

## Summer Activity Patterns of Three Rodents in the Southwestern Yukon

B.S. GILBERT,<sup>1</sup> D.B. CICHOWSKI,<sup>1</sup> D. TALARICO<sup>1</sup> and C.J. KREBS<sup>1</sup>

(Received 19 March 1985; accepted in revised form 7 August 1985)

**ABSTRACT.** The small mammal communities of the boreal forest in the SW Yukon are diverse and little is known about the underlying reasons for this species richness. Niche differentiation through staggered periods of activity is one way in which similar species may avoid potential interference competition. In this study we describe the activity pattern of three rodents (the deer mouse, the northern red-backed vole, and the singing vole) from the summer solstice to the autumnal equinox. Activity was measured on two white spruce plots by checking live-traps at 2 h intervals over a 24 h period. We did this at monthly intervals between June and September 1984. The deer mouse was strongly nocturnal throughout the summer, while the northern red-backed vole and the singing vole were active both day and night. During the nocturnal period of deer mouse activity, approximately 80% of the red-backed vole population was active, and we conclude that there is no evidence of temporal niche differentiation between these two species. Only deer mice showed a seasonal change in activity pattern. As the days became shorter, deer mice became active earlier, so that by September they were active 4 h earlier than they were in June.

**Key words:** deer mice, *Peromyscus maniculatus*, northern red-backed vole, *Clethrionomys rutilus*, singing vole, *Microtus miurus*, activity time, Yukon, competition

**RÉSUMÉ.** Il existe diverses communautés de petits mammifères dans la forêt boréale du sud-ouest du Yukon dont on connaît peu quant aux raisons de leurs nombres. La différenciation de niche par l'échelonnement des périodes d'activité présente une façon suivant laquelle les espèces semblables évitent toute intervention compétitrice. Au cours de cette étude, nous décrivons le cycle d'activité de trois rongeurs (la souris sylvestre, le campagnol à dos roux boréal et le campagnol chanteur) à partir du solstice d'été jusqu'à l'équinoxe d'automne. Leur activité fut mesurée sur deux sections d'épicéas blancs à l'aide de la vérification de pièges à récipient à des intervalles de deux heures sur une période de 24 heures. L'étude se poursuivit par intervalles mensuels entre juin et septembre 1984. La souris sylvestre était surtout nocturne tout au cours de l'été, tandis que le campagnol à dos roux boréal et le campagnol chanteur étaient actifs jour et nuit. Durant la période d'activité nocturne de la souris sylvestre, environ 80% de la population de campagnols à dos roux était actifs, ce qui nous amena à conclure qu'il ne semble pas y avoir de différenciation de niche entre ces deux espèces. A mesure que les jours se raccourcissaient, les souris sylvestres devinrent actives plus tôt, de sorte qu'en septembre, elles étaient actives quatre heures plus tôt qu'elles l'étaient en juin.

**Mots clés:** souris sylvestre, *Peromyscus maniculatus*, campagnol à dos roux boréal, *Clethrionomys rutilus*, campagnol chanteur, *Microtus miurus*, période d'activité, Yukon, compétition

Traduit pour le journal par Maurice Guibord.

### INTRODUCTION

Interspecific competition can be an important influence on the composition and structure of a community, and differences in niche structure (habitat, food or activity time) are often interpreted as responses to competitive pressures (Schoener, 1983). In this paper we explore the importance of temporal patterns of activity as a niche component in three species of rodents in the southwestern Yukon. Differences in the activity time of sympatric animals have been reported in lizards (Pianka, 1975), snakes (Mushinsky and Hebrard, 1977) and desert rodents (O'Farrell, 1974). Can differences in activity time reduce the effects of competition (as defined by Birch, 1957)? Competition for food could be lessened by adopting staggered periods of activity if food resources are refreshed quickly or if different resources are available. The example of diurnal (Falconiform) and nocturnal (Strigiform) raptors is often posed as an example of how two species have lessened competition by exploiting temporally segregated prey. Field work by Jaksic *et al.* (1981) in Chile has indicated high food-niche overlap between these two groups despite differences in their foraging activity. Interference competition is now viewed as a more plausible explanation for those differences in temporal activity (Carothers and Jaksic, 1984; Jaksic, 1982).

