Diurnal patterning of eight activities in 14 species of muroid rodents

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The diurnal patterning of locomotion, stereotypy, grooming, eating, drinking, sleeping, postural readjustment, and inactivity was studied in 14 species of muroid rodents in the laboratory using a visual observation technique. *Microtus canicaudus*, *M. montanus*, *M. ochrogaster*, and *M. pennsylvanicus* exhibited acyclic activity patterns, while *Peromyscus eremicus*, *P. gossypinus*, *P. leucopus*, *P. maniculatus bairdi*, *P. polionotus*, *Calomys callosus*, *Mus musculus*, and *Onychomys leucogaster* displayed nocturnality in their behavioral patterning. *Rhabdomys pumilio* exhibited crepuscular activities and *Neofiber alleni* displayed a complex pattern of nocturnality. Species differed in total amount of time spent per day for all activities but eating. The acyclicity of *Microtus* species appears to be related to high metabolic rates and a semi-fossorial life-style.

The purpose of this study was to provide a comparative assessment of activity patterns exhibited in the laboratory by members of a number of species belonging to the superfamily Muroidea. In order to furnish an adequate account of rodent activity patterns, a broad foundation of descriptive data should be available for a substantial number of species that bear close phylogenetic relatedness but typically occur throughout a wide range of habitats.

Previous investigators have evaluated the activity patterns of a large number of muroid species, concentrating primarily on species from the genera *Microtus* and *Peromyscus* (e.g., Layne, 1971; O. P. Pearson, 1960). A variety of methods have been utilized in these studies. Field studies of rodent activity patterns have included the use of direct field observations (e.g., Thompson, 1977), photographic techniques (e.g., Carley, Fleharty, & Mares, 1970), trapping records (e.g., Birkenholz, 1963; Daan & Slopsema, 1978), radio-telemetry (e.g., Shields & Sjöberg, Note 1), track counts in the substrate (cited in Falls, 1968), and the smoked card technique (e.g., Sheppe, 1965). Although data drawn from the field by the use of such techniques provide an accounting of animal behavior under naturally encountered conditions, the behavior under consideration is additionally influenced by such uncontrolled factors as climatic changes, food availability, and other ecological variables. In addition, each technique has drawbacks stemming from inherent biases in the estimation of the actual occurrence of activities. Laboratory measurements, while not providing a description in the natural environment, have an advantage in allowing the control and manipulation of particular variables believed

to influence the behaviors in question. Procedures used in the laboratory by various investigators include the use of running wheels (e.g., Kavanau, 1967), various types of stabilimeter cages (e.g., Stinson, 1960), direct observational techniques (e.g., Choate, 1972), the monitoring of food and water delivery systems (e.g., Toates, 1978; Toates & Ewart, 1977), gates, treadles, and photocell beams activated by movement from one area to another (e.g., Cheeseman, 1977), ultrasonic measurement devices (e.g., Peacock, Hodge, & Thomas, 1966), and metabolic rate monitors (e.g., Hart, 1952). The purpose of this study was to provide quantitative information on various individual activity patterns for a number of rodent species in a laboratory setting and to endeavor to relate such data to the phylogeny and ecology of these species.

EXPERIMENT 1

Method

Subjects. A total of 165 animals from 14 species of muroid rodents served as subjects. The following species were included: *Peromyscus eremicus* (cactus mice), *P. gossypinus* (cotton mice), *P. leucopus* (white-footed mice), *P. maniculatus bairdi* (deer mice), *P. polionotus* (old field mice), *Microtus canicaudus* (gray-tailed voles), *M. montanus* (montane voles), *M. ochrogaster* (prairie voles), *M. pennsylvanicus* (meadow voles), *Calomys callosus* (laucha de campo), *Mus musculus* (house mice), *Neofiber alleni* (round-tailed muskrats), *Onychomys leucogaster* (northern grasshopper mice), and *Rhabdomys pumilio* (African striped mice). With the exception of *N. alleni*, 12 males of each species between 90 and 120 days of age were observed. Nine *N. alleni* were used, and they ranged in age from 5 to 44 months. All animals were laboratory bred. Females were excluded from the study to avoid the imposition of estrous cycle variation on the results.

