Seasonal Variations in Circadian Rhythms of Deer Mice, in Northwestern Canada

LUCIUS L. STEBBINS[1]

ABSTRACT. Circadian rhythms of *Peromyscus maniculatus* were studied at Heart Lake, Northwest Territories, in winter and spring of 1965-1966. Daily peaks of activity were of longer duration and higher amplitude in spring than in winter. In winter deer mice were frequently observed in torpor and most activity occurred at night. In spring daily peaks of activity began before dark and extended 4 to 5 hours into daylight of the next morning.

RÉSUMÉ. *Variations saisonnières dans le rythme circadien de la Souris à pattes blanches,* Peromyscus maniculatus, *dans le Nord-ouest du Canada.* Au cours de l'hiver et du printemps 1965-66, on a étudié le rythme circadien de *Peromyscus maniculatus* à Heart Lake, Territoires du Nord-Ouest. Les sommets d'activité quotidienne étaient de plus longue durée et de plus grande amplitude au printemps qu'en hiver. En hiver, on observait souvent la Souris à pattes blanches dans un état de torpeur et presque toute son activité se produisait la nuit. Au printemps, les périodes d'activité maximale commençaient avant la nuit et se terminaient de 3 à 4 heures après l'aube du jour suivant.

РЕЗЮМЕ. *Сезонные изменения в жизнедеятельности оленьей мыши* Peromyscus maniculatus *в северо-западной Канаде.* Обсуждаются изменения в жизнедеятельности P. maniculatus, исследованные в районе озера Харт (Северо-Западные территории) зимой и весной 1965-66 гг.

INTRODUCTION

Daily and seasonal variations in activity of *Peromyscus maniculatus* were studied at Heart Lake, Northwest Territories (60°50′N., 116°40′W.) during the winter and spring of 1965-1966. The purpose of the study was to test whether circadian rhythms of deer mice at a subarctic latitude would vary in response to season as greatly as those of other small northern animals (Erkinaro 1961; Peiponen 1962; Grodzinski 1963; Folk 1964; Andreasson and Muller 1969; Gerell 1969).

Relationships between torpor and activity were also studied. Causal relationships between survival and either decreased activity or torpor had been suggested for several species (French *et al.* 1966; Hudson 1967; Kontogiannis 1968; Crowcroft and Godfrey 1968).

METHODS AND MATERIALS

Activity

Activity of 2 male and 1 female *P. maniculatus* in cages measuring 30 x 30 x 60 cm. placed on the forest floor in a quiet, natural area was studied. The deer mice were trapped locally prior to the experiment.

[1]University of Lethbridge, Alberta, Canada.

Relevance of results from a small sample of caged animals with a constant and ample food supply to activity of natural populations is unknown. Techniques used to monitor the activity of animals in natural conditions (Pearson 1960; Folk 1964) are desirable, but of little value under conditions of this study.

In nature deer mice use their cheek pouches to forage for winter food stores (Hamilton 1939, 1942; McCabe and Blanchard 1950; King 1968). Caged deer mice in this study did the same. If deer mice in nature can store sufficient food for winter, nutrition and feeding behaviour of animals in this study may not have been altered.

Between 16 November 1965 and 18 March 1966, the 3 deer mice were placed in one cage because of the reported facilitation of torpor by huddling (Howard 1951) and because in nature crowding of up to 20 deer mice per nest in winter has been reported (Howard 1951). I have personally counted 28 deer mice in one nest discovered in late March at Lethbridge, Alberta, Canada.

The cage was provided with a nest box which measured 8 x 8 x 16 cm. and was insulated on all surfaces by 2.5 cm. of styrofoam. Terylene fibre was provided for nesting material. A swinging door in a tunnel at the entrance to the nest box operated a mercury switch in an adjacent box. The switch activated a 20-pen Esterline Angus event recorder in a nearby trailer.

In this way activity occurring inside and outside the nest box was not recorded but the number of entrances and exits to and from the nest was taken as an index of total activity. Though this is not as desirable as measurement of total activity, attempts at measuring activity within the nest failed due to clogging of switches by snow, seeds, nesting material, feces, and ice, and studies of activity outside the nest were limited by snow and ice during all but the last 6 weeks of the study.

Sunflower seeds and Purina laboratory mouse food were fed *ad libitum*. Cage and nest box were cleaned, and fresh food added once a month. The cage was filled with and covered by snow between 16 November and 28 March, after which partial snow-cover persisted until 3 May. The animals had to tunnel to find food or exercise. The only protection from rain was the nest box.

