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Two Possible Determinants of the Timing of Daily Episodes of Behavior in Rats

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WIDMAN, D. R. AND W. TIMBERLAKE. *Two possible determinants of the timing of daily episodes of behavior in rats.* PHYSIOL BEHAV **58**(6) 1227–1236, 1995.—The present experiment examined endogenous ultradian rhythms and regulatory metabolic processes as two potential determinants of daily out-of-nest episodes (ONEs) and feeding episodes (FEs) in rats living in a 24-h environment. Two types of photoperiod were used: a Standard 12:12 h L/D schedule and a Skeleton 12:12 h schedule. During each type of photoperiod rats were exposed to 4 feeding conditions of 7 to 12 days each: (a) a baseline of ad lib food and water; (b) food restricted to the diurnal (inactive) portion of the cycle; (c) both food and water restricted to the inactive period; and (d) return to baseline. Time series analyses of nocturnal ONEs in baseline revealed a strong circadian rhythm and weaker ultradian rhythms with periods between 2 and 6 h. Analyses of FEs, though, revealed a general absence of circadian rhythms but strong ultradian rhythms with periods similar to those observed in ONEs. When food and water were restricted to the inactive part of the cycle, ONEs showed no change in frequency, but a decrease in average duration and changes in ultradian periodicities. The results indicated control of daily episodes of behavior in rats by ultradian oscillators that are weaker and more variable in effect than those found in voles, but similar in period.

Ultradian rhythms Circadian rhythms Episodic behavior Out of nest behavior
Feeding behavior Regulatory metabolic processes

MOST animals that use nests, burrows, or other relatively safe, permanent shelters must leave these locations at intervals to find food, water, and reproductive partners. When and how often an animal leaves the relative safety of its shelter has important implications for its survival and reproduction. Thus, we might expect the frequency, duration, and temporal distribution of out-of-nest episodes (ONEs) to depend on proximate variables such as metabolic demands, predator pressure, and the spatial and temporal distribution of food (3). However, to the extent that the temporal characteristics of ONEs are determined by similar selection pressures and/or homologous mechanisms, we can expect similarities across modestly related species, such as laboratory rats and voles.

In the case of voles, considerable research has documented their tendency to leave the nest in regular episodes (1,2,10). The primary hypothesis explaining these out-of-nest episodes (ONEs) proposes an ultradian rhythm of nest-leaving controlled by oscillators with a fixed period entrained to the light-dark cycle (5). This rhythm has been linked closely to feeding episodes by several authors (1,2,7), who reported that voles always ate during ONEs and during those ONEs in the diurnal part of their activity cycle engaged only in behavior required to obtain food.

Daily episodes of feeding also are shown by rats housed in laboratory environments without nests. However, researchers from Richter (12) to LeMagnen (8) have invoked regulatory metabolic processes rather than an ultradian oscillator to explain these feeding episodes (FEs) in rats. In this view, episodic behavior is produced by increases in hunger over time followed in turn by eating, satiation, and quiescence. The positive correlation between amount eaten and delay to the next feeding episode reported by LeMagnen (8) can be taken as support for this regulatory view. Lehmann (7) proposed a similar regulatory explanation for ONEs in voles.

Recent work by Gerkema and van der Leest (6) attempted to test the regulatory view of ONEs in voles by depriving them of food for a period typically sufficient for several ONEs to occur and monitoring the results on the timing of subsequent ONEs. If regulatory processes control ONEs, then the increased deprivation should have increased their frequency and/or duration. However, the authors found no such changes. Additional studies cast more doubt on the regulatory explanation of ONEs by showing no effects of enforced changes in rest and activity on the characteristics of subsequent ONEs.

The general purpose of the present study was to provide

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further information about the characteristics and control of daily ONEs and feeding episodes (FEs) in rodents. Previous work in our laboratory has shown that rats maintained in a 24-h environment with a nest show seemingly regular ONEs and FEs during the active portion of their cycle (see 9). While out of the nest, rats mainly eat, drink, run, and walk about. The specific purpose of the present experiment was to determine the relative contributions of ultradian rhythms and regulatory metabolic processes to the control of daily episodes of behavior in laboratory rats.

The contribution of ultradian rhythms to daily episodic behavior was evaluated using time series analyses (Fourier transforms) of continuously recorded ONEs and FEs. If ultradian rhythms control these behavioral episodes we expect marked frequency peaks in the density spectrum of a Fourier analysis between a period of 2 and 6 h. The contribution of regulatory metabolic processes to ONEs was tested directly by removing first food and then both food and water from the nocturnal (active) portion of the photoperiod schedule. If regulatory metabolic processes control ONEs, we should see a dramatic drop in their frequency and duration in the absence of nocturnal food availability. Finally, these potential determinants were examined during both a Standard L/D photoperiod and a Skeleton photoperiod to examine the potential effect of light in suppressing the expression of ultradian and regulatory determinants (see 15).

METHOD

Subjects

Four female Sprague–Dawley rats bred at Indiana University served as subjects. They were 1 yr old at the start of the experiment and had lived in the apparatus under a 12:12 h L/D cycle for approximately 9 mo. Subjects were allowed ad lib access to food and water within the apparatus except where noted.

Apparatus

The apparatus (Fig. 1) consisted of a 30.5 cm square chamber with a covered nest and a running wheel attached to separate walls of the chamber. Food and water dispensers were attached to a third wall of the chamber (see 9 for a more detailed description). Food (94 mg pellets, Formula #F0058, Bioserve, NJ) and water (distilled) were constantly available except during conditions of nocturnal restriction (see below). Location of the animal in the apparatus, running, eating and drinking were sampled every 4 s. Running was assessed through photobeam interruption of a flag mounted on the outside of the wheel. Eating and drinking were defined as the removal of either a food pellet or 0.05 ml of water from the food or water source. Location was assessed via switches in the floors of the nestbox and the central chamber.

