicities (Fig. 2).

However one looks at them, these cycles persisting in constant conditions, unsynchronized between individual dormice (*5, 13*), of long duration and yet dependent on body temperature, must be considered a new category of endogenous cycle. As exciting, perhaps, is the opportunity that this phenomenon offers to analyze the physiology of rhythms of long duration. Detailed studies of exactly how hibernation and weight change are related, and of other factors that influence weight gain or loss, should prove instructive. Finally, apart from the rhythmical aspects of this cycle, it is worth noting that the cycle has practical value. For those studying the mechanisms involved in spontaneous obesity, the cycle can be used [for example (*14, 15*)] to compare phases of fattening and slimming without having to wait a year. For those studying hibernation, it offers a way of obtaining hibernation at any time of year, even midsummer, without resorting to food deprivation.

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