Housing conditions and Apparatus. All animals were maintained on a reversed 16:8 h photoperiod. For *Microtus* species, the lights came on at 2000 h and went off at 1200 h. For all other species, the lights came on at 1730 h and went off at 0930 h. White light was provided via overhead room illumination with dim red

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light continuously present. All animals except *N. alleni* were individually housed in clear plastic cages, 29×19×13 cm. *N. alleni* were housed in cages measuring 38×20×48.5 cm. San-i-cel was used as a substrate for all animal cages. Food and water were continuously available. *Microtus* and *Neofiber* were provided with both Purina laboratory animal and rabbit chows, while all other species were fed only Purina laboratory animal chow.

Procedure. The animals were placed into clean cages with new substrate and immediately transferred to the testing room to adapt to room conditions for 60 h prior to the beginning of recording periods. One of two observers conducted all recordings. Interobserver reliability was calculated on the basis of 100 measurements each for three *P. m. bairdi* and three *M. ochrogaster*. Interobserver agreement for the two observers was obtained by dividing the number of agreements by agreements plus disagreements and multiplying by 100. Interobserver reliability for individual activity patterns ranged from 97% to 100%. An average of 12 animals (range 6-18) were observed across each 24-h recording period. Observations were conducted every other hour within a 24-h period. Although this method entailed periodic disturbance of the animals, a 10-20-min period of adaptation to the observer served to minimize such intrusion. Little, if any, change in an animal's behavior was noted in the period prior to observations. Within each observation hour, the behavior of each animal was recorded once every 60 sec, using an instantaneous sampling procedure (Altmann, 1974). Behaviors were recorded by the observer on a checklist. An attempt was made to maintain a consistent scan duration, that is, the amount of time per complete scan of animals under observation at a given time. Scan durations varied as a function of light-dark phase, the number and species of animals being observed, and the individual observer, ranging from approximately 10 to 40 sec per minute interval. Each animal was observed for one complete 24-h cycle. Animals from various species were tested during the same cycle. That is, for any one 24-h period, any combination of species having similar light onset-offset times was observed. Each animal was scored as emitting or engaging in one of the following, mutually exclusive behaviors: sleep—behavioral quiescence with the eyelids closed; inactivity—behavioral quiescence with the eyelids open; postural readjustment—whole-body readjustments which occurred during bouts of sleep or inactivity, for example, stretching, yawning, etc.; locomotion—moving about the cage, sniffing, exploring the substrate; stereotypy—repetitive, relatively invariable movements, for example, back flips, gnawing of the cage, continuous circling, etc.; grooming—preening, scratching, licking, and biting of the animal's own body; eating—manipulation or ingestion of food items and substrate; and drinking—contact with the tip of the water-bottle spout and ingestion.

Results

Hour-by-hour analysis. Individual behavioral patterns were grouped into two broad composite categories: composite activity—locomotion, stereotypy, grooming, eating, and drinking—and composite inactivity—sleep and postural readjustment. The individual category of inactivity was not included in this analysis because of its apparent lack of relationship to other measures. The measure of inactivity may have been too inclusive to accurately assess sleep-related behaviors. As defined, inactivity included events such as freezing, which often occurred during bouts of locomotion and stereotypy as well as other measures of composite activity.

Figures 1a, 1b, 1c, and 1d present the percentage of intervals within an hour in which the animals engaged in composite activity or inactivity over the

course of 24 h. Four different activity patterns are to be noted. First, nocturnality is the most prevalent daily pattern. All species of the genus *Peromyscus* exhibited composite activity cycles with a unimodal activity peak occurring at approximately the midpoint of the dark phase. Similar nocturnal activity patterns were also apparent for *C. callosus*, *M. musculus*, and *O. leucogaster*.

The second pattern is that demonstrated by the *Microtus* species, which shows the greatest departure from diurnal patterning of any sort. Activity patterns of *Microtus* appeared acyclic in that no rhythmicity of any sort is apparent on an hour-by-hour analysis.

A third pattern is exhibited by *R. pumilio*, which appeared unique in exhibiting a very marked crepuscular rhythm with activity peaks occurring immediately prior to light onset and offset.

The fourth pattern, characteristic of *N. alleni*, was complex, with a general increase in activity in the dark phase but a sharp curtailment of activity in the middle of that phase.

Generally, the daily trends of composite activities and inactivities were paralleled by similar patterning for the individual behaviors included in each category. However, some behaviors, for example, eating and drinking, often occurred at such low rates as not to appear to exhibit any cycle for some species.