Procedure

The experiment used two photoperiod schedules: a Standard 12:12 h L/D schedule with light onset occurring at 0600 h, and a Skeleton 12:12 h. schedule with two half-hour light pulses, one at 0600 and the other at 1800. Each photoperiod schedule was in effect for four feeding conditions: Baseline (BASE), Food in Day Only (FDO), Food and Water in Day Only (FWDO), and Recovery of Baseline (RBASE). Both the BASE and RBASE conditions consisted of ad lib access to food and water. FDO consisted of restricting access to food to the diurnal (inactive) portion of the photoperiod. In FWDO access to both food and water was restricted to the inactive part of the photoperiod. Conditions generally lasted 12 days with the exceptions of the BASE of the

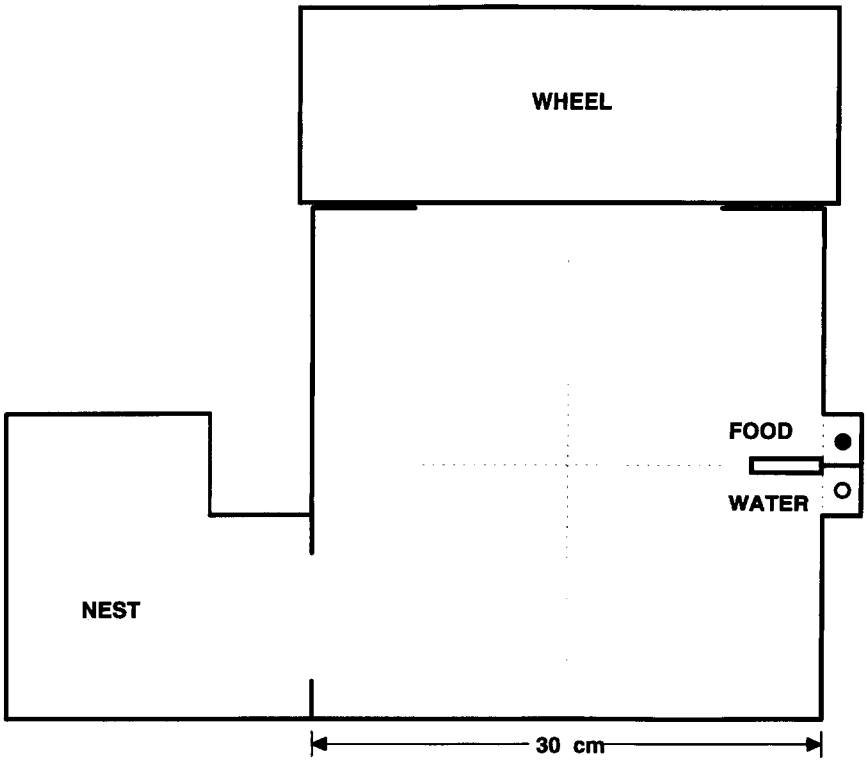

FIG. 1. Diagram of the apparatus.

Standard photoperiod schedule (10 days) and the FDO and FWDO conditions of the Skeleton schedule (10 and 7 days, respectively).

Animals were considered out of nest any time the nest floor switch was not activated during a 4-s period. These 4-s bins of data were then summed into 20-min bins for analysis. An eat was recorded when a food pellet was removed during any 4-s period. As with the out of nest data, the 4-s bins of eat data were summed into 20-min bins for analysis.

Data Analysis

The data were subjected to two types of analysis. A fourier transform was applied to the ONE and FE data during the nocturnal (active) periods of each BASE and FWDO condition. We restricted our analysis to the active portion of the photoperiod schedule because Fourier analysis looses robustness when it is used on data that results from markedly different processes (4). In the case of circadian rhythms of activity there is ample evidence that different processes determine behavior during the active and inactive periods of the cycle (e.g., 11). For example, constant bright light conditions will decrease the duration of daily activity in certain species of nocturnal rodents (11). If our light conditions suppress activity then this would have the effect of altering the spectra towards longer periods.

The resulting density spectra were smoothed. Smoothing involves averaging the original spectral density function across a specific number of weighted points (a window). This smoothing window is passed through the entire range of spectra and the resulting data transformation is examined. We used a Parzen weighting function with a window size of 15. The effect of smoothing is to enhance peaks of reliable periodicities in the time series while damping those peaks which represent noise. For example, a rhythm of 6 h will typically generate strong peaks of 6 h but will also, through "leakage," generate weaker peaks at periods surrounding the 6 h peak. Smoothing should enhance the 6 h peak while damping the others, resulting in greater confidence in the peaks which appear in the resultant spectral function.

The second type of analysis involved a repeated measures analysis of variance (ANOVA) on the average daily frequency and duration of ONEs during the nocturnal portion of the photoperiod schedule. For the purpose of this analysis, ONEs were defined as any time the animal was out of the nest for at least eight 4-s intervals during any 10 min bin. Median values were calculated from the final six days of each condition within each photoperiod schedule. These medians were then averaged for the condition and photoperiod schedule. ANOVA was performed on these average medians with photoperiod schedule (Standard or Skeleton) and condition (BASE, FDO, FWDO, and RBASE) serving as within subject variables. Tukey's LSD tests were used to compare among conditions. Significance was set to $p < .05$ for all tests.