The small mammal fauna of the SW Yukon is rich for a subarctic location, and several habitats contain two or more species of rodents. We will focus on two abundant species: the

deer mouse, *Peromyscus maniculatus*, and the northern red-backed vole, *Clethrionomys rutilus*, and one uncommon one, the singing vole, *Microtus miurus*. The deer mouse and the red-backed vole often share the same habitat, although in previous experiments we were unable to find strong evidence of competition between them (Gilbert and Krebs, 1984). The singing vole is usually found in alpine tundra habitats in this area; however, we located a few colonies in the boreal forest at lower elevations. At these lower elevations, singing vole populations intermingle with populations of deer mice and red-backed voles. Our work revolved around two questions: Do these rodents have different periods of activity that could allow them to avoid competition? How does the activity pattern of these rodents vary seasonally with changes in day length? The latter question is based on the fact that daylight at this latitude varies over the snow-free season from 19.5 to 12 h.

### METHODS

Our study area is located in the southwestern Yukon at the south end of Kluane Lake (60°58'N, 138°28'W). In this paper we analyze live-trapping data collected on two study areas (GE and SM) being monitored as control populations for other studies. Each grid (2.3 ha) consists of a 10 × 10 network of stations (15 m apart) with a single Longworth trap prebaited at each station. Trapping technique was similar to our previous studies (see Gilbert and Krebs, 1984). Minimum trappability

<sup>1</sup>Department of Zoology and Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C., Canada V6T 1W5  
©The Arctic Institute of North America

estimates (Krebs and Boonstra, 1984) exceeded 85% for all three species during this study.

Both study areas are located in a white spruce (*Picea glauca*) forest, but they differ in several ways. The GE grid is located on an old alluvial fan and it has more shrubs and larger spruce trees with a much heavier cone crop than the SM grid. The most abundant rodents on this plot in 1984 were deer mice and red-backed voles, although a few singing voles and least chipmunks (*Eutamias minimus*) also appeared during the study. The SM grid has a strong north-facing aspect, and unlike the GE grid there are patches of permafrost. Consequently the spruce trees are much smaller, shrubs occur more sparsely and the ground cover of moss is more extensive. Only red-backed voles and singing voles were abundant in this area and there were very few deer mice, chipmunks and tundra voles (*M. oeconomus*).

We monitored activity at approximately monthly intervals beginning near the summer solstice and finishing near the autumnal equinox (see Fig. 1 for exact dates). During each sampling period we would begin with one night of routine trapping followed immediately by a 24 h period when we checked all traps at 2 h intervals. During each 24 h period we sampled both areas simultaneously except for two occasions. In June the 24 h sample on SM was actually a composite of data collected during two periods spaced four days apart, and in September we were only able to monitor one area. Finally, our technique was slightly different in July on the SM area. We attempted to bolster our sample size of singing voles by trapping a perimeter line 30 m from the normal grid with 52 traps spaced 15 m apart. We recognize that sample sizes are small for singing voles in this study, but we include these data here because little is known about this uncommon vole (Youngman, 1975). Cloud cover was sparse during all four sampling periods and the phase of the moon (last quarter) was also similar for all four.

