

Summer and Autumn Temporal Activity of the Montane Vole (*Microtus montanus*) in the Field

Abstract

Because little is known of the temporal activity of the montane vole (*Microtus montanus*) under natural conditions, this field study was undertaken to elucidate the summer and autumn activity patterns. Laboratory studies suggest this species is more nocturnal when subject to long photoperiods that simulate summer conditions. The temporal activity of the montane vole was continuously monitored 3-5 days/week May-November, over two successive years, in an old-field grassland in southeastern Washington. Live traps, instrumented with timer mechanisms that documented capture times, were checked twice daily. Voles were active at all hours of the day and night but both sexes and all age groups were predominately diurnal. In June, September, October, and November, 1989, the diurnal activity was significantly greater than expected ($p < 0.05$). A diurnally bimodal activity pattern was apparent during the summer months. Activity was reduced during the highest daytime temperatures. It is suggested that photoperiod, ambient temperatures, energetic requirements, predatory pressures, and interspecific competition may influence the temporal activity pattern.

Introduction

Temporal activity patterns are an important aspect of better understanding the ecological niche of a species, however, little had been published about the temporal activity of the montane vole (*Microtus montanus*) when Madison (1985) extensively reviewed the literature on activity rhythms of *Microtus*. The few published studies he cited were all conducted in the laboratory (Seed and Khalili 1971, Baumgardner *et al.* 1980, Dewsbury 1980, Rowsemitt 1981, Rowsemitt *et al.* 1982). While laboratory investigations on the activity rhythms of the montane vole have continued (Rowsemitt and Berger 1983, Rowsemitt 1986, 1989, 1991), only Claypool (1984) has reported on the temporal activity in the field for this species.

Numerous field studies on activity rhythms have been conducted on *Microtus* species other than the montane vole. Madison (1985) concluded in his review that the activity schedule through the diel period of most species is flexible and that the free-running rhythms during constant light or darkness (Calhoun 1945, Seed and Khalili 1971, Lehmann 1976, Daan and Slopeema 1978) supported the existence of circadian rhythms. Field studies on voles often find diurnal or crepuscular activity, whereas voles under laboratory conditions (including *M. montanus*) are reportedly nocturnal (Calhoun 1945, Heidt 1971, Seed and Khalili 1971, Herman 1977, Rowsemitt *et al.* 1982, Claypool 1982, 1984).

Rowsemitt *et al.* (1982) demonstrated in the laboratory that a change in photoperiod can induce male *M. montanus* to shift its locomotor activity

from a nocturnal to a diurnal pattern. Rowsemitt (1991) recently compared those results with running wheel activity of female *M. montanus* and observed nocturnal activity under long photoperiods to be less likely in females than in males.

Field studies have also shown some *Microtus* species emphasize diurnal activity during the winter and then shift to crepuscular or nocturnal activity in the summer (Baumler 1975, Carley *et al.* 1970, Erkinaro 1961, Lehmann 1976). Ambrose (1973) reported a tendency for *M. pennsylvanicus* to be diurnal during the summer in natural environment enclosures.

Differences in the temporal activity of age and gender of some microtine species have been reported by several investigators (Pearson 1960, Evans 1970, Baumler 1975, Lehmann and Sommersberg 1980). This study investigates the temporal activity of the montane vole in the field during summer and autumn to elucidate the patterns of activity with respect to gender and ages, and to determine if this species is more nocturnal than diurnal in the summer.

Materials and Methods

Study Area

The 2.6 ha study area is in an old-field grassland surrounded by wheat fields immediately west of Robison Pond (300 m), 5.6 km n.w. of Walla Walla, (n.e. quarter, section 7, T7N, R36E), Walla Walla Co., WA. The site is dominated by teasel (*Dipsacus sylvestris*) and a variety of grasses (*Agropyron* sp., *Bromus* spp., *Festuca* sp., *Poa* spp.,

and *Polypogon* sp.). Fuel reduction burning in the area is practiced every few years, and most recently in November, 1989.