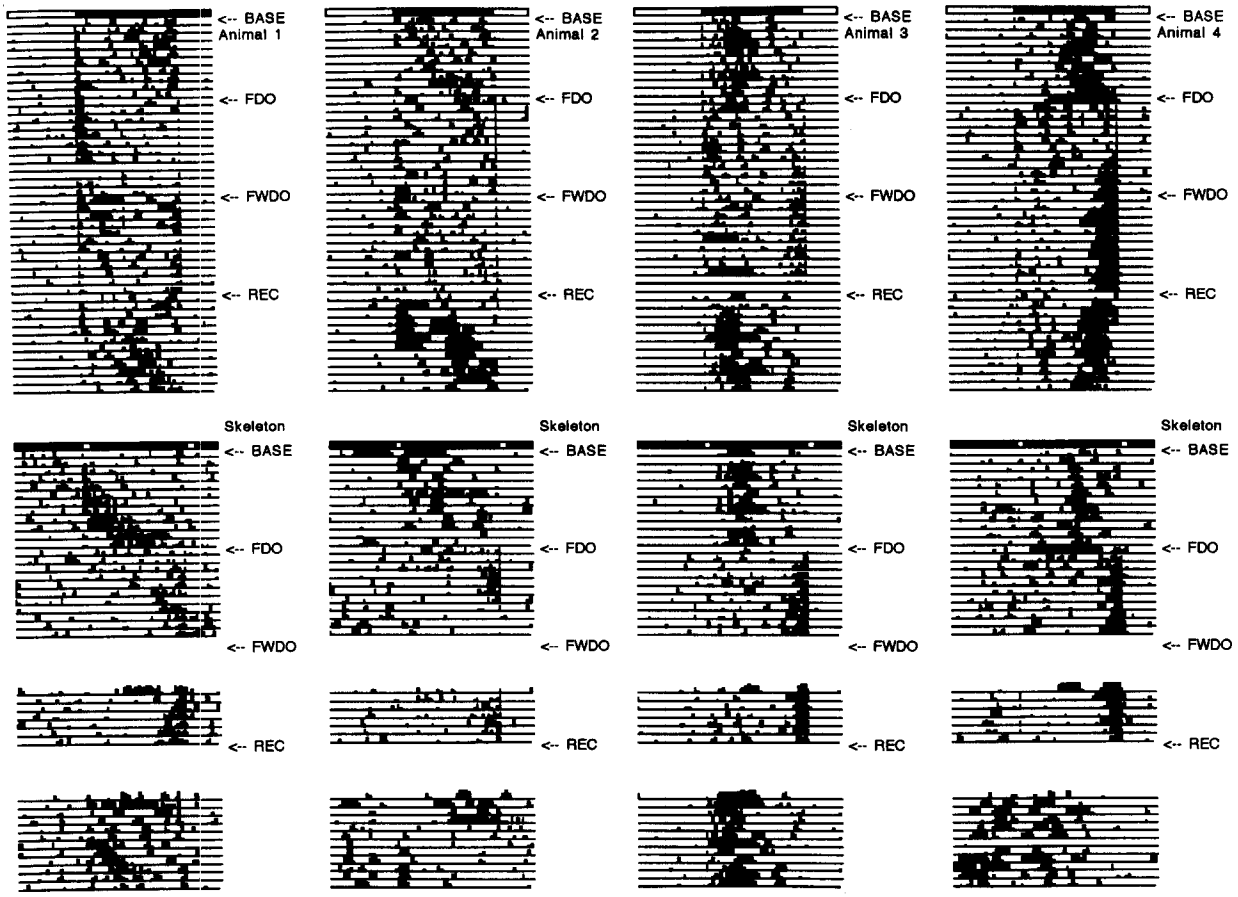

FIG. 2. Actograms of ONEs for each photoperiod schedule (Standard and Skeleton) and feeding condition (BASE, FDO, FWDO, & RBASE) for each animal. The height of the bar indicates the amount of behavior during a 20 min bin.

Results

Actograms of out-of-nest episodes (ONEs) for each animal for all feeding conditions in both Standard and Skeleton photoperiod schedules are shown in Fig. 2. Actograms of FEs for each animal over the BASE conditions for each type of photoperiod schedule are shown in Fig. 3. Careful examination of both sets of actograms indicates the episodic nature of behavior. Animals tended to remain in the nest most of the time, exiting (Fig. 2) and eating (Fig. 3) several times a night.

Out-of-Nest Episodes (ONEs) in Baseline (BASE)

Figures 4 and 5 display the density spectra for each animal in the BASE condition for the Standard and Skeleton photoperiod schedules respectively. The largest frequency peak occurs at the

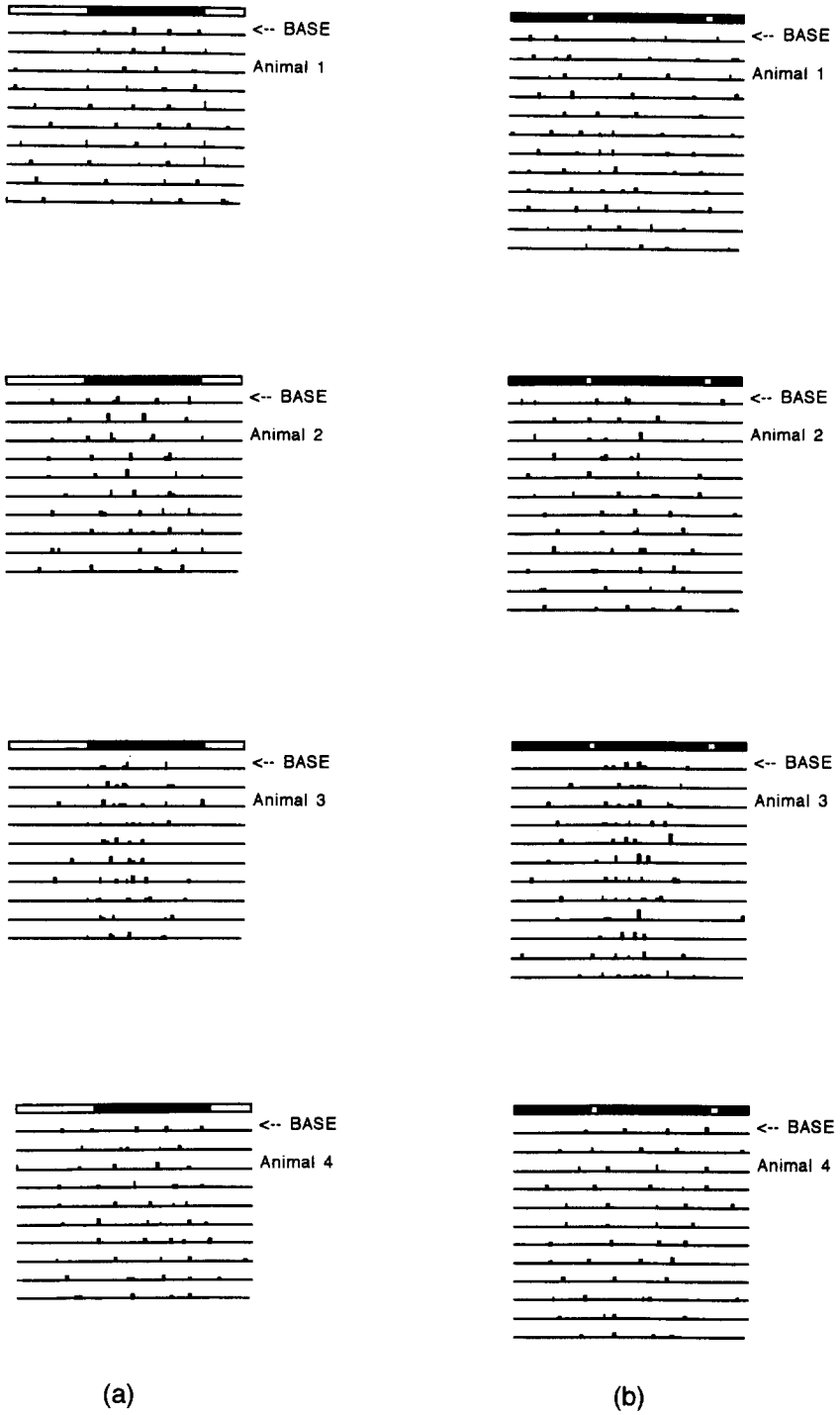

FIG. 3. Actograms of FEs for each animal in the BASE condition of both the (a) Standard and (b) Skeleton photoperiod schedules. The height of the bar indicates the amount of behavior during a 20 min bin.