Although data collected by instantaneous sampling are not appropriate to assess the sequence of activity patterns, it was independently noticed by both observers that rather long bouts of grooming typically preceded sleep.

Phase-by-phase analysis. Nocturnal ratios, indexes derived by calculating the total time spent in a given activity in the dark phase divided by the total time spent in that activity in the light phase, were obtained for all species for each behavior pattern. These were corrected for differences in duration of the light and dark phases. Graphic representation of these ratios is depicted in Figure 2. Values greater than one represent a higher percentage of behavior occurring nocturnally, whereas values of less than one denote a greater proportion of behavior occurring during the light phase. The nocturnal ratios of each behavior category show close agreement with the patterning of the composite indexes. In general, locomotion, stereotypy, grooming, eating, and drinking show similar periodicity, while sleep and postural readjustment show an inversely related time course but a similar periodicity. Inactivity shows the largest departure from cyclicity, showing no clear pattern across species.

Activity levels. The percentage of time that members of a species engaged in a particular behavior during the light phase, dark phase, and the entire day is shown in Table 1. These data exhibit some similarity within genera and a larger disparity among

Figure 1. Percentage of intervals per hour spent in composite activity and inactivity for 14 species of muroid rodents in Experiment 1. Composite activity includes locomotion, stereotypy, grooming, eating, and drinking. Composite inactivity includes sleep and postural readjustment. The area underneath the dark bar represents the dark phase of the photoperiod. (a) Pe = *P. eremicus*; Pg = *P. gossypinus*; Pl = *P. leucopus*; Pmb = *P. maniculatus bairdi*; Pp = *P. polionotus*; (b) Mc = *M. canicaudus*; Mm = *M. montanus*; Mo = *M. ochrogaster*; Mp = *M. pennsylvanicus*; (c) Cc = *C. callosus*; Mm = *M. musculus*; Ol = *O. leucogaster*; and (d) Na = *N. alleni*; Rp = *R. pumilio*.

Figure 2. Nocturnal ratios of eight activities for 14 species of muroid rodents in Experiment 1. Nocturnal ratios are indexes derived by calculating the percentage of intervals spent in a given activity in the dark phase divided by the percentage of intervals spent in that activity in the light phase. Key: Pe = *P. eremicus*; Pg = *P. gossypinus*; Pl = *P. leucopus*; Pmb = *P. maniculatus bairdi*; Pp = *P. polionotus*; Mc = *M. canicaudus*; Mm = *M. montanus*; Mo = *M. ochrogaster*; Mp = *M. pennsylvanicus*; Cc = *C. callosus*; Mm = *M. musculus*; Na = *N. alleni*; Ol = *O. leucogaster*; Rp = *R. pumilio*.

genera. One-way analyses of variance were conducted examining the percentage of intervals for the total day spent in each behavior for all 14 species. All tests showed highly significant differences between species, with p levels often substantially lower than $p < .001$ [locomotion, $F(13,154) = 2.27$; stereotypy, $F(13,154) = 2.58$; grooming, $F(13,154) = 8.54$; drinking, $F(13,154) = 12.07$; sleep, $F(13,154) = 3.03$; postural readjustment, $F(13,154) = 3.69$; and inactivity, $F(13,154) = 20.09$]. Only eating failed to show any significant differences when analyzed across species [$F(13,154) = 1.14$, $p < .33$].

EXPERIMENT 2

Although data obtained in Experiment 1 strongly suggested significant differences in the cyclicity of *Microtus* and *Peromyscus* species, the possibility could not be excluded that the disparity between genera was due to the different diets and times of light onset/offset to which the genera were exposed. Experiment 2 was conducted to assess the influence of these two variables on *Microtus* and *Peromyscus* activity patterns.

Method

Twelve male *M. ochrogaster* were maintained on Purina Lab Chow and exposed to a reversed 16:8 h photoperiod, with light onset at 0930 h. Twelve male *P. m. bairdi* were exposed to a similar photoperiod, except that light onset was at 1200 h. The diet of these animals was Purina Rabbit Chow. All animals were under these conditions for 2 weeks prior to the beginning of behavioral observations. All other procedures were as stated in Experiment 1.