Data Collection

Data were collected over 13 months in May-July, and September-November, 1989, and May-November, 1990. Sherman live traps (six in 1989 and 18 in 1990), instrumented with timing mechanisms, were spaced 5 m, baited with oats and carrots (during summer months) and left open continuously for two, three (June, 1990) or five (June and July, 1989, and July and August, 1990) consecutive days each week. The traps were checked and baited twice each day. Captured voles were sexed, weighed, aged (adults > 33 g; subadults 22-33 g; juveniles < 22 g), ear-tagged with Monel no. 1 tags (National Band and Tag Co., Newport, KY), and released. The timing mechanisms on the traps are a modification of a field timer described by Jenness and Ward (1985) and are powered with 4-rechargeable AA batteries. The timers are activated with a magnet switch when the trap door shuts. Elapsed time is read from eight light emitting diodes (LED) recording 5, 10, 20, 40, 80, 160, 320, and 640 minutes respectively, to accumulate 1275 min (= 21 hrs 15 min) from the time the trap door shuts. Any combination of LED's could be recorded, and the total elapsed time indicated, subtracted from the time of recording, documented the capture time within a 5 min accuracy. Traps were covered with a 2500 cm² vinyl tarp for protection against the elements. Ambient temperature and relative humidity were continuously recorded with a hygrothermograph (Model 5020, Qualimetrics Inc., Sacramento, CA). Mean ambient temperatures were determined for every even hour, all days of the month, for each month. For May, July, and September, 1989, temperature-humidity data were recorded for only 17, 19, and 15 days respectively.

Data Analysis

A capture index was developed to reflect the trapping success each month. The index was based on the total number of voles captured, divided by the total number of trap-nights and trap-days X 100. An analysis of the 495 capture times showed only 6.4% (32) to represent crepuscular activity, thus the 12 (2.4%) captures during morning twilight were pooled with diurnal captures and the 20

(4.0%) captures during evening twilight were included with the nocturnal captures. The sunrise and sunset times for each month were averaged to calculate the percent of lightness during the 24 hr. The monthly capture frequencies (%) for each even hour of the 24 hr day were determined by using the nearest hour of capture.

I tested the null hypothesis that no difference existed in the observed occurrence of voles between day and night. I took changing daylength into account and calculated the expected values from the true proportions of daylength over the sampling period. For example, in June it was light on the average 65% of the 24 hr day. The χ^2 test was used to test the differences between the expected number of diurnal occurrences and the observed number of diurnal occurrences and differences were considered statistically significant at the 0.05 level.

Results

A total of 482 individual *Microtus* were trapped 495 times. Based on weight, there were 97 juveniles, 215 subadults, and 170 adults. Individuals were seldom recaptured, and in 11 of 13 months, 80-95% of the captures were one time captured individuals. The greatest number of voles were caught during July and August, 1990, and the fewest in October and November, 1989, while the greatest trapping success was May-July, 1989 (Figure 1).

The percent difference between the percent of light in the 24 hr day, taking changing daylength

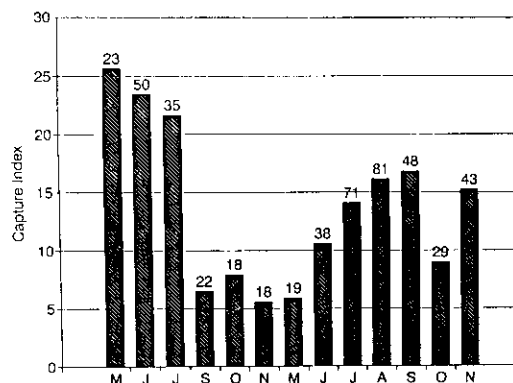


Figure 1. Capture indices, based on the total number of voles captured divided by the total number of trap-nights and trap-days X 100, reflect the trapping success for each month. Numbers above each bar represent the total voles captured.

into account, and the percent of diurnal vole activity observed is shown for each month in Figure 2. Vole activity was never more nocturnal than expected. In 1989 diurnal activity was significantly greater than expected in June ($\chi^2 = 10.63$, $p < 0.001$), September ($\chi^2 = 8.54$, $p < 0.001$), October ($p < 0.05$), and November ($p < 0.05$). In July, 1989, the vole activity was strongly diurnal ($\chi^2 = 3.23$, $p < 0.1$). There was a strong difference between the percent of diurnal activity in 1989 and 1990.