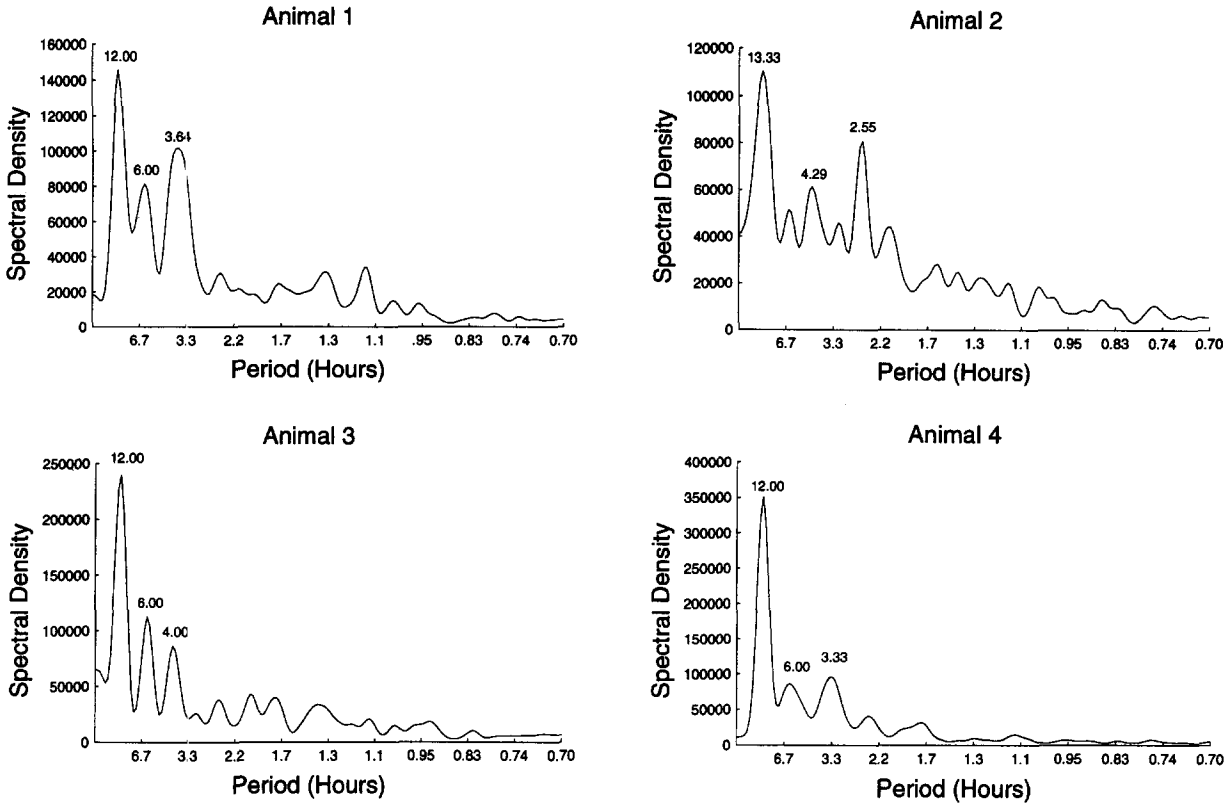

FIG. 4. Density spectra of ONEs for each animal in the Standard Base condition. Each spectrum was smoothed using a Parzen function with a window of 15 points. Although the data does not allow for accuracy below tenths of an hour resolution, peaks labeled in the figures are labeled in hundredths of an hour resolution for clarity.

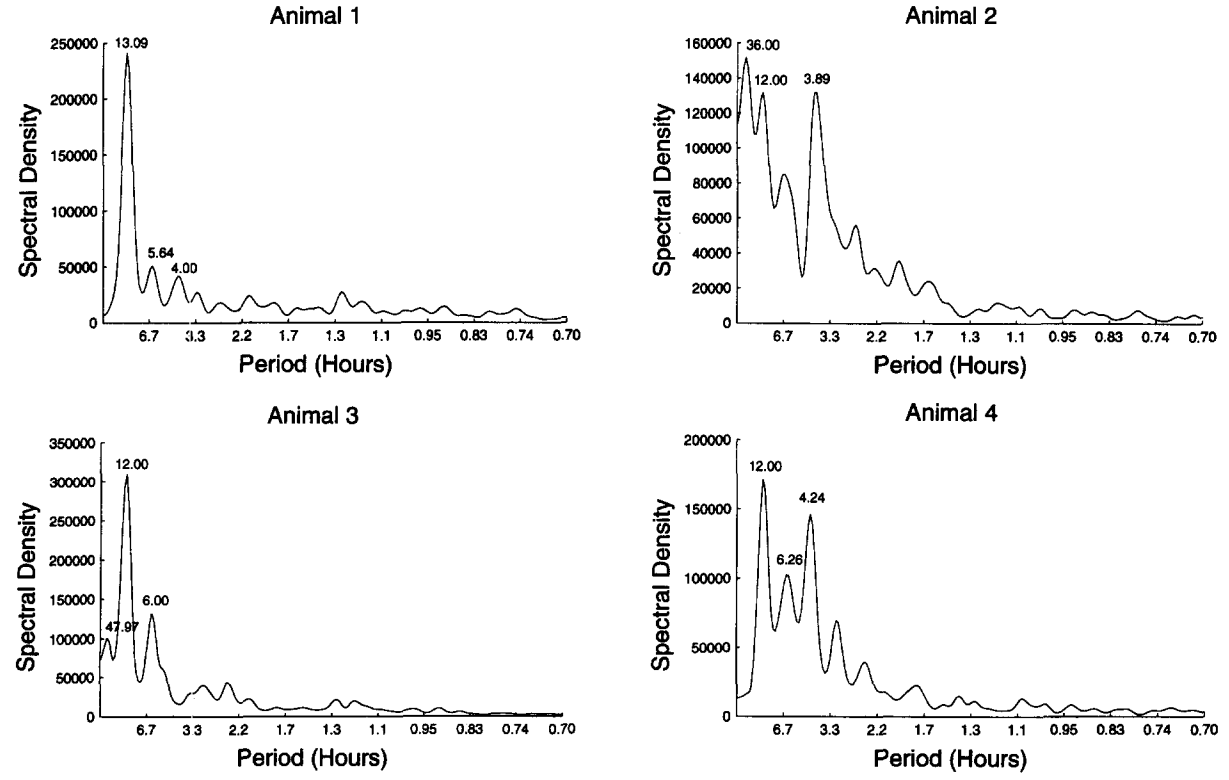

FIG. 5. Density spectra of ONEs for each animal in the Skeleton Base condition. Each spectrum was smoothed using a Parzen function with a window of 15 points.

