

Annual Cycle of Patterns of Activity Rhythms in Beaver Colonies (*Castor canadensis*)*

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Summary. Beavers studied under natural conditions near Québec City, Canada, displayed a yearly cycle of patterns of activity rhythms. In winter, the beaver colonies had a free-running circadian rhythm of period length 26.25 to 28.0 h, with or without relative coordination, depending on available light intensity, which in turn depends on ice and snow cover conditions; in summer, their activity rhythm followed a "normal" 24 h period. Transitions between these two patterns suggest that annual variations in the beaver's physiological state affect their reaction towards the presence or absence of a Zeitgeber.

Introduction

Evidence that a beaver family (*Castor canadensis*) living in SW Canada under uncontrolled, natural conditions displayed during the winter months a free-running circadian rhythm of activity with a period length of about 27 h has been recently produced by Bovet and Oertli (1974). The purposes of the present paper are to check that the case described by these authors was not an exceptional and/or local one, and to study the pattern of occurrence of this phenomenon under various habitat and microclimate conditions.

Material and Methods

Four different free-living beaver colonies were monitored in the course of this one and a half year study in the vicinity of Québec City, Canada (about 4000 km east of Bovet and Oertli's, 1974, study area). Three of them were located in Parc des Laurentides within a quadrilateral limited by the 47°17' N, 71°06' W, 47°19' N and 71°12' W lines of latitude and longitude, at an altitude of about 750 m. The fourth colony was within Cap Tourmente National Area (47°05' N, 70°47' W), near the shore of St-Lawrence River, at an altitude of about 5 m.

These two areas have quite different winter temperature conditions. Parc des Laurentides, due to its altitude, is not subject to several thawing periods in the course of the winter, and freeze-up is continuous from the date of first freeze-over (early November) to the sudden and irreversible spring thawing which occurs at some time between early March and early May depending on the location (stream or lake). For the Cap Tourmente study area, owing to its more temperate climate and to its location on a fast running stream, winter conditions were much more fluctuating: partial open water alternated throughout winter with transparent or snow covered ice.

Table 1 sums up several pertinent characteristics of the four colonies and locations studied. The "presumed composition" figures are based on many incidental observations made visually outside the freezing period and acoustically (through earphones) at various times during the study. Our initial hopes were to monitor colony 2 from mid-summer throughout

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Table 1. Characteristics of the beaver colonies monitored

Beaver colony	Presumed composition	Period monitored	Location	Habitat	Winter conditions freeze-up	Type of recording
1	2 adults	Dec. 24, 1972 to Apr. 23, 1973	Rivière Noire, Parc des Laurentides	rapid river	(Nov. 15) through to Mar. 4	Tape recorder (2 min/30 min)
2	2 adults 1 yearling 1 kit	Aug. 4 to Sept. 14, 1973	Route 33, Forêt Montmorency	pond formed by blocked stream	—	Tape recorder (2 min/30 min)
3	2 adults 2 yearlings 1 kit	Nov. 1, 1973 to Jun. 5, 1974	Lac Huppé Parc des Laurentides	lake	Nov. 4 through to May 1	Tape recorder (2 min/30 min)
4	2 adults (4 muskrats)	Nov. 17, 1973 to May 29, 1974	Rivière Friponne, Cap Tourmente	pond and rapid river	Intermittently from Nov. 17 to Apr. 2 (see Fig. 3)	Event recorder (continuous)

winter, but the beavers disappeared on Sept. 14, 1973, as the probable result of the activities of a poacher. Recordings from colony 1 also ended abruptly when beavers were forced away by a high flood on April 23, 1973 and did not return.

The technique for monitoring the beaver's activity at the three locations in Parc des Laurentides was similar to that developed by Bovet and Oertli (1974). Two omnidirectional microphones (Shure 575S), introduced in the roof of the beaver lodge, one over the feeding shelf, the other over the sleeping quarters, were connected to a tape recorder (Roberts 610 X) which was automatically turned on by a time clock for two minutes every half-hour.

For the Cap Tourmente colony, we modified the technique so as to obtain continuous recordings. One microphone in the beaver lodge was connected to a home-made electronic noise activated trigger circuit coupled to an event recorder (Esterline Angus Minigraph). A noise in the lodge resulted in one mark on the recording paper, continuous noise produced a compact block of overlapping lines. Chart speed was set at 5 cm/hr and hourly time signals were given by a clock coupled to another channel of the recorder. The sensitivity threshold of the apparatus could easily be adjusted and was verified periodically by means of a second microphone coupled to earphones.

At all four locations, the instruments were stored near the lodges in a propane heated, insulated, plywood shed, and were powered by 12VDC and/or 6VDC car batteries. Each location was visited once or twice weekly for maintenance and chart or tape renewal.

The analytical procedures for the acoustic recordings made in Parc des Laurentides (colonies 1, 2, 3) were similar to those of Bovet and Oertli (1974). We consider that the beavers were active during any half-hourly two-minutes bout of recording when gnawing and chewing noises were heard on the tapes. The actograms thus obtained (Figs. 1, 2) were then analysed by means of periodograms (Enright, 1965a) to find out what period lengths, if any, were implied in the activity pattern (see for instance Fig. 4).