A bimodal diurnal activity pattern appeared during July through October, both years (Figs. 3 and 4). The greatest activity period occurred most frequently during the 3 hr period before sunset and subsequent to peak ambient temperatures. In November, 1990, the activity was greatest (25.5%) during the 3 hr period before midnight; in September, 1990, it was greatest during the 3 hr period following sunrise. The period of least activity in 11 of the 13 months was between midnight and sunrise. In September, 1990, between 1000 and 1600 hrs, there was 9% less activity than between midnight and sunrise. Between 0800 and 1400 hrs in October, 1990, there was 46% less activity than between midnight and sunrise. In seven of the 13 months, no voles were captured at the 2200, 2300, or 2400 hr, and in nine of the 13 months none were captured during the 0200 hr.

The sex ratio of captured males to females averaged 1:1.1. There was no significant difference at the $P < 0.05$ level of the male:female captures during any month. Throughout the 13 month trapping period, the vagrant shrew (*Sorex vagrans*), the deer mouse (*Peromyscus maniculatus*), the western harvest mouse (*Reithrodontomys megalotis*), and the house mouse (*Mus musculus*) were other species periodically captured.

Discussion

The obvious diurnal summer activity, and other temporal patterns found in this study, are similar to patterns described by Claypool (1984) in the only field study on temporal activity previously reported for this species. He described monthly activity patterns over a two year period of a population of montane voles near the southwest edge of the Great Salt Lake in Utah. The voles at his field site, at 41° N, experienced a photoperiod pattern (summer solstice is 15 h 09 min) similar to

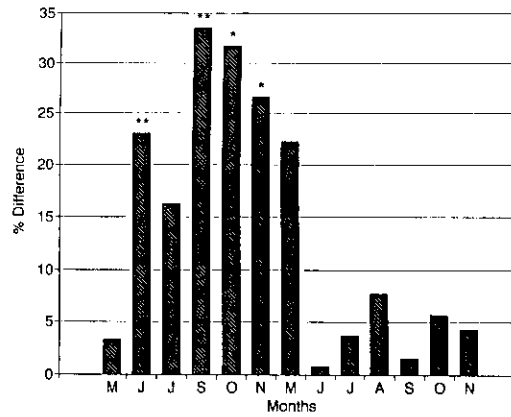


Figure 2. The percent of differences between the percent of light in the 24 hr day, taking changing daylength into account, and the percent of diurnal vole activity observed each month. Significant differences: *, $P < 0.05$; **, $P < 0.001$.

the photoperiod at this 46° N site (summer solstice is 15 h 45 min). He described vole activity as predominately diurnally bimodal in the summer and activity at all hours in the summer and fall. He reported late afternoon activity peaks in October and November, and a decrease of activity during the hottest period of the day.

There was no difference in activity patterns of males and females seen in this study. Claypool (1984) did not collect field data on gender difference for *M. montanus*. Rowsemit (1991) recently reported a major difference in the temporal distribution of laboratory running wheel use by female *M. montanus* under long (16 h light : 8 h dark) and short (8 h light : 16 h dark) photoperiods, than what she and her colleagues had previously found for males (Rowsemit *et al.* 1982). She found that females were less likely than males to be nocturnal under a long photoperiod. She feels that laboratory running wheel use, under long photoperiods, increases nocturnality to a greater degree than would be found under natural conditions. *M. pennsylvanicus* females have been found to be more diurnal than males by some (Evans 1970, Madison 1985), but other studies of this same species reported no difference in gender activity (Madison 1985). Pearson's (1960) study of *M. californicus* and Baumler's (1975) investigation of *M. agrestis* found no difference in activity patterns of males and females.