On 18 March each deer mouse was placed in a separate activity cage. This was done because it was doubtful that the high level of activity of the 3 mice in spring could be accurately measured by a single recording device and because it is doubtful whether the communal arrangements of winter persist through spring and summer (King 1968).

For analysis the total number of trips across the entrance to the nest was averaged for each 2-week period and hourly averages were graphed.

Weather

Aerial and ground surface temperatures were recorded continuously with a Yellow Springs Instrument Sequencing Telethermometer (Model 80) and recorder (Model 47) placed near the activity experiments.

Ground surface temperatures were recorded about 2 cm. under the surface of the lichen or leaf litter cover. Air temperatures were recorded 1.5 m. above the surface of the forest floor by means of a thermistor sheltered from direct radiation by pine boughs.

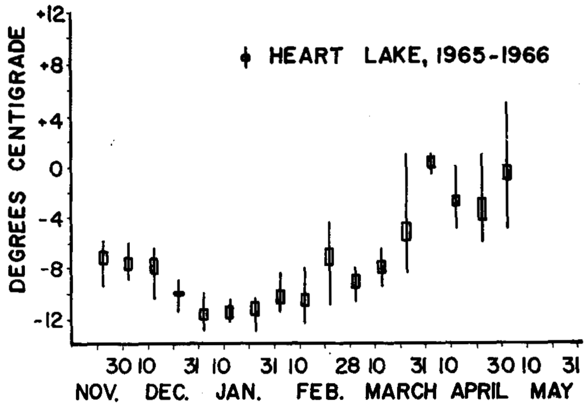


FIG. 1. Subnivean temperatures at Heart Lake. The values are plotted for each third of the month, 1-10, 11-20, and 21 to end. The vertical line indicates the range. The boxes enclose the range from the mean maximum to the mean minimum.

Solar illumination 60 cm. above the forest floor was recorded continuously by a Rustrak recorder and Silicon cells combined into a field instrument (Stebbins 1968).

RESULTS

Microclimate

Subnivean temperatures are given in Fig. 1. The first snow fell in early October 1965 at Heart Lake, but melted within a few days. The permanent winter snow-cover then began in late October and persisted through 4 May 1966.

Between 8 March and 5 May 1966, nest-box temperatures were taken (Fig. 2). Nest-box temperatures were colder than those of the forest floor because the nest box was, due to accumulation of snow under the cage, still about 10 cm. above the forest floor.

Lowest temperatures were probably recorded in the nest box when mice were out of the box. The nest box was cold-saturated during cleaning on 7 March and required 11 hours to warm from −26°C. to the rather steady temperature of −12°C.

Because deer mice nested in the snow outside the insulated nest box for most of January and February where they were frequently seen in a torpid condition, a gap in the record exists.

Activity

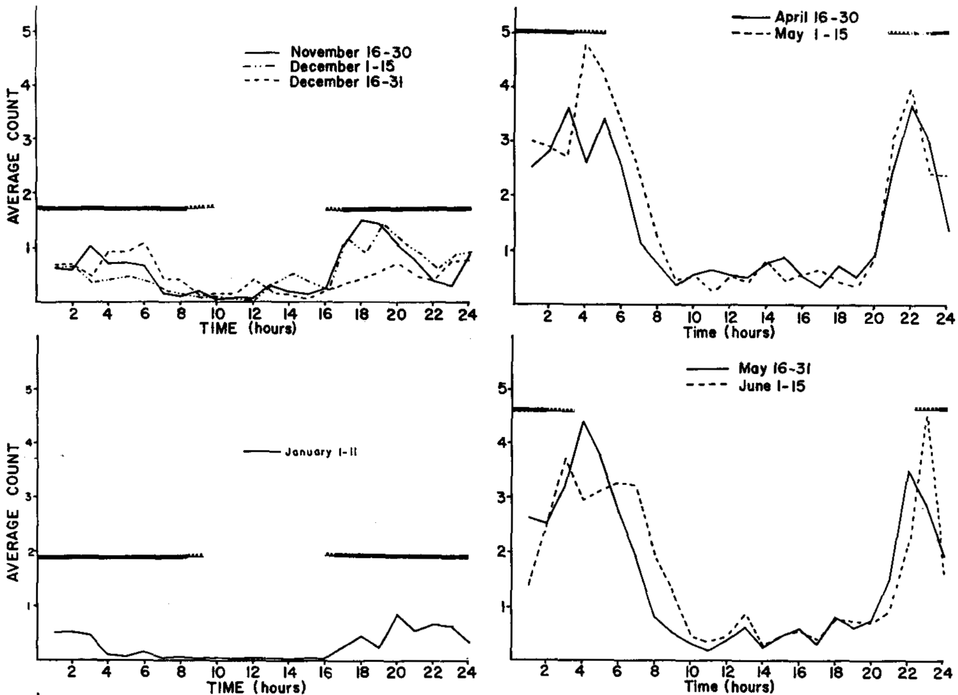
Circadian rhythms are given in Fig. 3. From 16 November 1965 to 11 January 1966, activity was low during the day, began to increase at dusk, reached a low peak before midnight, and declined again to the low daytime value before dawn. A similar pattern was observed from 1 to 8 March.