Analysis of the graphic recordings obtained from colony 4 was more complex since in addition to the two adult beavers, at least four muskrats are thought to have lived regularly or intermittently inside the beaver lodge during winter (see Table 1). Visual outside observations made during the spring, coupled with listening in the lodge through earphones, have shown

that compact blocks of overlapping lines on the graph could only be produced by intense beaver feeding. Even intense eating activity of several muskrats did not achieve the necessary noise volume to produce such blocks. Therefore to analyse only data from beaver activity, the procedure was as follows. The charts were divided into consecutive three-minute bouts (480 bouts per 24 h). We consider that there was beaver activity during any three-minute bout when one or more blocks of overlapping lines could be seen on the chart. To facilitate the making and reading of the actograms produced for that colony (Fig. 3), we made a further simplification: ten consecutive three-minute bouts were coupled so as to form a 30-min group; a group is represented on the actograms as "active" when six or more of its ten bouts contained blocks of overlapping lines. However, the periodographic analysis of these data (e.g. Fig. 4B) is based on the detailed series of 480 bouts per 24 h.

Neither technique (tape nor event recorder) allowed for individual identification of the beavers in a colony and therefore all actograms and periodograms produced pertain to the colony as a whole.

Results

The results obtained from colony 2 showed that during the summer, beavers display a "normal", 24 h activity rhythm and, with activities beginning in the mid-afternoon and stopping in the early morning, are chiefly nocturnal. The actograms and periodograms obtained, being essentially similar to those presented earlier by Bovet and Oertli (1974, their Fig. 2B) for the same season, have not been illustrated in this paper.

During the course of the winter, all three beaver colonies monitored (1, 3 and 4) showed a free-running circadian activity rhythm of average period length 26.5, 28.0 and 26.25 h respectively (see Figs. 1, 2 and 3).

Two of the colonies (3 and 4) were monitored early enough in the fall to show the autumnal transition period between the summer and winter rhythms. In the case of colony 3, the transition period started quite early and was rather complex. When the lake surface began to freeze (Nov. 2), the beavers decreased their period length down to a value of 23.5 hours for several days (Fig. 5A), then increased it gradually to 27 h. During the next three weeks (Nov. 18 to Dec. 12), the periodograms indicate the presence of two distinct period lengths of 24 and 27 h (Fig. 5B). Due to a malfunction of the recording equipment between Dec. 15 and Dec. 22, the autumnal transition of colony 4 does not appear clearly (Fig. 3). However, the results suggest a faster and simpler transition from the 24 h to the 26.25 h rhythm, than was the case for colony 3.

Three complete shifts between winter and summer rhythms were obtained. In two of these (colonies 3 and 4), the transition was quite simple and appeared as a progressive reduction of the period length until it was 24 h, without the beavers necessarily displaying a normal summer type of phase relationship between their cycle and that of the Zeitgeber. Minor adjustments of the period length to exactly 24 h, and of the phase of rest and activity bouts to a normal summer pattern followed over a few weeks. In the case of colony 1, the transition period was more complex. After a first reduction in period length and several days on a 24 h rhythm (Mar. 12 to 24), the beavers shifted back to a free-running 26.5 h rhythm. Several days later, another passage to a 24 h rhythm occurred, again followed by a period of free-running rhythm. Four such shifts were observed from Feb. 20 to Apr. 20 (see Fig. 1).