Results

Figure 3 presents the percentage of intervals within an hour in which *M. ochrogaster* and *P. m. bairdi* engaged in composite activity and composite inactivity over a 24-h period. It is apparent that *P. m. bairdi* exhibits a marked nocturnality while *M. ochrogaster* displays a relatively acyclic pattern of activity.

To compare the amount of time engaged in individual activities by *M. ochrogaster* and *P. m. bairdi* in Experiments 1 and 2, t tests were performed. There were essentially no differences for *M. ochrogaster*, except that animals in the first experiment displayed more postural readjustment [$t(11) = 3.91$, $p < .01$].

P. m. bairdi in Experiment 1 exhibited less grooming [$t = 3.89$, $p < .01$] and more eating [$t = 2.65$, $p < .05$] than *Peromyscus* in Experiment 2.

Table 1
Mean Percentages of Total Day, Light, and Dark Phases of Eight Behaviors for 14 Species of Muroid Rodents

	Percent- age	Loco- motion	Stereo- typy	Groom- ing	Eat- ing	Drink- ing	Sleep	Postural Read- justment	Inacti- vity
<i>P. eremicus</i>	Dark	17.74	22.15	13.89	16.25	1.70	11.67	.56	15.80
	Light	2.22	.85	8.35	4.22	.35	62.60	1.30	19.98
	Day	7.40	7.95	10.20	8.23	.80	45.62	1.05	18.59
<i>P. gossypinus</i>	Dark	21.91	14.03	13.54	11.53	1.81	8.44	.80	26.56
	Light	4.67	.16	7.41	2.41	.12	44.43	1.72	38.49
	Day	10.42	4.78	9.46	5.45	.68	32.43	1.41	34.51
<i>P. leucopus</i>	Dark	10.62	2.05	20.90	14.72	.80	29.41	1.32	19.83
	Light	3.49	.00	12.41	5.94	.17	65.10	1.70	11.34
	Day	5.87	.68	15.24	8.87	.38	53.21	1.57	14.17
<i>P. m. bairdi</i>	Dark	9.93	36.84	11.35	16.98	.35	11.81	.90	11.84
	Light	3.65	.71	7.24	4.41	.23	74.81	1.28	7.52
	Day	5.74	12.75	8.38	8.60	.27	53.81	1.16	8.96
<i>P. polionotus</i>	Dark	17.85	32.15	9.06	18.09	.49	9.06	.28	13.06
	Light	2.47	3.66	6.06	2.55	.17	77.62	1.53	5.82
	Day	7.59	13.16	7.06	7.72	.59	54.77	1.12	8.23
<i>M. canicaudus</i>	Dark	6.42	4.13	18.30	6.94	2.19	42.64	1.25	17.78
	Light	5.78	1.46	15.24	6.94	2.12	46.18	1.39	20.02
	Day	6.00	2.35	16.26	6.94	2.14	45.00	1.34	19.27
<i>M. montanus</i>	Dark	12.50	7.22	13.19	8.78	2.50	39.72	1.80	14.27
	Light	8.09	2.95	11.79	10.16	2.76	51.53	2.00	10.75
	Day	9.56	4.38	12.26	9.70	2.67	47.59	1.93	11.92
<i>M. ochrogaster</i>	Dark	4.13	5.52	11.84	6.18	1.18	53.96	2.26	14.05
	Light	5.28	2.40	8.26	5.87	1.53	69.08	1.89	5.42
	Day	5.02	3.44	9.46	5.97	1.41	64.04	2.01	8.50
<i>M. pennsylvanicus</i>	Dark	7.74	5.31	13.54	4.27	2.99	53.54	1.98	12.74
	Light	7.31	1.30	11.30	5.38	3.26	59.08	2.14	10.30
	Day	7.45	2.64	12.05	5.01	3.17	57.23	2.08	11.11
<i>C. callosus</i>	Dark	13.92	10.76	19.90	28.75	1.91	3.54	.28	22.08
	Light	4.41	.00	9.25	4.34	.10	41.96	1.42	36.61
	Day	7.00	3.59	12.80	12.48	.71	29.16	1.04	33.10
<i>M. musculus</i>	Dark	30.49	3.78	19.20	14.34	.94	8.68	.35	23.23
	Light	7.36	.00	16.41	5.28	.16	47.20	1.32	22.24
	Day	15.07	1.26	17.34	8.00	.42	34.36	1.00	22.57
<i>N. alleni</i>	Dark	21.71	5.09	7.78	9.21	5.51	44.03	1.57	5.09
	Light	5.93	.28	9.19	5.90	3.12	69.28	1.67	6.20
	Day	11.19	1.88	8.72	7.01	3.92	60.86	1.71	5.83
<i>O. leucogaster</i>	Dark	19.20	32.15	9.65	16.98	2.36	15.24	.83	12.27
	Light	3.00	1.18	6.82	2.57	.47	83.16	1.86	1.08
	Day	8.40	11.50	7.77	7.37	1.10	60.52	1.52	1.97
<i>R. pumilio</i>	Dark	9.41	3.33	8.40	4.41	.73	54.44	1.08	18.19
	Light	15.78	6.96	8.11	9.79	1.27	27.12	1.34	29.64
	Day	13.66	5.75	8.21	8.00	1.09	36.23	1.25	25.82