12-h point for most animals in each condition. Given that we omitted the 12 h of the inactive part of each daily cycle because markedly different processes appear to be involved (4), this peak most likely indexes the periodicity of the circadian rest-activity cycle. Near 12-h peaks are shown by Animal 2 under the Standard photoperiod (13.3 h) and Animal 1 under the Skeleton photoperiod (13.1 h). In the Skeleton photoperiod schedule Animals 2 and 3 also showed peaks at periods longer than 24 hr. Examination of the respective actograms (Figs. 2 and 3) suggests that these peaks are due to less than adequate entrainment to the respective photoperiod.

In addition to circadian and some infradian peaks in the BASE condition, all spectra showed noticeable peaks at shorter periods. These included 6.0 h peaks (3 of 4 animals in the Standard photoperiod and 1 of 4 animals in the Skeleton schedule), and several other peaks between 2 and 6 h (except for Animal 3 under the Skeleton schedule). The 6.0 h peak probably reflects harmonic processes related to the 12 h peak. Peaks at shorter periods, though, most often occurred at nonharmonic intervals (Standard: Animal 1—3.6 h, Animal 2—2.6 and 4.3 h; Animal 3—4.0 h; Animal 4—3.3 hr. Skeleton: Animal 1—5.6 and 4.0 h; Animal 2—3.9 h; Animal 4—4.2 h).

Figure 6 shows the average median frequency (a) and duration (b) of nocturnal ONEs for both photoperiod schedules and each feeding condition. Diurnal ONEs were excluded for two reasons: first, because they were minimal and would add little to the results,and second, to maintain consistency with the rationale and implementation of the Fourier analysis. The average median scores were calculated over the final 6 days of each feeding condition. ANOVA revealed no significant effects of photoperiod schedule, feeding condition, or their interaction on the frequency of ONEs (all F's < 4.89, all p's $> .113$). ANOVA on the average median duration of ONEs also showed no main effect of photoperiod schedule, $F(1,3) = .09$, or interaction of photoperiod schedule and feeding condition, $F(3,9) = 3.47$. However, the main effect of feeding condition was significant, $F(3,9) = 4.63$. Tukey LSD tests showed that only the FWDO condition differed significantly from the BASE and RBASE conditions.

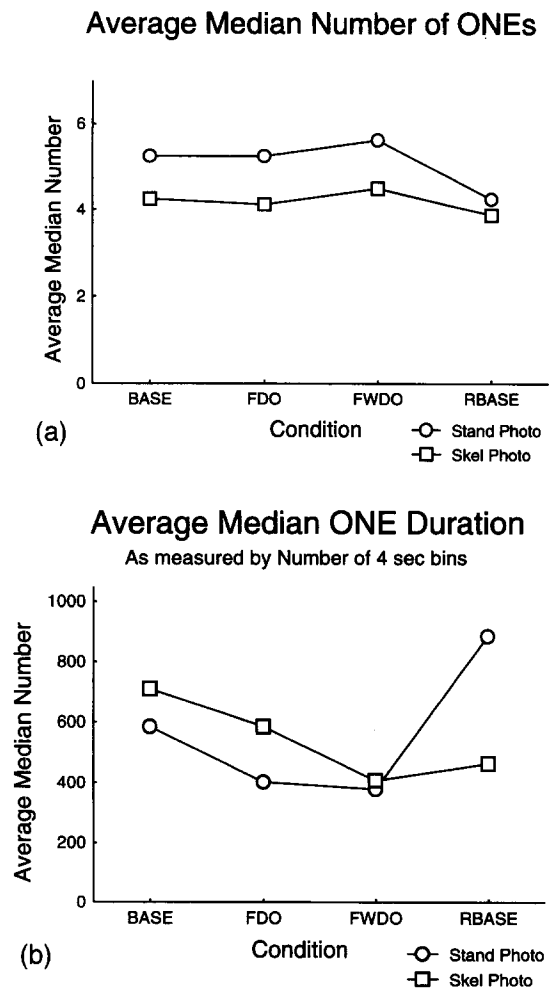

FIG. 6. (a) Average median number and (b) average median duration of ONEs as indexed by the number of 4 s bins within each ONE as a function of photoperiod schedule (Standard and Skeleton) and condition (BASE, FDO, FWDO, & RBASE).

Feeding Episodes (FEs)

Time series analyses of FEs during the BASE condition of both photoperiod schedules are shown in Figs 7 and 8. The most striking aspect of these spectra is the absence of a circadian rhythm except for Animal 3. All animals, though, showed peaks at periods between 0.7 and 4.4 h. As in the case of ONEs, there were similar but not identical periods of peaks for the Standard and Skeleton photoperiod schedules.

A visual comparison of these spectra of FEs with those of ONEs under the BASE conditions of the Standard and Skeleton photoperiods (Figs. 4 vs. 7 and 5 vs. 8) also showed several similar though not identical periods in the 2 to 6 h range. Animal 1 had a ONE peak at 3.6 h and an FE peak at 3.8, a difference of 0.2 h. Animal 2 had two similar peaks, one differing by 0.5 h and the other by 0.1 h. Animal 4 had one peak which differed by 0.1 h. In the Skeleton photoperiod schedule, only Animals 2 and 4 showed similar peaks, which differed by 0.1 h.

ONEs in the Food-and-Water-in-Day-Only Condition (FWDO)

Finally, we compared the frequency spectra for ONEs during the FWDO and BASE conditions under both Standard and Skeleton photoperiod to determine whether the rhythms observed in the BASE conditions had been affected by metabolic processes related to the FEs. Spectral density functions for each animal for the FWDO condition in both the Standard and Skeleton photoperiod schedules are presented in Figs. 9 and 10, respectively. We chose the FWDO condition (rather than the FWD condition) because it showed the greatest changes in the characteristics of ONEs relative to baseline.

Comparison of the Standard BASE and FWDO spectra (Figs. 4 vs. 9) showed that for three of the four animals the ultradian peaks were considerably altered in the absence of nocturnal food and water. Animal 4 changed less, though removal of food and water did cause the loss of the sole ultradian component in the BASE condition. Examination of the Skeleton BASE and FWDO spectra revealed similar effects (Figs. 5 vs. 10). Though change occurred for all animals, the form it took varied. One consistent change was a decrease in the relative importance of the circadian rhythmicity in the Standard photoperiod of the FWDO condition. Other changes characterized individual animals. For example, the spectra for Animal 3 appeared to increase in complexity under the FWDO condition as though the presence of ingestive behavior pulled together disparate rhythms. In contrast, the spectra for Animal 4, if anything, appear to decrease in complexity, as though the presence of food increased the number of rhythms present.