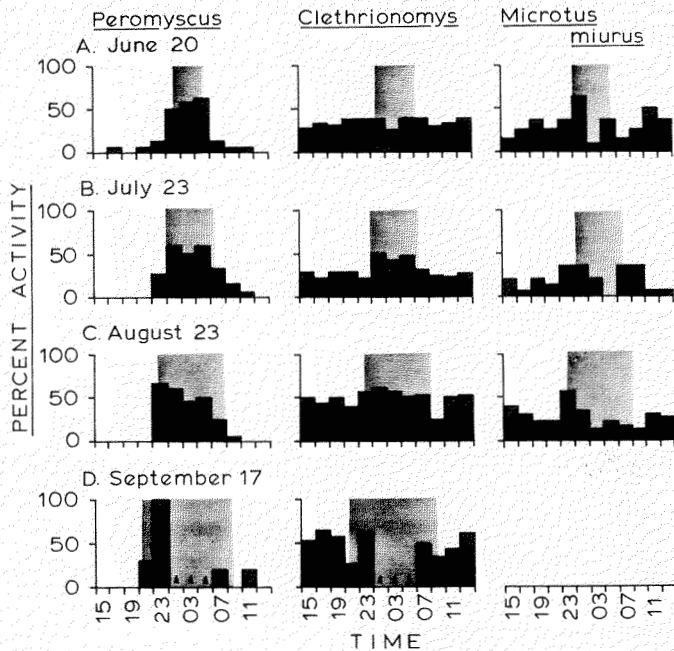


FIG. 1. Percentage of animals caught in each 2 h period over the 24 h sampling time for deer mice (*Peromyscus maniculatus*), northern red-backed voles (*Clethrionomys rutilus*) and singing voles (*Microtus miurus*). Night hours are shaded. Time expressed as Pacific Standard Time.  $\blacktriangle$  = no data available. In September no sample could be obtained for *Microtus miurus*. Sample sizes for these data are given in Table 1.

## RESULTS

We have used two methods of analyzing our data on activity patterns. The first is simply the number of animals caught in any 2 h period expressed as a percentage of all individuals caught in the entire 24 h period. We assume that any animal caught at least once was potentially eligible for capture during all other periods. We first analyzed our data separately for each area and sex, and since we could detect no difference between them ( $\chi^2$  test), we have pooled the data for both areas and sexes in Figure 1. The deer mouse appears to be strongly nocturnal throughout the season, while both northern red-backed voles and singing voles have a more even pattern of activity and seem active both night and day. Deer mice also show a seasonal shift in activity associated with the change in daylight. They become active earlier in the evening, so that by September they are active 4 h earlier than in June. We do not see a similar shift at the other end of their nocturnal period of activity. Deer mice were active until 0700 (Pacific Standard Time) in all samples from June until September.

Our second method summarizes the tendency for an animal to be caught during daylight hours using a simple formula, the group diurnality index ( $D$ ), described by Hoogenboom *et al.* (1984). The index ranges from a value of +1 when all captures occur during the day to -1 when all captures are at night. This analysis (Table 1) supports our graphical interpretation that the deer mouse is largely nocturnal. Red-backed voles and singing voles have most values of  $D$  near zero, which agrees with our earlier summary that these species are active day and night. We cannot explain why the diurnality index for red-backed voles in July departs so far from zero. Perhaps there is some avoidance of warmer temperatures. The diurnality index can also show seasonable changes of activity. The index for deer mice becomes more negative over the summer. There is no seasonal trend apparent in the data for the other two species.

TABLE 1. Diurnality Index of Hoogenboom *et al.* (1984). Values range from +1 when all captures are in daytime to -1 when all captures are at night. Data for both sexes and grids are pooled. Sample sizes (no. of captures) in parentheses.

	<i>P. maniculatus</i>	<i>C. rutilus</i>	<i>M. miurus</i>
June 20	-.69 (26)	+.06 (76)	-.01 (14)
July 23	-.73 (22)	-.27 (137)	+.04 (14)
August 23	-.87 (20)	-.11 (123)	-.12 (23)
September 17	-.90 (13)	+.06 (52)	—

Is there any evidence that deer mice use the nighttime period to avoid contact with certain segments of the red-backed vole population? These species do not have disjunct patterns of activity over the course of the day. However, if some particular class of the red-backed voles population tended to be less active during the middle of the night, then deer mice might profit by becoming more active. We calculated the proportion of the red-backed vole population active during the evening period of intense deer mice activity (Table 2). Adults of both sexes and juveniles are very active during this period, and we conclude that deer mice are exposed, during their brief active period, to most (usually over 80%) of the red-backed vole population.