Daytime and nighttime activity increased in mid-March, and the nocturnal peak of activity became bimodal. During this time the mice seemed to begin and stop their daily peak of activity at about the same time each day, although the days were lengthening. As a result, by early April the nocturnal peak of activity was beginning before dusk and continuing after dawn.

From mid-April to mid-May this trend intensified. The mice were nearly inactive at midday. Their activity began to increase about 2 hours before dark, and peaked at full darkness. After a depression in early morning there was a second peak near dawn with activity gradually declining during the next 3 to 4 hours of daylight.

From mid-May to mid-June, when the dark period was only about 3 hours, the major change was a continued extension of activity into the early daylight hours. By 15 June a high level of activity persisted for 6 hours after dawn.

Total daily activity was much higher in summer than in winter. When the study began in mid-November the mean daily minimum temperature in the subnivean environment was already near $-8\,°C$. (Fig. 1). The increase in activity in late March 1966 coincided with the spring warming trend and the loss of snow cover over the top of the cage.



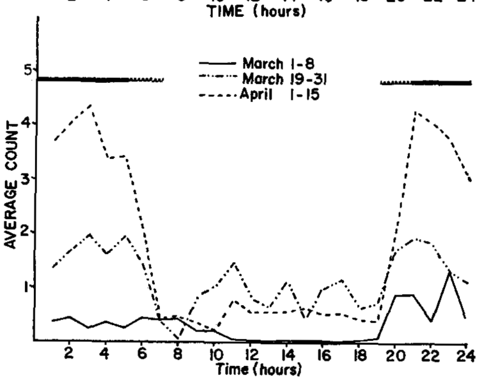


FIG. 2. Temperatures taken at the top of the nest box during the activity experiments at Heart Lake. The vertical line indicates the range, the boxes enclose the range between the mean maximum and the mean minimum. Temperatures are plotted for each third of the month.

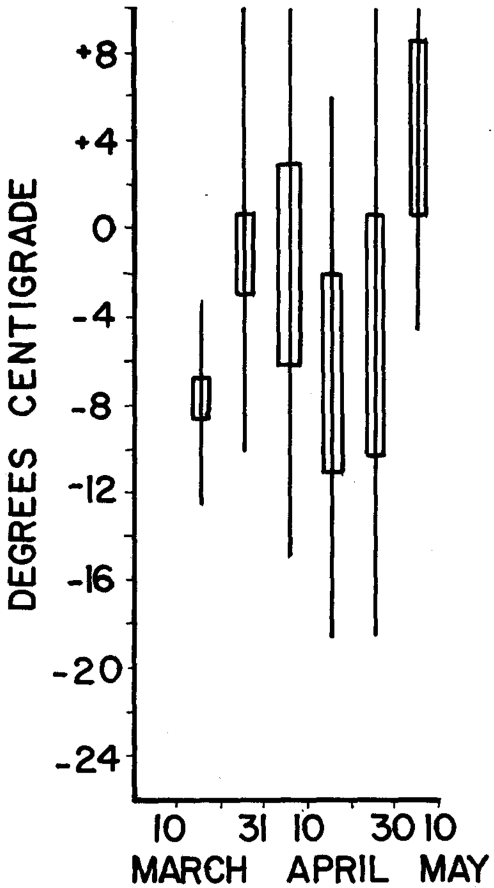


FIG. 3. Circadian rhythms of 2 male and 1 female *P. maniculatus* tested at Heart Lake. The term "average count" refers to the average number of times a gate at the entrance of the nest box was crossed by the animals. Time is given with hour 0100 through hour 2400 abbreviated to hour 1 through hour 24. Periods of darkness are indicated by vertical striped lines across the top of the graph. The short line with loops indicates the range of variation in photoperiod during the test period.