Thus, while there is a slight amount of variability in levels of individual activities, it should be emphasized that there were no differences in either composite activity, composite inactivity, or individual activity patterns (not shown) between *M. ochrogaster* and *P. m. bairdi* tested in Experiments 1 or 2.

GENERAL DISCUSSION

The data reveal a marked difference between the activity rhythms of the two primary genera in this study. Those animals belonging to the genus *Peromyscus*

showed a nocturnal periodicity, while the *Microtus* exhibited an essentially acyclic pattern. All other species studied, with the exception of *R. pumilio* and *N. alleni*, exhibited nocturnally active behavior patterns, although the pattern of *N. alleni* is complex. *R. pumilio* was the sole species studied which displayed a crepuscular rhythm of activities.

Previous research on *Peromyscus* species indicates strong nocturnality within the genus. This is true for all of the species included in this study, including *P. maniculatus* (Carley et al., 1970), *P. gossypinus* (Layne, 1971), *P. polionotus* (Ehrhart, 1972), *P.*

Figure 3. Percentage of intervals per hour spent in composite activity and composite inactivity for *M. ochrogaster* and *P. m. bairdi* in Experiment 2. Composite activity includes locomotion, stereotypy, grooming, eating, and drinking. Composite inactivity includes sleep and postural readjustment. The area under the upper dark bar represents the dark phase of the photoperiod of *P. m. bairdi*; the area under the lower dark bar represents the dark phase of the photoperiod of *M. ochrogaster*.

leucopus (Behney, 1936; Hill, 1972; Johnson, 1926; Orr, 1959; O. P. Pearson, 1947), and *P. eremicus* (Kavanau, 1978). One exception to such findings is for *P. eremicus*, which McNab and Morrison (1963) have studied in its desert habitat. They found that cactus mice were essentially crepuscular and believed this to be partially a function of high ambient temperature (35°C). Stinson (cited in Falls, 1968) has provided sufficient evidence concerning the regulatory effect of temperature on activity. Given the moderate temperatures maintained in this study, the present finding that *P. eremicus* is nocturnal is probably congruent with previous data.

Activity patterns of *Microtus* have not been as thoroughly studied as those of *Peromyscus*, nor are the data so consistent within the genus. *M. pennsylvanicus* has been reported as being diurnal (Emlen, Hine, Fuller, & Alfonso, 1957) and acyclic (Hamilton, 1937a, 1937b). The activity patterns of *M. montanus* have likewise been reported to be diurnal (Petterborg & Negus, Note 2), nocturnal (Petterborg & Negus, Note 2), and acyclic (Maser & Storm, 1970). *M. ochrogaster* periodicity has been reported as being both diurnal (Carley et al., 1970; Martin, 1956) and nocturnal (Calhoun, 1945). We have been unable to locate any reports of activity patterns for *M. canicaudus*. All *Microtus* in this study uniformly displayed acyclic activity patterns.

Mus musculus is a nocturnal species (e.g., Aschoff, 1960), although some crepuscularity has been reported when activities are assessed via a stabilimeter cage (Aschoff & Honma, 1959). Our findings indicate that this species is strongly nocturnal.

The activity patterns of *N. alleni* have not been intensively studied, but what information does exist suggests that this species is primarily nocturnal (Birkenholz, 1963, 1972). The nocturnal periodicity

reported by Birkenholz is in general agreement with the data reported here, although he does note the finding of diurnal activity by one investigator.