TABLE 2. Proportion of northern red-backed vole (*C. rutilus*) population active between 2300 and 0700 h (PST). Areas pooled. Sample size in brackets.

	June 20	July 23	Aug. 23	Sept. 17
Adult male	80.5 (41)	87.0 (23)	90.5 (21)	85.7 (7)
Adult female	92.9 (28)	100.0 (20)	80.9 (21)	87.5 (8)
Juveniles	42.8 (7)	90.4 (94)	95.1 (81)	70.3 (37)
Total	81.6 (76)	91.2 (137)	91.8 (123)	75.0 (52)

## DISCUSSION

The main question in this study was whether the time of daily activity differs between species so that some animals avoid the effects of interspecific competition? Our analysis of red-backed vole-deer mouse and red-backed vole-singing vole activity reveals that their activity patterns are unrelated and there is no evidence that they might be avoiding competition by temporal separation of activity. Both red-backed voles and singing voles seem active throughout the day, and this may be associated with their herbivorous diet. The even pattern of activity throughout the day is correlated with a low quality diet (Hansson, 1971), and Daan and Slopsema (1978) hypothesize that regular and frequent periods of food intake are required to optimize the fermentation process by intestinal bacteria.

Our secondary interest was to consider the influence of seasonal changes in daylight on the temporal patterns of rodent activity. Only one species, the deer mouse, exhibited a shift in its nocturnal pattern from June to September. Deer mice became active earlier in the evening as the hours of daylight decreased; however the end of its nocturnal activity remained constant throughout the summer. The detailed field results obtained by Harling (1971) on deer mice in Vancouver (49°N) indicate that activity began 1 h after sunset and ended at least 1 h before sunrise. Harland and Millar (1980) found that the end of nocturnal activity for nonbreeding female white-footed mice (*Peromyscus leucopus*) was related to overnight temperature. At lower temperatures the activity period was extended. In theory the duration of activity integrates several variables including energy acquisition (foraging) and energy use (metabolism). The slight differences between the duration of deer mouse activity in our northern study compared with Harling's results may reflect some adjustment to foraging strategies related to ambient temperature.

Data presented by O'Farrell (1974: Fig. 4) suggest that deer mice in Nevada are active for only 10 h after sunset during the summer, while during the remainder of the year they were active for 12 h. Deer mice in our study were only active for approximately 6 h-day during June, and it is interesting to speculate on the effects of this possible limitation on foraging time. The peak of deer mouse breeding activity coincides with the summer solstice, so animals have very reduced opportunities for foraging at a time when energy demands may be approaching a seasonal maximum (Millar, 1979). Female breeding success is enhanced by supplemental feeding, but the contribution of food supply by itself cannot be separated from social influences (Gilbert and Krebs, 1981). The northwestern limit of deer mouse distribution occurs at approximately 63°N (Youngman,

1975), and we wonder if further dispersal is limited by the short nights during the breeding season, which may restrict foraging activity below some critical energy threshold?

Several techniques have been used for measuring the activity of secretive small mammals — e.g., laboratory measures of feeding rate or running behaviour on an activity wheel (Daan and Slopsema, 1978), remote sensing (Madison, 1981; Harling, 1971), and live-trapping. In the laboratory one can make continuous, detailed measurements of activity, but these advantages must be weighed against the difficulty of interpreting how well the results describe wild populations. Live-trapping can provide large amounts of field data, albeit with at least two drawbacks. Activity measurements cannot be instantaneous, as logistical constraints and the danger of interrupting normal animal activity require some interval between trap checks. Secondly we must assume that animals will enter the traps as a part of their daily round when they are active. This assumption would be upset if animals were trap-shy. We cannot tell if animals avoid traps over a short period of time (less than 24 h); however, we can calculate an estimate of trappability between regular biweekly trapping sessions. Trappability ranged from 85-90% for all species in 1984.