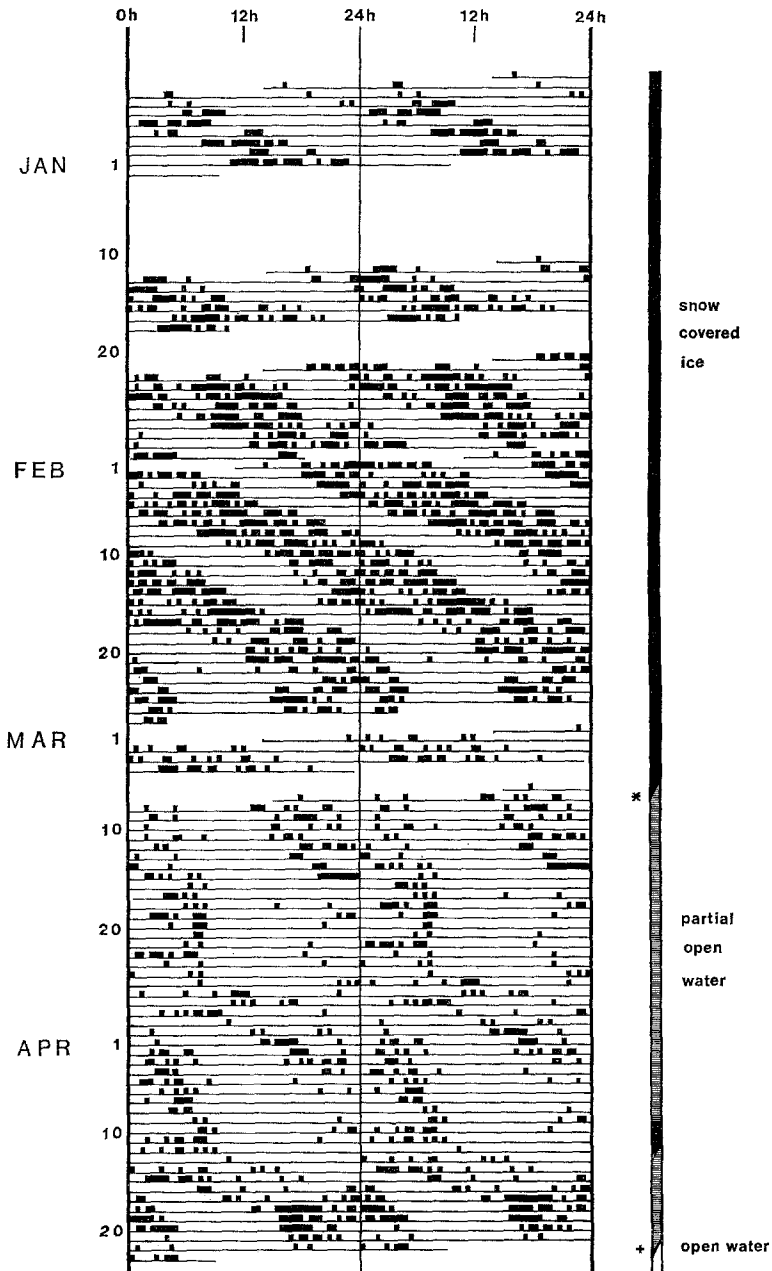


Fig. 1. Actogram of colony 1, from Dec. 24, 1972 to Apr. 23, 1973. Observed ice and snow conditions on the river are represented on the right of the actogram. *Beavers out for the first time. + Break-up of the ice, beaver dam carried away, beavers leave the site. Note: For all actograms, each horizontal line gives the results for a pair of consecutive days

Fig. 2. Actogram of colony 3, from Nov. 1, 1973 to Apr. 26, 1974. Observed ice and snow conditions on the lake are represented on the right of the actogram. The arrows point to the snow falls of more than 10 cm per 24 h, as recorded at a meteorological station 6 km away from the lake, from Nov. 1 to Dec. 31. The numbers refer to the height (in cm) of each of those snow falls