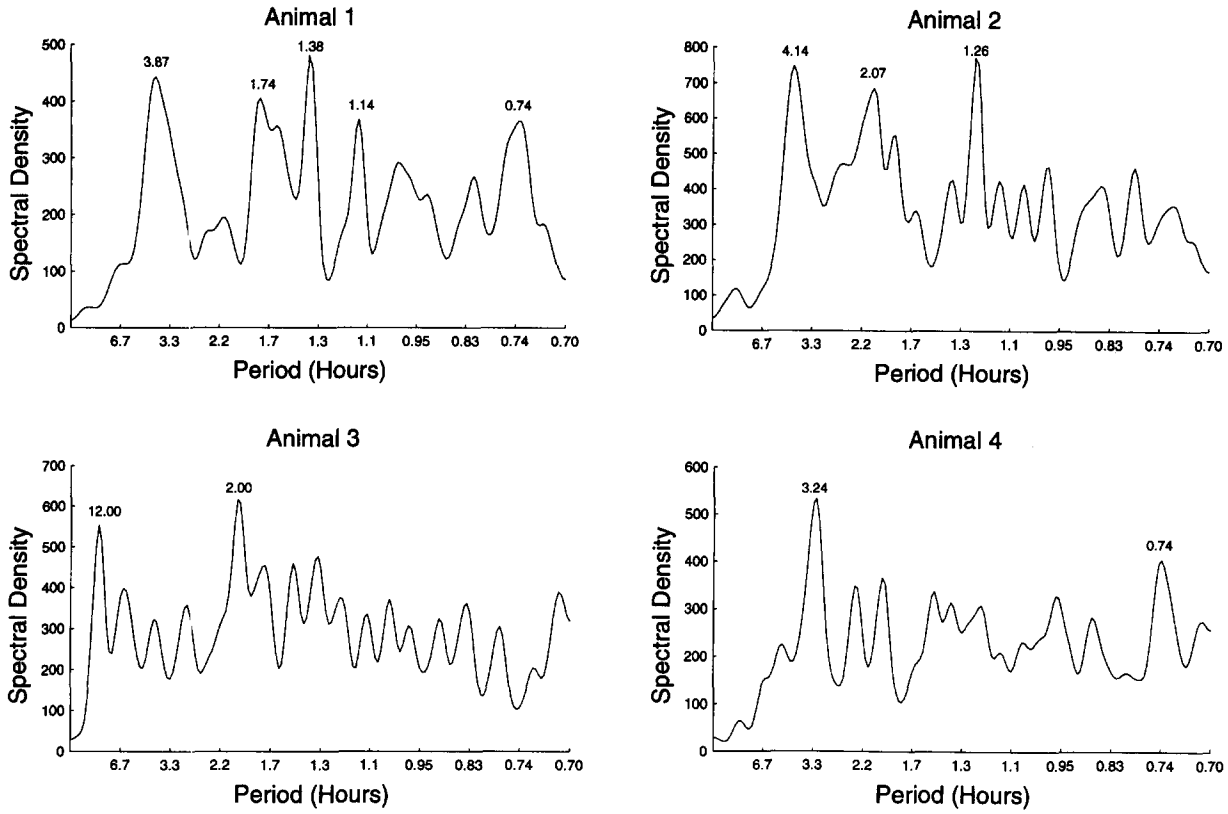

FIG. 7. Density spectra of FEs for each animal in the Standard Base condition. Each spectrum was smoothed using a Parzen function with a window of 15 points.

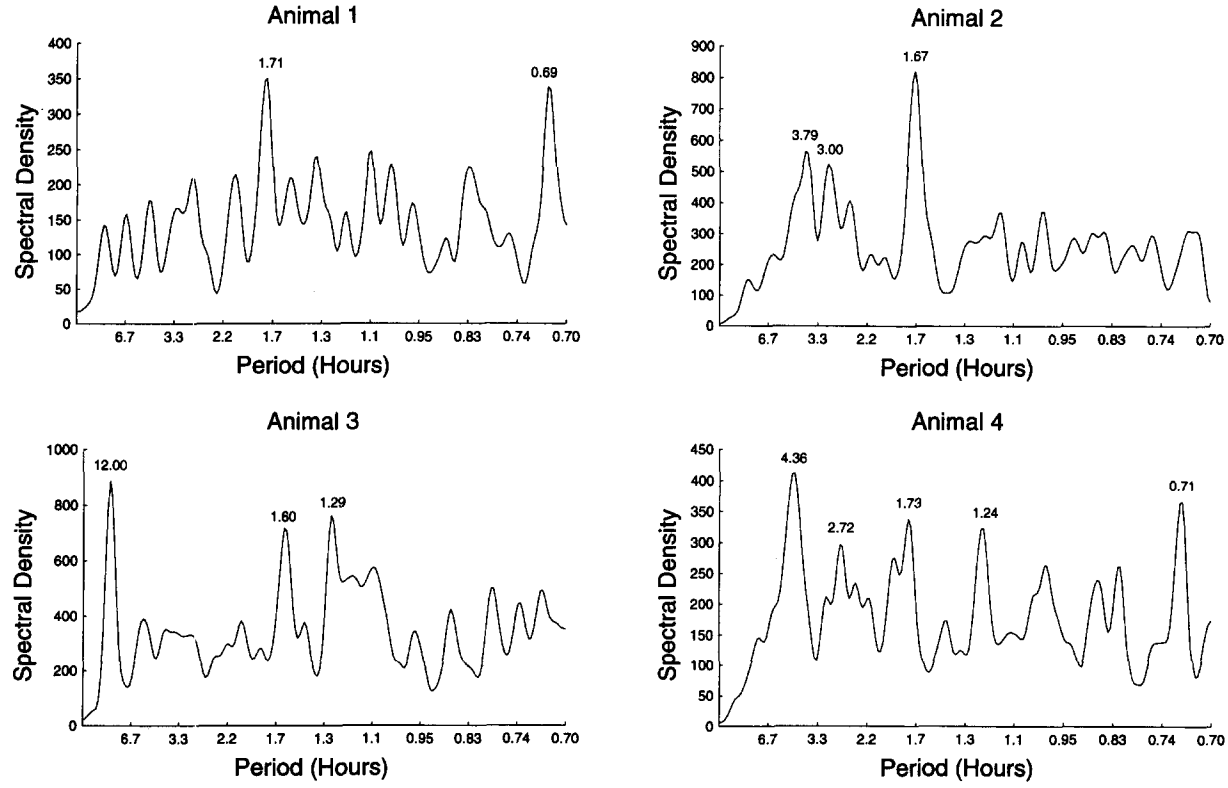

FIG. 8. Density spectra of FEs for each animal in the Skeleton Base condition. Each spectrum was smoothed using a Parzen function with a window of 15 points.