DISCUSSION

The lower activity in winter may be related to seasonal changes in energy use or to torpor. Decreased activity in small homeotherms exposed to extended cold stress in winter has been suggested as an adaptive mechanism for energy conservation. Kontogiannis (1968) has shown that moderate activity greatly raises the minimum temperature at which the white-throated sparrow can survive and maintain body weight. Kendeigh (1949), Davis (1955), McNab (1963) and West (1968) have shown that energy used for activities other than thermoregulation is greatly decreased in winter in the house sparrow (*Passer domesticus*), ptarmigan (*Lagopus lagopus*), and *Peromyscus* spp. As a result, energy-requiring activities other than thermoregulation, such as growth, reproduction, and high levels of activity are postponed until cold stress is lessened.

Another factor directly related to energy budget and activity is torpor. Deer mice underwent periods of torpor at Heart Lake. During early January and early March there was almost no activity during the day and little at night. The deer mice were removed from their cage while torpid and found to fit the description of torpid deer mice by Howard (1951). They were found asleep or lethargic, either in the nesting material or in the snow outside the nest. They had a slow breathing rate, moved their limbs slowly when walking, let their tails drag, and made no attempt to run or escape. When the temperature moderated somewhat in late March and early April, the mice were no longer observed in torpor, and their general level of activity increased considerably.

It has been suggested that torpor in *Peromyscus* spp., *Perognathus* spp., *Dipodomys* spp. and *Eutamias* spp. is an adaptation to increase survival during a variety of unfavourable conditions, particularly when food is in short supply (Howard 1951; Hudson 1967; Bartholomew and Cade 1967; Cade 1968; French *et al.* 1966).

Further study will be required to explain the adaptive value of torpor and reduced activity recorded in this study.

In winter only weakly-defined nocturnal peaks of activity occurred. Similar nocturnal patterns of activity in winter have been reported at more southerly latitudes (Behmy 1936; Falls 1953; King 1968). In spring daily peaks of activity began from 1 to 2 hours before onset of darkness and persisted from 4 to 6 hours into daylight of the next morning. Thus in spring the activity consisted almost equally of crepuscular, nocturnal, and diurnal activity. Such behaviour has not been previously reported in *Peromyscus* spp.

These seasonal changes in phase remain unexplained, but their absence in this species at more southerly latitudes may indicate a response of this normally nocturnal species to the brevity of darkness in summer at northern latitudes.

One may presume that activity occurring during daily peaks of activity in homeotherms is in some way directly related to various patterns of behaviour which have survival value. Reproductive, nesting, territorial, and foraging behaviour have all been shown to contribute to circadian rhythms in small mammals (Wald and Jackson 1944; Cloudsley-Thompson 1960; Muul 1965; Kikawa 1964; Gerell 1969; Crowcroft and Godfrey 1968; King 1968). It has also been suggested that expression of a nocturnal or diurnal preference in a variety of animals is secondary to satisfaction of basic food and energy requirements (Chitty and Shorten 1946; Miller 1955; Williams 1959).

In this study, the spring changes in phase of the circadian rhythms occurred as growth became more rapid and reproduction began (Fuller 1969; Fuller *et al.* 1969). Perhaps as spring progressed, activity associated with growth and reproduction increased and, being at first restricted to the dark hours of the day by a nocturnal preference characteristic of this species in winter, contributed to the development of the well-defined nocturnal peaks of activity. Then as spring advanced and the number of hours of darkness decreased a time may have been reached when the animals were no longer able to satisfy their physiological needs within the time limits imposed by photoperiod. Their peaks of activity then began to extend into the daylight hours of morning. Further studies of the latitudinal range of this pattern of behaviour may support or disprove this proposed explanation.

ACKNOWLEDGEMENTS

I wish to acknowledge financial support received from the National Research Council of Canada and the University of Alberta, and to thank Dr. W. A. Fuller and Dr. G. E. Folk for their personal and professional encouragement.

REFERENCES

ANDREASSON, S. and K. MULLER. 1969. Persistence of the diel activity phase shift in *Cottus poedilopus* (Pisces) after transfer from 66° to 55° northern latitude. *Oikos*, 20: 171-74.

BARTHOLOMEW, G. A. and T. J. CADE. 1967. Temperature regulation, hibernation and aestivation in the little pocket mouse, *Perognathus longimembris*. *Journal of Mammalogy*, 38(1): 60-71.

BEHMY, W. H. 1936. Nocturnal explorations of the forest deer mouse. *Journal of Mammalogy*, 17: 225-30.

CADE, T. J. 1968. Observations in torpidity in captive chipmunks of the genus *Eutamias*. *Ecology*, 44(2): 255-61.

CHITTY, D. and M. SHORTEN. 1946. Techniques for the study of the Norway rat *(Rattus norwegicus)*. *Journal of Mammalogy*, 27: 63-78.

CLOUDSLEY-THOMPSON, J. L. 1960. Adaptive function of circadian rhythms. *Proceedings of the Cold Springs Harbor Symposium on Quantitative Biology*, 25: 345-57.