R. pumilio has been reported to be chiefly diurnal (Choate, 1972; Delany & Neal, 1966; Roberts, 1951; Shortridge, 1934). These reports are not consistent with the results of this study or those of Dewsbury and Dawson (1979), in which *R. pumilio* displayed a marked crepuscular rhythmicity for wheel running. Choate (1972), however, has conducted a combined laboratory and field investigation of *Rhabdomys* behavior. He, too, has found *Rhabdomys* to be largely diurnal, as assessed by visual observations recorded on an event recorder. The partial discrepancy between the results reported here and those of Choate may be attributable to his use of a smaller number of animals (two) and a different photoperiod (12:12) than used in this study. Furthermore, it should be noted that if one were to consider the nocturnal ratios derived from our data (see Figure 2), in fact, *R. pumilio* may best be described as being diurnal/crepuscular in its patterning of activities.

As has been previously reported (Bailey, 1971), we have found *O. leucogaster* to be primarily nocturnal. We have been unable to locate any data pertaining to activity patterns of *C. callosus*. Our findings of strong nocturnality for this species appear typical for most rodents.

Table 2 presents information on species included in this study, including their periodicity, mode of living, and basal metabolic rates (BMR).

Metabolic rates obtained for other species of the genera *Microtus* and *Peromyscus* not included in this study appear quite similar to those included in this study. Basal metabolic rates (cc O₂/g/h) for 15 taxa of *Peromyscus* species range from 1.03 to 1.79 (Glenn, 1970; MacMillen, 1965; McNab & Morrison, 1963;

Table 2
Periodicity of Rodents Included in This Study Together With Information on Mode of Living and Basal Metabolic Rates

Species	NR	Mode of Living	Basal Metabolic Rate* (cc O ₂ /g/h)	Source (BMR)
<i>P. eremicus</i>	4.49	terrestrial	1.48-1.60 (1.56)	McNab & Morrison, 1963; Macmillen, 1965
<i>P. gossypinus</i>	4.25	semiarboreal	1.72	Glenn, 1970
<i>P. leucopus</i>	2.23	semiarboreal	1.46-1.63 (1.55)	Morrison, 1948
<i>P. m. bairdi</i>	4.65	terrestrial	1.55-1.65 (1.60)	Morrison, 1948
<i>P. polionotus</i>	5.21	terrestrial/semifossorial	1.79	Glenn, 1970
<i>M. canicaudus</i>	1.20	semifossorial	2.50	McNab, Note 3
<i>M. montanus</i>	1.24	semifossorial	2.65	Packard, 1968
<i>M. ochrogaster</i>	1.23	semifossorial	2.20	McNab, Note 3
<i>M. pennsylvanicus</i>	1.19	semifossorial	2.77	Wiegert, 1961
<i>C. callosus</i>	4.16	terrestrial	N/A	
<i>M. musculus</i>	2.35	variable	1.53-1.79 (1.66)	Morrison, 1948
<i>N. alleni</i>	2.02	semiaquatic	.84	McNab, Note 3
<i>O. leucogaster</i>	5.72	terrestrial/semifossorial	1.30	Altman & Dittmer, 1971
<i>R. pumilio</i>	.63	terrestrial	N/A	

NOTE—NR = nocturnal ratios of composite activity.

*The BMR given in parentheses designates the figure used in computing the correlations described in the text.

Morrison, 1948; O. P. Pearson, 1947), while metabolic rates for 11 taxa of microtines (excluding *N. alleni*) range from 2.20 to 3.14 (Bienkowski & Marszalek, 1974; Daan & Slopsema, 1978; Gorecki, 1968; Hanson & Grodzinski, 1970; Packard, 1968; A. M. Pearson, 1962; O. P. Pearson, 1947; Wiegert, 1961; McNab, Note 3). Such disparity between genera appears to be correlated with the periodicity of activity patterns for the genera. A Pearson product-moment correlation coefficient was calculated to assess any relationship existing between basal metabolic rate and the nocturnal ratio of composite activity for the 12 species in this study for which both types of information were available. Although possibly suggestive of the direction of relationship, the degree of relationship appears to be moderate ($r = -.56$), perhaps attributable in part to the small number of species that could be examined here. When the relationship between BMR and composite inactivity is examined, however, a significant correlation was found to exist ($r = .64$, $p < .05$). When only *Microtus* and *Peromyscus* species were included in the analysis, substantially higher correlations were found to exist for both composite activity and BMR ($r = .79$, $p < .02$) and composite inactivity and BMR ($r = .89$, $p < .001$).