DISCUSSION

The data clearly show that laboratory rats are reliably episodic in their out-of-nest behavior (ONEs) and feeding episodes (FEs) under both Standard and Skeleton photoperiod schedules in a 24-h artificial environment. The frequency of nocturnal ONEs was remarkably constant across feeding conditions even when feeding was not allowed to occur during the nocturnal (active) portion of the cycle. However, the duration of ONEs decreased when food was restricted to the inactive portion of the photoperiod schedule.

Time series analyses in the form of spectral density functions produced by Fourier Transforms showed a strong circadian rhythm for ONEs but not FEs for three of the four animals in the baseline condition for both photoperiod schedules. Most importantly, the spectral density functions for both ONEs and FEs showed numerous peaks in the ultradian 2–6 h range with more peaks for FEs than for ONEs. The 2–6 h range of these peaks corresponds rather well to the time period of ultradian rhythms reported for voles (see 10, table 1; also 2, 5, 6). The ultradian peaks of FEs and ONEs were quite similar though not identical, suggesting that the two forms of episodic behavior shared some causal aspects as suggested by Lehmann (7) and Daan & Aschoff, (1). However, we know from the FWDO condition data that FEs and ONEs also show an important degree of independence. Finally, comparison of the spectral density functions of ONEs during the baseline condition with those when food and water were removed from the active part of the activity cycle (BASE vs. FWDO conditions) showed considerable change in periodicity, but the nature of the change was not consistent among animals.

These analyses showed very little effect of photoperiod schedule on the expression of episodic behavior. ONEs and FEs were almost exclusively concentrated in the active (nocturnal) portion of the rest activity cycle under both Standard and Skeleton photoperiods. Both circadian and ultradian cycles were expressed in both types of photoperiod. There were some alterations in the spectra as a function of Standard vs. Skeleton photoperiods, but most changes arguably were related to differences in the secureness of entrainment of the basic circadian activity rhythm. On the whole, our results support the argument that skeleton photoperiods generally have the same effect on behavior as normal photoperiods.

With respect to the determinants of the timing of episodic behavior in rats, the data clearly support an important contribution of ultradian rhythms to ONEs and FEs. Not only did all animals show rhythms in the 2–6 h range for nearly all conditions, ultradian rhythms continued to characterize ONEs even when food and water were removed from the active part of the cycle. This latter result raises the possibility that metabolic processes do not contribute at all to episodic behavior in rats. Instead, it might be argued that all daily episodic behavior, including feeding, is entirely controlled by "noisy" ultradian oscillators.

However, four aspects of these data suggest a role for processes related to feeding in determining daily episodic behavior. First, the periods of ultradian rhythms contributing to FEs, though very similar to, were not identical to the periodicities shown by ONEs. This suggested different determinants for the two behaviors. Second the average duration of ONEs was shortened when

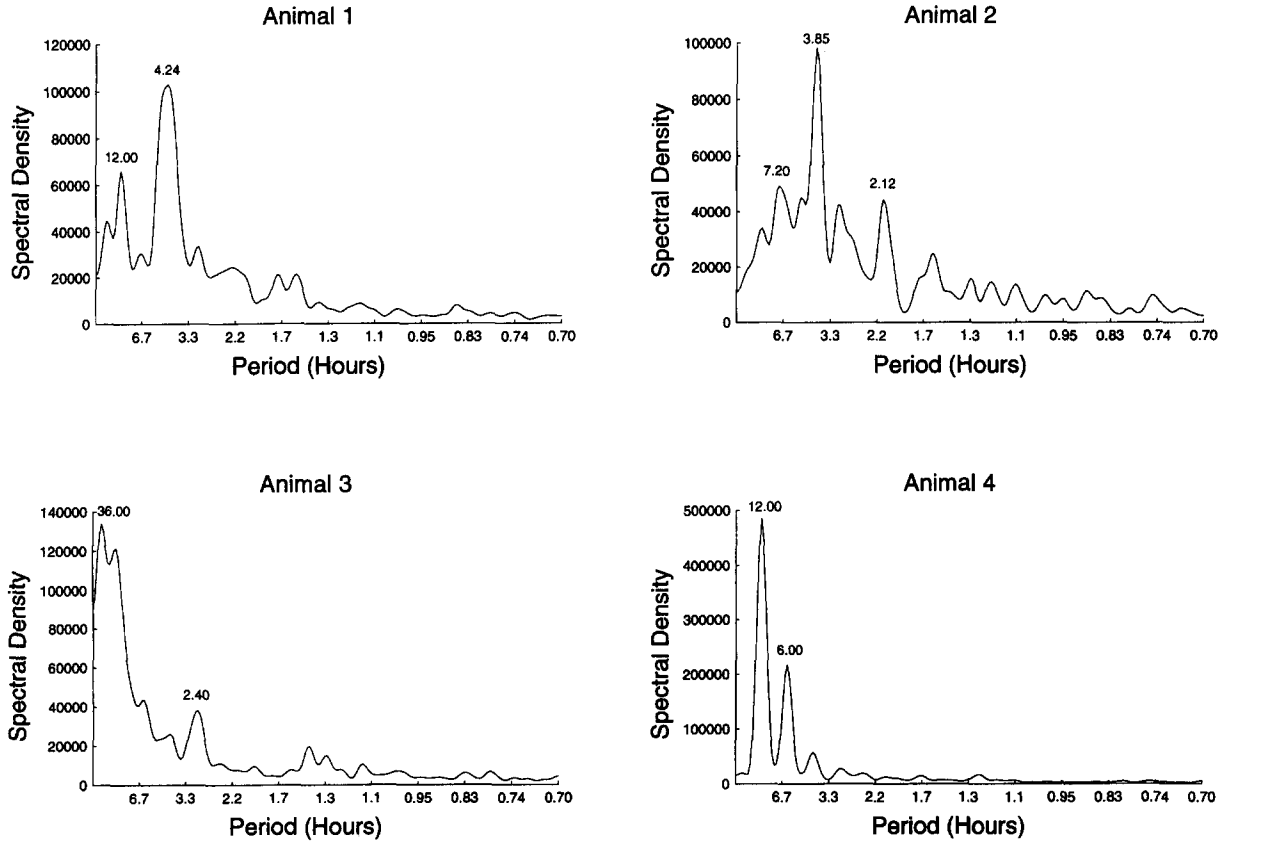

FIG. 9. Density spectra of ONEs for each animal from the Standard FWDO condition. Each spectrum was smoothed using a Parzen function with a window of 15 points.

access to food and water was removed from the nocturnal portion of the activity cycle. This result indicated that metabolic processes control at least the duration of episodic behavior. Third, the rhythmic aspects of ONEs was altered considerably when food and water were restricted to the inactive part of the cycle. In most cases, this alteration involved changes in the period of ultradian components (including a loss of an ultradian component in animal four). Fourth, the strength of the ultradian control of episodic behavior is not striking, at least relative to the importance of circadian control. Taken together, these data indicate that FEs and even ONEs are partially controlled by metabolic processes related to feeding even though independent ultradian rhythms appear to be the more important determinants.