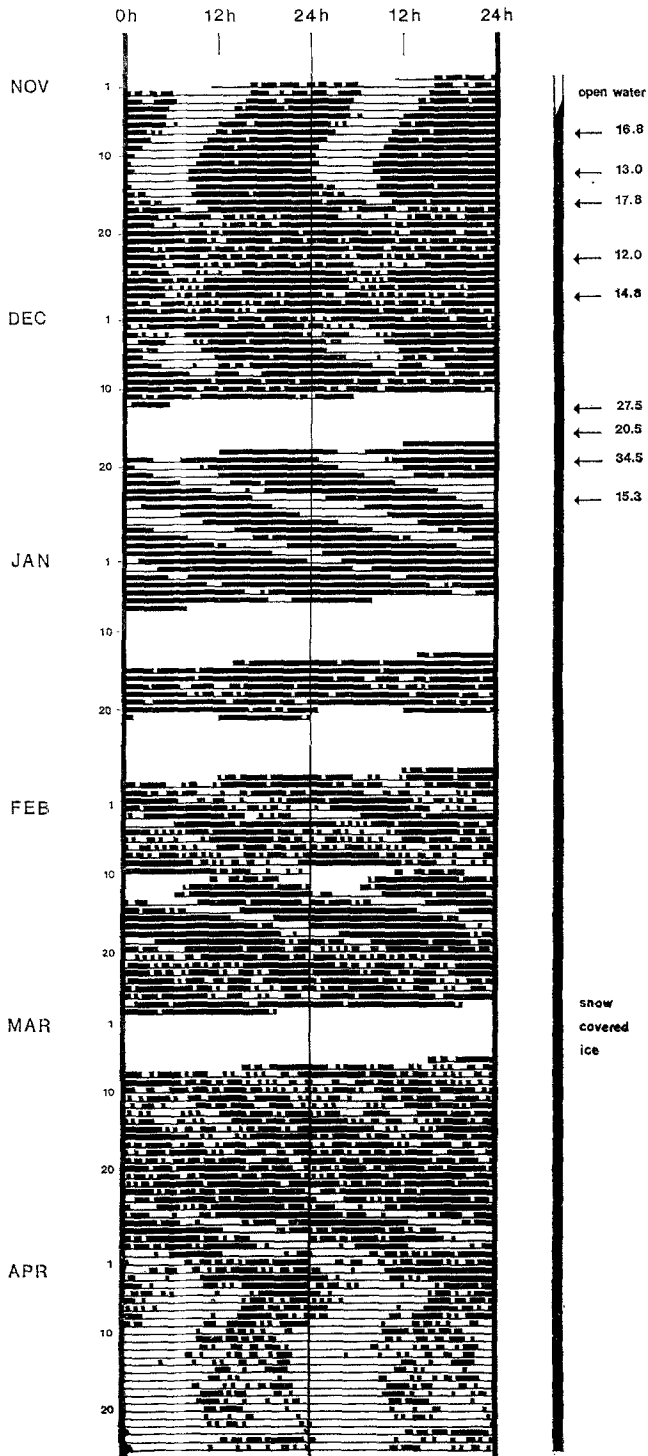


Fig. 2

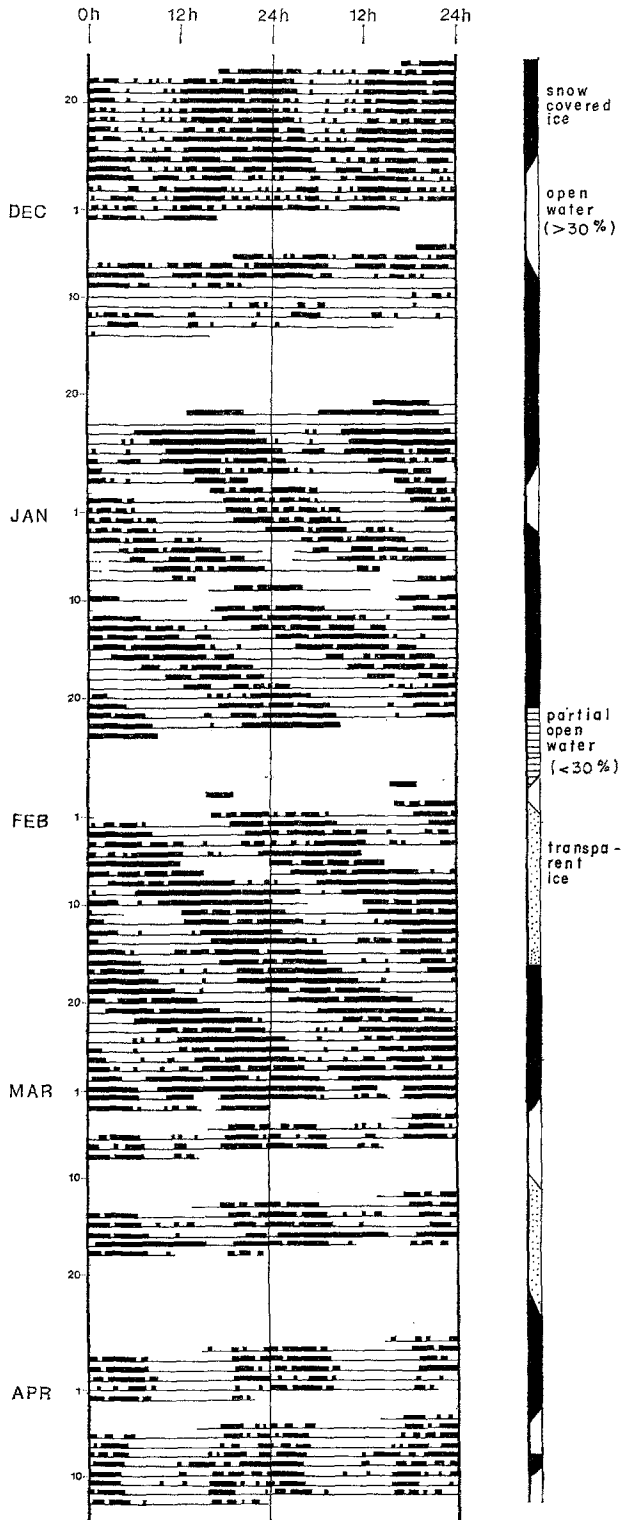


Fig. 3

Discussion

The obvious winter occurrence of a free-running circadian activity rhythm in all three beaver colonies studied confirms and extends the results presented earlier by Bovet and Oertli (1974).

A period length of 26–28 hours might at first seem surprising since according to the “circadian rule” (Aschoff, 1965; Enright, 1965b) a nocturnal animal like the beaver should react to a reduction in light intensity by a reduction in period length. Also surprising is the fact that colony 4 showed the same free-running rhythm as the other colonies in spite of the fact that beavers had direct access to land, and therefore to light several times during the winter (see Table 1 and Fig. 3). Finally, colony 3 autumnal transition, showing a reduction in period length, and colony 1 spring transition with four successive shifts from free-running to entrained rhythm, were strikingly different from other such cases related here, and from what was expected from previous works on circadian rhythms.

We shall see how all these seemingly surprising results can be combined to give an idea of the general mechanisms underlying the beaver’s annual cycle of daily or circadian activity patterns.