CROWCROFT, P. and G. GODFREY. 1968. The daily cycle of activity in two species of Sminthopsis (Marsupialis: Dasyuridae). *Journal of Animal Ecology*, 37: 63-75.

DAVIS, E. A., JR. 1955. Seasonal changes in the energy balance of the English Sparrow. *Auk*, 72: 385-411.

ERKINARO, E. 1961. The seasonal change of activity of *Microtus agrestis*. *Oikos*, 121: 157-63.

FALLS, J. B. 1953. Activity and local distribution of deer mice in relation to certain environmental factors. Ph.D. Thesis, University of Toronto.

FOLK, G. E., JR. 1964. Daily physiological rhythms of carnivores exposed to extreme changes in arctic daylight. *Federation Proceedings*, 23: 1221-28.

FRENCH, N. R., B. G. MAZA and A. P. ASCHWANDEN. 1966. Life spans of *Dipodomys* and *Perognathus* in the Mojave Desert. *Journal of Mammalogy*, 48: 537-48.

FULLER, W. A. 1969. Changes in numbers of 3 species of small rodents near Great Slave Lake, N.W.T., Canada, 1964-67, and their significance for general population theory. *Annales Zoologici Fennici*, 6: 113-44.

FULLER, W. A., L. L. STEBBINS and G. R. DYKE. 1969. Overwintering of small mammals near Great Slave Lake, northern Canada, in 1965-1966, and 1966-67. *Arctic*, 22: 34-55.

GERELL, R. 1969. Activity patterns of the mink *Mustella vison* Schreber in southern Sweden. *Oikos*, 20: 451-60.

GRODZINSKI, W. 1963. Seasonal changes in the circadian activity of small rodents (in Polish, English summary); *Ekologia Polska Seria* B, 9: 1-17.

HAMILTON, W. J., JR. 1939. *American mammals*. New York: McGraw Hill. 434 pp.

———. 1942. The buccal pouch of *Peromyscus*. *Journal of Mammalogy*, 23: 449-50.

HOWARD, W. E. 1951. Relation between low temperature and available food to survival of small rodents. *Journal of Mammalogy*, 32(3): 300-12.

HUDSON, T. W. 1967. Variations in the patterns of torpidity of small homeotherms. In: K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schonbaum, and F. R. South, Jr., eds. *Mammalian Hibernation III*. New York: American Elsevier Press. pp. 30-46.

KENDEIGH, C. S. 1949. Effect of temperature and season on energy resources of the English Sparrow. *Auk*, 66(2): 113-27.

KIKAWA, J. 1964. Movement, activity, and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *Journal of Animal Ecology*, 33: 259-95.

KING, J., ED. 1968. *Biology of Peromyscus*. Special Publication No. 2, The American Society of Mammalogists. 593 pp.

KONTOGIANNIS, J. E. 1968. Effect of temperature and excercise on energy intake and body weight of the White-Throated Sparrow *Zontrichia Albiiollis*. *Physiological Zoology*, 41(1): 54-64.

MCCABE, T. T. and B. D. BLANCHARD, 1950. *Three species of Peromyscus*. Santa Barbara, California: Rood Associates, 136 pp.

MCNAB, B. K. 1963. A model of the energy budget of a wild mouse. *Ecology*, 44: 521-32.

MILLER, R. S. 1955. Activity rhythms in the wood mouse, *Apodemus sylvaticus*, and the bank vole, *Clethrionomys glareolus*. *Proceedings Zoological Society of London*, 125: 505-19.

MUUL, I. 1965. Day length and food caches. *Natural History*, 74(3): 22-28.

PEARSON, O. 1960. Habits of harvest mise revealed by automatic photographic records, *Journal of Mammalogy*, 41: 58-74.

PEIPONEN, V. A. 1962. Zur aktivitat der graurotelmaus, *Clethrionomys rufocanus* (Sund.), im dauerlicht des arktischen sommers. *Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo'*, 17: 171-78.

STEBBINS, L. L. 1968. Seasonal changes in the circadian rhythms of some small northern rodents. Ph.D. Thesis, University of Alberta.

WALD, G. and B. JACKSON. 1944. Activity and nutritional deprivation. *Proceedings of the National Academy of Science*, 30: 255-63.

WEST, G. G. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. *Ecology*, 49(6): 1035-45.

WILLIAMS, G. 1959. Seasonal and diurnal activity of carabidae, with particular reference to *Nebria, Notiophilus*, and *Feronica*. *Journal of Animal Ecology*, 28: 309-14.