The present results show a number of similarities between the control of freely occurring daily episodic behavior in laboratory rats and in voles. As in the case for voles, ONEs in rats appear more related to ultradian oscillators than metabolic processes. Also, ONEs in rats persist in the absence of food, a finding apparently similar to that of Gerkema and van der Leest (6) in voles. Finally, voles display weaker ultradian rhythms, like rats, during periods when the majority of their daily activity is restricted to the night portion of the L/D cycle (14).

However, it is also important to point out several differences between the daily episodic behavior of voles and rats. First, though voles resemble rats in distinguishing between diurnal and nocturnal ONEs, they differ in their behavior during the diurnal part of the cycle. Undisturbed rats provided with nests remain almost completely quiescent during the "light" part of the cycle. In contrast, voles continue to show rhythmic ONEs, although their behavior during the ONEs is restricted almost entirely to eating (see 7,10). This persistence of ONEs seems likely related to the voles herbivorous diet.

Second, vole ultradian rhythms depend on the season. During "winter," that is, periods of longer dark than light, voles' activity becomes diurnal with the majority of activity occurring during the light portion of the L/D cycle. During these periods, voles show strong ultradian rhythms and little or no circadian rhythmicity in activity. During "summer" periods of longer light than dark, voles' activity becomes restricted to the night portion of the L/D cycle. During these periods, voles display much weaker ultradian rhythms and a strong circadian rhythm, a pattern more similar to that of the rat (14). Third, denial of food during feeding times slightly alters the ultradian period of ONEs in rats while it apparently does not in voles (6). This suggests that metabolic processes may be somewhat more important to the expression of episodic behavior in rats.

In short, the results of this experiment support the conclusions that control of episodic behavior in rats by ultradian rhythms, similar in period to but weaker in strength than those found in voles. Further, in partial contrast to voles, control of episodic behavior by ultradian rhythms in the rat is restricted to the nocturnal part of the cycle. These ultradian processes appear to be slightly altered, but in no way eliminated, by removal of food during the active part of the cycle.

When combined with the work on voles (1,2,5, and 6), the present data suggest that similar ultradian oscillators function in both rats and voles, but that local metabolic processes add more variance in rats than in voles. As a larger, social omnivore, rats

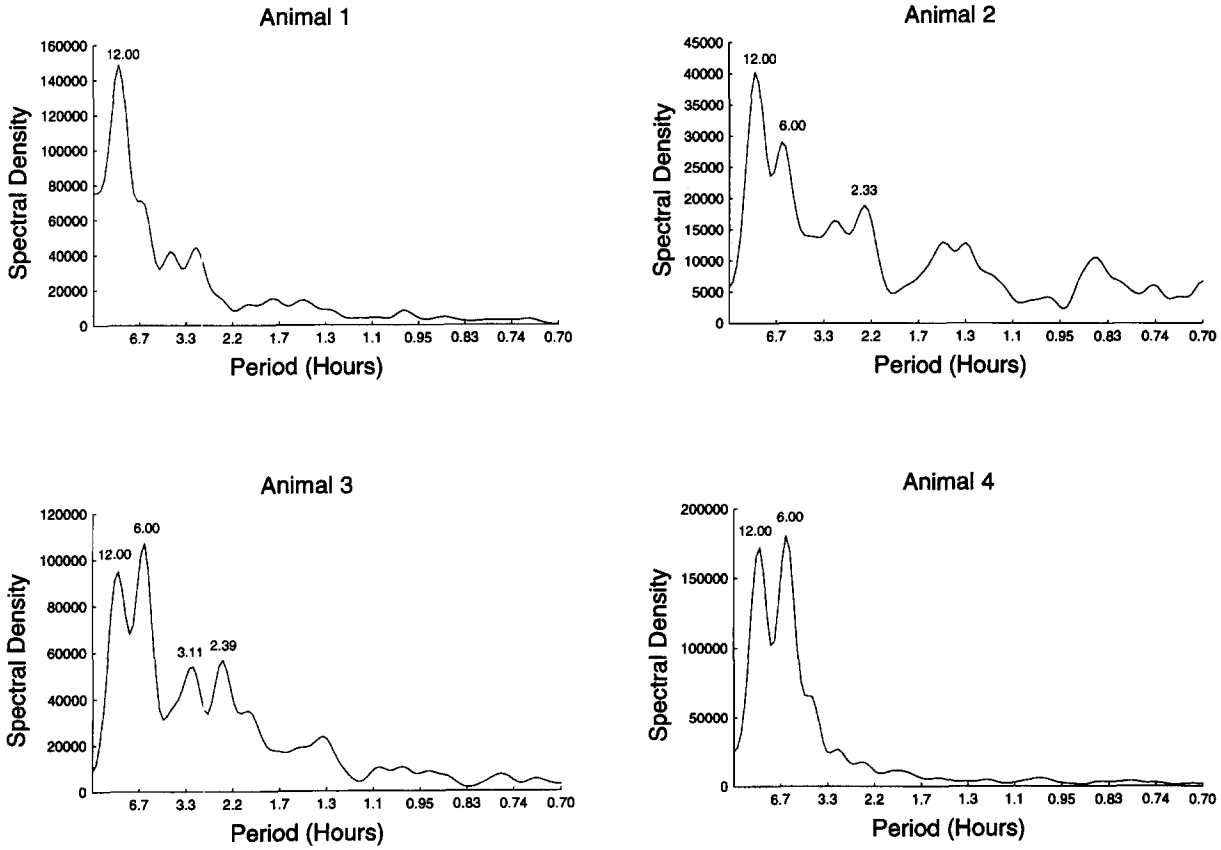

FIG. 10. Density spectra of ONEs for each animal under the Skeleton FWDO condition. Each spectrum was smoothed using a Parzen function with a window of 15 points.

may have evolved to take greater advantage than voles of learnable variation in food distribution and predator pressure. In contrast, the more constant feeding requirements of granivorous voles may have prevented dependence on such a strategy, instead producing population-wide ultradian rhythm-based synchrony in ONEs as an antipredator device based on flooding the environment with a large number of individuals at the same time. The result should be a decrease in the probability of any one individual being preyed upon (13). The changes to a more rat-like circadian behavior during the longer nights of winter when fewer predators are present can been seen as supporting this hypothesis.

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