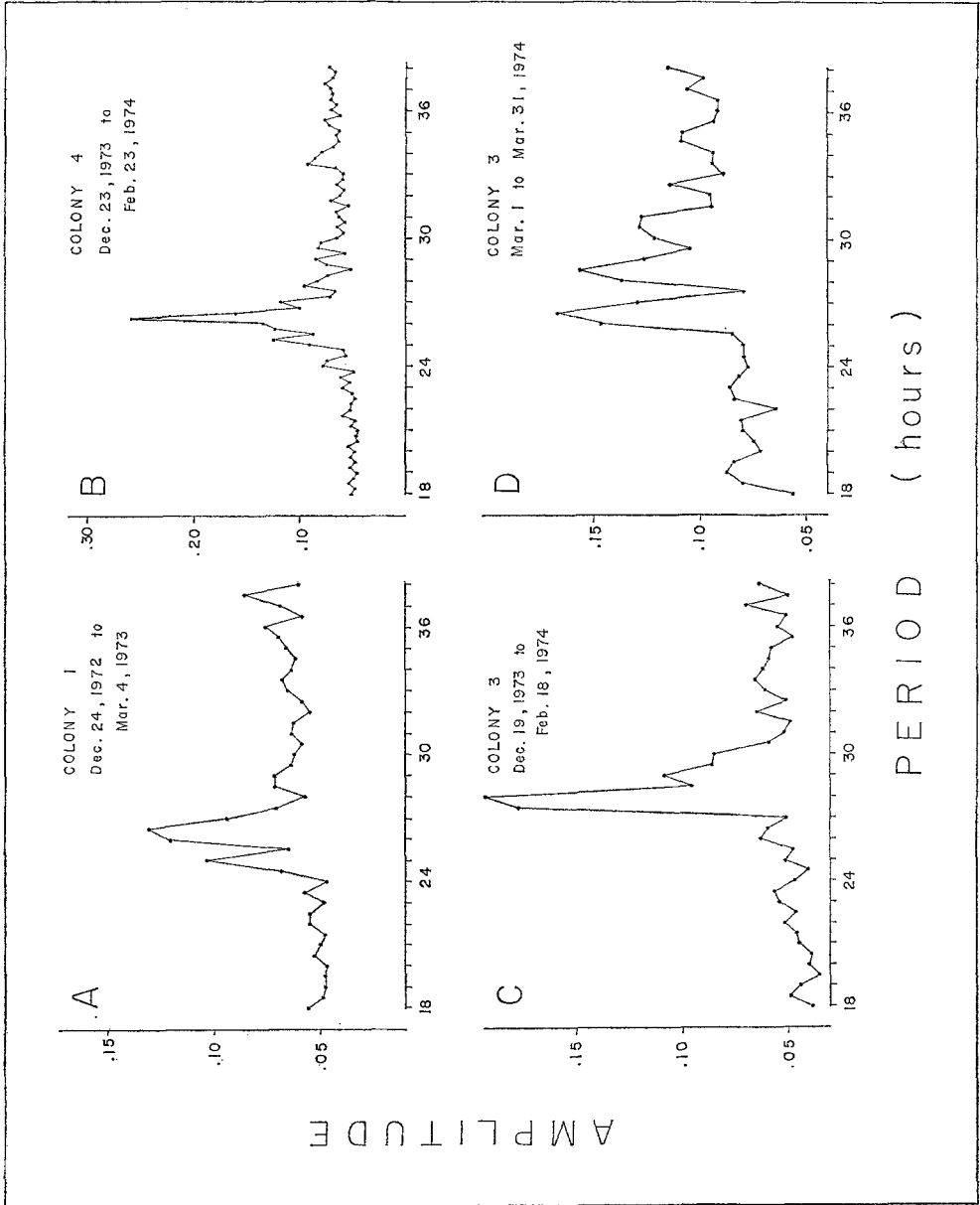
Light Conditions

The observed winter free-running rhythm raises the question of light conditions in the beaver’s environment. We have not been successful in obtaining winter measurements of underwater light intensity with a photocell (Lambda Instruments LI-212SR) placed in autumn, 40 cm under the surface of the water at the Cap Tourmente location. The receptor surface of the cell would become covered with fine particles after several days. However, light measurements under snow cover indicated the presence of about 1.5 lux under 25 cm of snow. Other experiments by various authors have all shown light intensity to be quite low (0–4 lux) under 25 to 50 cm of snow (Andreasson, 1973; Evernden and Fuller, 1972; Müller, 1970. See also light measurements under ice, Little *et al.*, 1972).

The results obtained during the fall transition period of colony 3 (Fig. 2, upper part) might suggest, at first sight, a relationship between the period length of the free-running cycle and the presumed light intensities in the beavers environment. At first, for a few days during and after freeze-up of the lake surface, at a time when the snow cover over the ice was negligible, the beavers followed a rhythm with a 23.5 h period length (see Fig. 5A). Then followed, from Nov. 13 to 18, a transition bout, the start and end of which might possibly be linked with a decrease in light intensity due to the snow falls of Nov. 13 and 17. From Nov. 18 to Dec. 12, a time with only two important snow falls on Nov. 24 and 29, the beavers followed a 27 h rhythm with strong relative coordination (Fig. 5B), this relative coordination suggesting that snow accumulation up to Dec. 12 was possibly not sufficient to stop all light-dark variations. From Dec. 12 to 18, the recording device failed to work. Finally, from Dec. 18 to Feb. 18, the beavers followed a 28 h rhythm without relative coordination (Fig. 4C); the