What is the significance of our conclusion that deer mice and red-backed voles have overlapping patterns of daily activity? When red-backed voles were experimentally removed, deer mouse populations showed no strong evidence of competitive release (Gilbert and Krebs, 1984); yet we know that these two species share similar habitats with high estimates of niche overlap (Krebs and Wingate, 1985). How can we reconcile the coexistence of these two species? Perhaps competition is avoided through niche differentiation by diet, microhabitat use or some other unidentified niche dimension. Alternately, competition itself may be unimportant because population densities of both Yukon species tend to be low and the threshold for competitive interactions may never be realized.

## ACKNOWLEDGEMENTS

We thank the following people for sharing the perils, both real and imagined, of the nighttime work: Karen Broughton, Alice Kenney, Kelly Nordin, Jeff Schmok and Mark Simpson. Carlos Galindo, Laura Jameson and Rob Purdy provided help in designing this experiment. It is a pleasure to thank Andy and Carole Williams and the staff of the Arctic Institute of North America for their help during our stay at the Kluane Lake Research Station. This research was supported by funds from the Natural Sciences and Engineering Research Council of Canada.

## REFERENCES

- BIRCH, L.C. 1957. The meanings of competition. *American Naturalist* 91:5-18.
- CAROTHERS, J.H., and JAKSIC, F.M. 1984. Time as a niche difference: the role of interference competition. *Oikos* 42:403-406.
- DAAN, S., and SLOPSEMA, S. 1978. Short-term rhythms in foraging behaviour of the common vole, *Microtus arvalis*. *Journal of Comparative Physiology* 127:215-227.
- GILBERT, B.S., and KREBS, C.J. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia* 51:326-331.
- . 1984. Competition between *Peromyscus maniculatus* and other small rodents in the boreal forest of the southern Yukon Territory. *Acta Zoologica Fennica* 172:51-56.
- HANSSON, L. 1971. Small rodent food, feeding and population dynamics. *Oikos* 22:183-198.

- HARLAND, R.M., and MILLAR, J.S. 1980. Activity of breeding *Peromyscus leucopus*. *Canadian Journal of Zoology* 58:313-316.
- HARLING, J. 1971. A technique for precisely timing captures of *Peromyscus maniculatus*. *Canadian Journal of Zoology* 49:1275-1277.
- HOOGENBOOM, I., DAAN, S., DALLINGA, J.H., and SCHOENMAKERS, M. 1984. Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis*. *Oecologia* 61:18-31.
- JAKSIC, F.M., GREENE, H.W., and YANEZ, J.L. 1981. The guild structure of a community of predatory vertebrates in central Chile. *Oecologia* 49:21-28.
- \_\_\_\_\_. 1982. Inadequacy of activity time as a niche difference: the case of diurnal and nocturnal raptors. *Oecologia* 52:171-175.
- KREBS, C.J., and BOONSTRA, R. 1984. Trappability estimates for mark-recapture data. *Canadian Journal of Zoology* 62:2440-2444.
- KREBS, C.J., and WINGATE, I. 1985. Population fluctuations in the small mammals of the Kluane region, Yukon Territory. *Canadian Field-Naturalist* 99:51-61.
- MADISON, D.M. 1981. Time patterning of nest visitation by lactating meadow voles. *Journal of Mammalogy* 62:389-391.
- MILLAR, J.S. 1979. Energetics of lactation in *Peromyscus maniculatus*. *Canadian Journal of Zoology* 57:1015-1019.
- MUSHINSKY, H.R., and HEBRARD, J.J. 1977. The use of time by sympatric water snakes. *Canadian Journal of Zoology* 55:1545-1550.
- O'FARRELL, M.J. 1974. Seasonal activity patterns of rodents in a sagebush community. *Journal of Mammalogy* 55:809-823.
- PIANKA, E.R. 1975. Niche relations of desert lizards. In: Cody, M.L., and Diamond, J.M., eds. *Ecology and evolution of communities*. Cambridge, MA: Belknap Press. 292-314.
- SCHOENER, T.W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240-285.
- YOUNGMAN, P.M. 1975. Mammals of the Yukon Territory. *National Museums of Canada Publications in Zoology* No. 10. 192 p.