Mann-Whitney U tests were conducted comparing *Microtus* and *Peromyscus* species on the measures of composite activity, composite inactivity, and BMR. Although none of the *Microtus* data were overlapping with those of the *Peromyscus* species, only a comparison of composite activity between the two genera was found to be statistically significant ($p < .008$).

Microtus species are believed to be one of the few forms of small mammals which exhibit substantial activity in the daytime, due in part to feeding within dense cover and having great food requirements (Cloudsley-Thompson, 1961). All *Microtus* species

studied share what is an essentially semifossorial existence (e.g., Hooper & Hart, 1962), live in moderately cold environments, and appear to require feeding at regular intervals throughout the day (Daan & Slopsema, 1978; Hatfield, 1940; Kavanau & Havenhill, 1976). Such ecological factors which relate directly to energetic requirements have determined, in part, the relatively high metabolic rates these animals exhibit as compared to those of other muroid rodents. Because of the high nutritional and energetic requirements imposed by such factors, it follows that these semifossorial rodents would by necessity evolve in such a way as to regulate their food intake so as to meet the demands of their high metabolism. One strategy for maintaining such high levels of energy intake might be to exhibit relatively acyclic patterns of locomotion and exploration along with concomitantly high levels of ingestive behavior at all times of the day.

One very interesting, and potentially conflicting, piece of information pertains to the finding that eating was the only behavior which, when analyzed in terms of percentage of 24 h spent in that activity, failed to show significant species differences. All other individual activities showed remarkably large species differences for such percentages. If, as has been hypothesized here, voles exhibit acyclic behavior patterns due to high energetic requirements, why then should all species show equivalent values for time during the day spent eating? One possibility is that our measure of eating was too unrefined to assess accurately the true percentage of time spent in eating behavior. Nibbling the substrate was included in this category due to the inability to distinguish food from all other foreign items under the current testing conditions. Furthermore, both duration of eating bouts and the type and amount of food consumed may differ substantially among the genera.

Several qualifications must be made regarding the

data obtained in this study. First, it should be noted that the photoperiods were step-changed. Kavanau (e.g., 1967) has demonstrated, for at least some of the species included in this study, that the presence of artificial twilights may influence the running speed of rodents in running wheels.

Second, Rusak and Zucker (1975) have reviewed evidence suggesting that the addition of a continuously darkened area to a laboratory environment, analogous to a nesting site in the natural habitat, may alter activity and feeding patterns exhibited by at least some species of rodents. The animals in this study had no such available area.

Finally, the animals in the two primary genera in this study were maintained on different diets and were subject to different times of light onset/offset. The particular settings of light onset/offset and the selection of the diets employed in this study were those which had proven optimal for the maintenance of laboratory breeding in these species. Data obtained in Experiment 2 strongly suggest that the influence of these variables is negligible, at least under the conditions employed in this study. When the diet and times of light onset/offset were reversed for *P. m. bairdi* and *M. ochrogaster*, both species continued to exhibit the patterns of cyclicity found for these animals in Experiment 1.

Of interest here is the recent work by Daan and Slopsema (1978) with *Microtus arvalis*, which is characterized by a high metabolic rate and acyclic activity rhythm. They assessed short-term activity patterns in the field via trapping records and then monitored running-wheel activity and ingestive behavior in the laboratory with the same animals. While running-wheel activity was exhibited virtually only during the dark phase, feeding occurred throughout both light and dark phases. When the photoperiod was altered, subjecting the animals to continuous darkness, both running-wheel activity and feeding activity remained the same as that shown on a LD 12:12 photoperiod. The only disparity was that the temporal patterning now approximated a cycle of slightly greater than 24 h in length. This finding, along with that of Lehmann (1976) with *M. agrestis*, which was exposed to continuous light, strongly suggests that this meal patterning is of endogenous origin and not dependent on light changes.

In summary, the acyclicity of *Microtus* species appears to be determined in part by their relatively cold habitat, which serves to promote high metabolic rates in these animals. So as to maintain these metabolic rates while ingesting low nutritional food, *Microtus* must apparently remain active throughout the day, unlike the nocturnal activity typical of most rodents.

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