Fig. 3. Actogram of colony 4, from Nov. 17, 1973 to Apr. 13, 1974. Observed ice and snow cover conditions on the pond and adjacent stream to which beavers had access are represented on the right of the actogram

Fig. 4. Periodograms illustrating the presence (A, B, D) or absence (C) of relative coordination. Time unit for A, C and D is 30 min; for B: 15 min



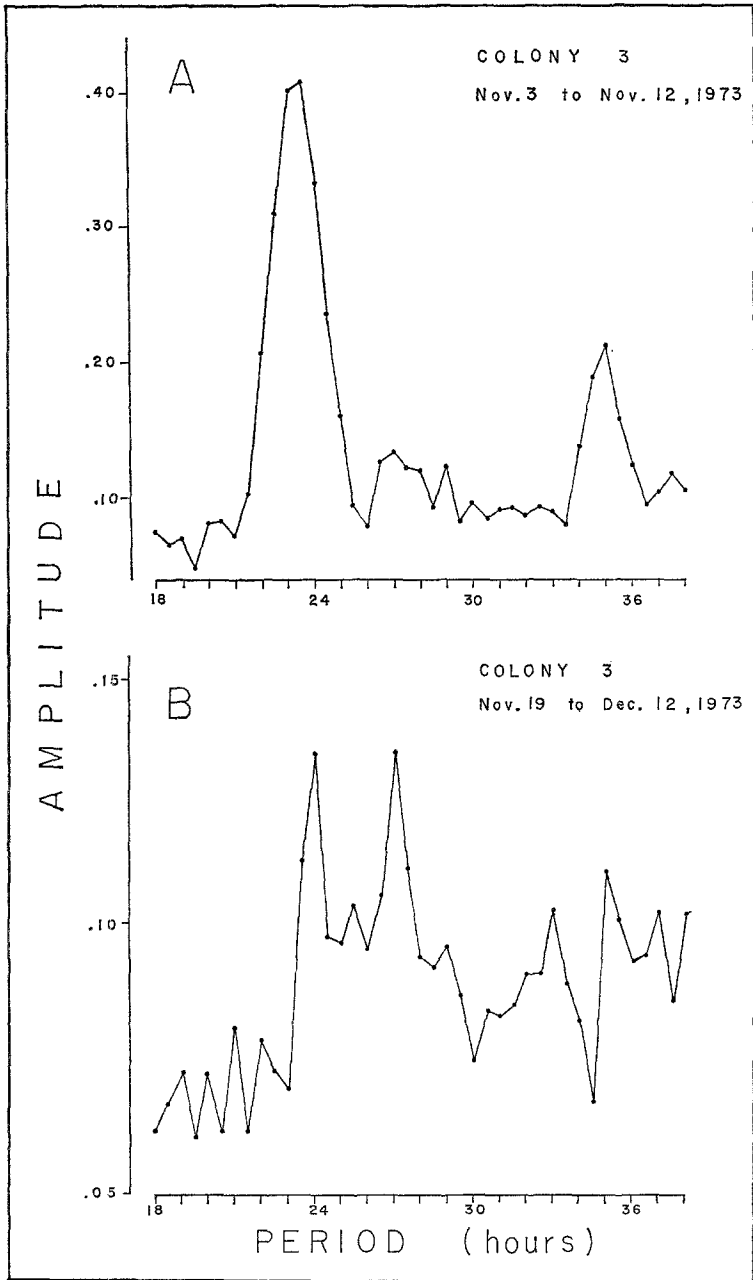


Fig. 5. Periodograms of the autumnal transition of colony 3 (time unit: 30 min)

disappearance of the relative coordination might possibly be linked with the heavy snow falls of Dec. 14, 17 and 20. For the remainder of the winter, the lake was covered with an estimated 60-70 cm of ice, and from 80 cm of wind-packed snow

over the center of the lake to more than 2 m on the sides (as measured in January and March). This autumnal pattern of changes in period lengths, in itself, is reminiscent of a phenomenon documented by Pohl (1972), namely that in nocturnal mammals kept in constant light conditions, there is a "critical light intensity" (about 0.01 lux) at which the period length of the free-running rhythm is shortest, and over *and* under which the period length becomes greater. In our case, the shift from a 23.5 h to a 27–28 h rhythm could possibly be considered as corresponding to a decrease of light intensities below the critical value. We do not think, however, that this is true, because none of the similar decreases of light intensity which must have necessarily occurred in the environment of colony 4 (see Fig. 3) has ever induced a 23.5 h period length; and also because none of the observed transitions from a winter free-running 26–28 hours rhythm, to a summer entrained 24 h rhythm (Figs. 1, 2 and 3) has ever contained a clear 23.5 h period length bout, although the "critical light intensity" value must have been reached through the progression of the melting process.

Furthermore, the beavers of colony 4 were in an environment where some light-dark fluctuations were present all winter, through either patches of open water, transparent ice or thin snow cover. Maximum measured winter cover was 30 cm of ice with 10–50 cm of snow. It should be noted that although patches of open water were present within 40 m of the lodge of colony 4 (sometimes as close as 10 m), never were any beaver or beaver tracks seen around these holes between the end of the lodge mud-covering activity (Nov. 15) and their first trip outside to get food (March 5). There is a possibility that beavers in winter "deliberately" avoid lighted areas, or never wander further than their food reserve until a shortage of food occurs.

As far as snow and ice conditions go, colony 1 was in an intermediate situation between colonies 3 and 4, and was probably subject to small light-dark variations too. Snow cover, although deep in front of the lodge, was rather thin at both extremities of the pond.

Relative Coordination

The occurrence of light-dark cyclic cues in the winter environment of some of our beavers is further revealed by the obvious signs of relative coordination¹ in the actograms of both colonies 1 and 4 (Figs. 1 and 3). There is a marked tendency to reduce the period length whenever the free-running cycles come to be in a nearly "normal" summer phase relationship with the Zeitgeber (i.e., when the beginning of the activity bout happens to occur in the mid-afternoon). This relative coordination can also be shown on the periodograms as a secondary peak for a period length smaller than that of the free-running period (see Fig. 4).

It is interesting to note that colony 3 does not show any signs of relative coordination during most of the winter (Fig. 4C). This supports the idea that these beavers were in complete darkness. Evernden and Fuller (1972) have shown that while snow cover reduces light intensity to near-zero values during early and mid-winter, there is a rapid increase of light intensity in late winter and early spring although snow depths remain the same. Correspondingly, winter results of colony 3

¹ Relative coordination (in this context): partial, temporary entrainment of the rhythm by a weak Zeitgeber (see Aschoff, 1965; Enright, 1965b).

show appearance of relative coordination in late winter (March 1), long before the first signs of snow melting (Fig. 4D).

An extreme case of relative coordination can be found in the spring results of colony 1 (Feb. 22 to Apr. 23). When the rapid increase in light intensity occurred, because of the thinner snow cover, light dark variations were much stronger than for colony 3 at the same season. Relative coordination, already present, was enhanced to the point where there was complete entrainment of the rhythm for as much as 10–12 days in a row before the free-running rhythm would take over again.

Bovet and Oertli (1974) were extremely cautious about relative coordination in the recordings they made from Feb. 19 to Apr. 2, 1970 (their Figs. 1A and 2A₁, A₂, A₃). We have re-analysed their data by compiling a single periodogram for all their 1970 winter results. This periodogram gives a main peak at 28 h (free-running period) and a clear secondary peak at 24 h (relative coordination). With regard to our own results, it seems obvious that what they described as apparent phase-shifts in the free-running rhythm was in fact strong, short-term relative coordination. Since the results they obtained between Dec. 16, 1970 and Jan. 26, 1971 do not show any signs of relative coordination (their Fig. 2C), their colony displayed a pattern analogous to that of our colony 3, with relative coordination appearing only during late winter and early spring.

Temperature and Metabolic Depression

Numerous studies over a wide variety of organisms have shown that temperature has only a slight effect on the period length of overt rhythms. Values of Q_{10} are very seldom higher than 1.1 or 1.2, and quite often range between 1.0 and 1.1 (see review in Bünning, 1967: pp. 46–59). With respect to the results of those studies, we do not think that changes in outside temperature might have affected the period length of the beavers activity rhythm, especially since the ambient temperature in the beavers winter environment rarely drops below 0° C (Stephenson, 1969).

Physiological changes associated with hibernation have been found to produce a marked effect on the period of the underlying rhythms of bats (Menaker, 1961). Subjected to the same temperature and lighting conditions, summer bats showed a free-running body temperature rhythm of average period length 22.5 h, while winter bats kept a period of 25 h. Northern beavers do not hibernate (the results of this study are one proof of this); they do however “possess a winter metabolic depression induced by decreasing light intensity in the autumn”, as described by Aleksiuik and Cowan (1969) (see also Novakowski, 1967). According to them, body temperature is kept at a normal value, but metabolism is reduced to a low maintenance level. Their findings also strongly suggest the presence of an endogenous annual physiological cycle: the winter depression is triggered by decreasing light intensity, but beavers must be in a certain “prepared state” before entering the depression, otherwise light intensity changes will remain ineffective; they have shown, for instance, that constant darkness imposed on beavers in late April does not induce the metabolic depression.

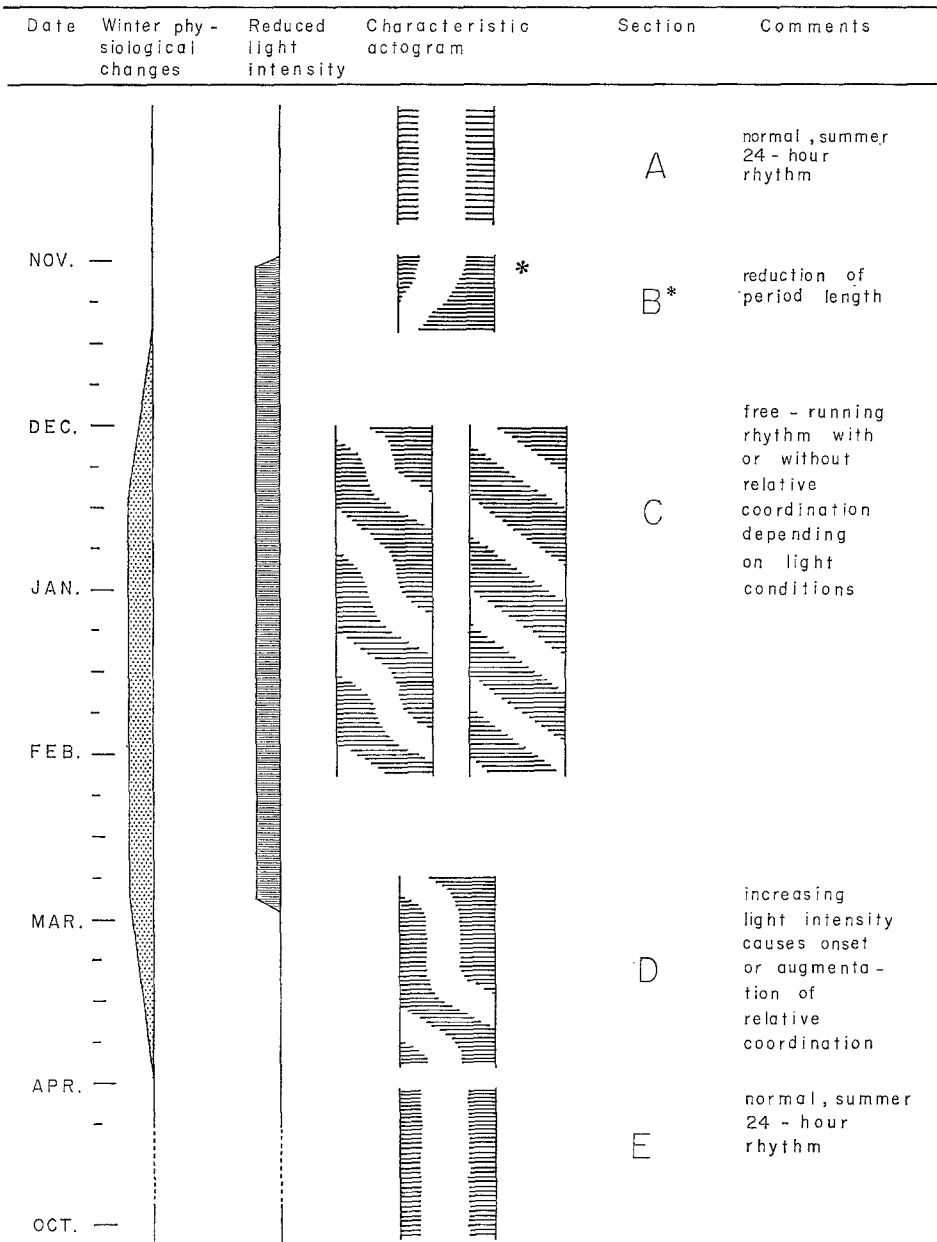


Fig. 6. Annual cycle of patterns of activity rhythms in relation to physiological changes and available light. *Section B applies only to those colonies where reduction in light intensity occurs before the start of winter physiological changes in beavers

These facts about winter physiological changes in bats and Northern beavers lead us to formulate the hypothesis that the 26-28 h period length of the rhythm displayed by our beavers might be, in some way, linked to their winter metabolic

depression. The unique occurrence, in early November, of a bout of activity cycles with a period length of 23.5 h could indicate that the beavers of colony 3 had perhaps not yet reached the necessary "prepared state" for the metabolic depression at that time of the year.

Annual Cycle of Activity Rhythm

Fig. 6 is an attempt to combine all data obtained on beaver rhythms into a general yearly cycle of activity rhythms in relation to presumed physiological state and available light intensity. The summer situation (sections A and E) requires no additional comments; a 24 h rhythm is maintained, entrained by normal light-dark Zeitgeber. We do not possess much information on the time of onset of winter physiological changes (sections B and C). Nov. 15 seems an approximate date (based on colony 3) at which winter metabolic depression could be initiated by a reduction in light intensity. However, it should be noted that colony 4 switched to a free-running rhythm much later (Dec. 22). There may be differences in the time of onset of winter physiological changes associated with local winter conditions; or it may be that these changes were present in all beavers by mid November, but availability of the near full-strength Zeitgeber maintained colony 4 on a 24 h rhythm (this coincides well with observed snow cover conditions). The last days of February seem to bring rapid changes in available light intensity in all colonies (section D). Depending on snow cover, there is either onset (colony 3) or increase (colony 1) of relative coordination, even to the point where this coordination becomes absolute (i.e. 24 h rhythm), as for colony 4.

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