A bimodal activity pattern during the day was also reported for the montane ovle by Vaughan

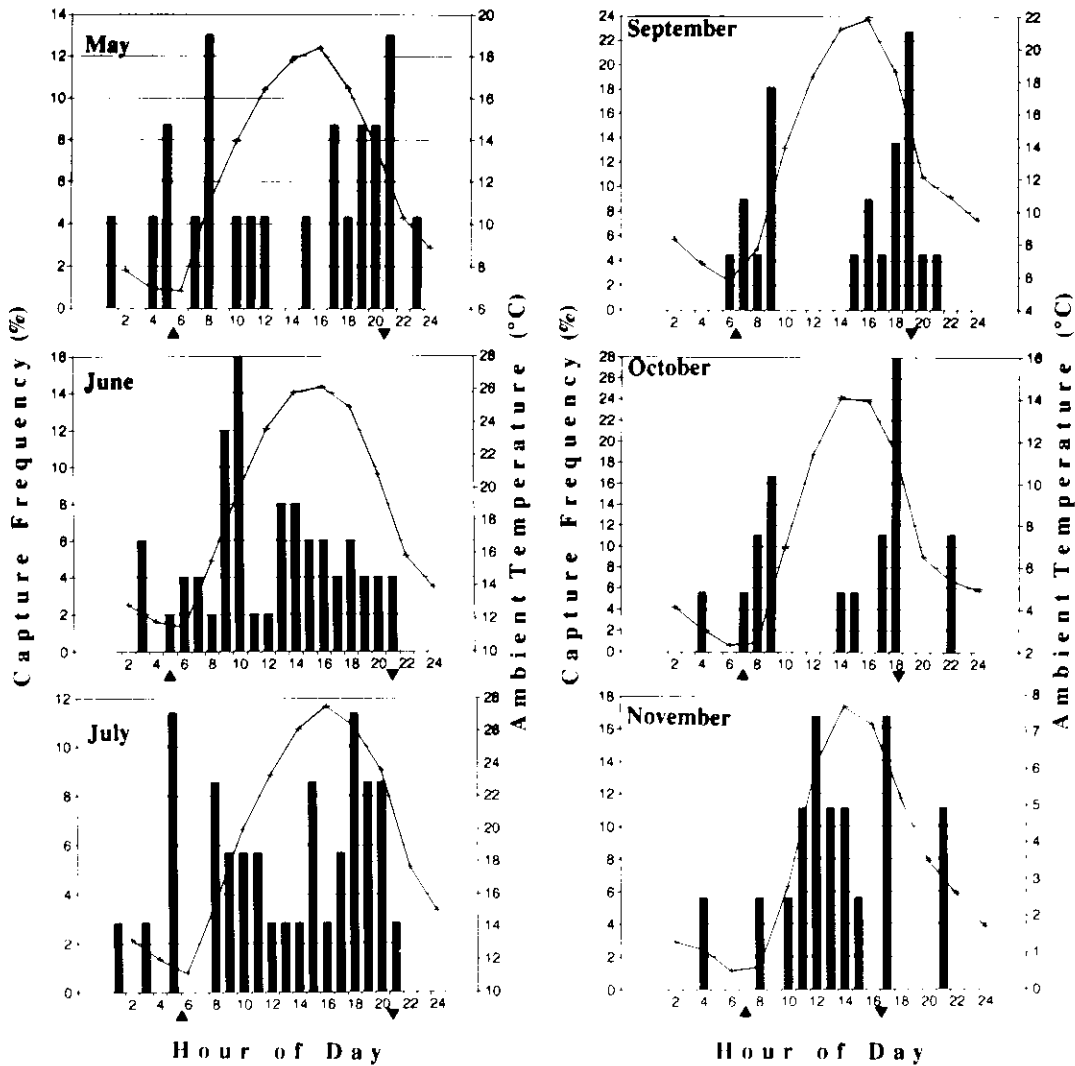


Figure 3. Capture frequencies and mean ambient temperature line through the hours of the day for each month of 1989. Upward and downward arrows at hours of day indicate the mid-month time of sunrise and sunset.

(1974). The highest summer temperatures in this study were typically 25-30°C and occurred from 1400-1800 hr. Packard (1968) reported that montane voles could not withstand temperatures much above 31°C. High daytime temperatures reportedly depressed the daytime activity in *M. californicus* (Pearson 1960) and *M. pennsylvanicus* (Getz 1961).

The activity at all of the day and night hours reported here probably reflects the energetic

requirements of the montane vole. Vaughan (1974) found the stomach contents of *M. montanus* to be entirely forbs and grasses. A low-quality herbivorous diet requires *Microtus* spp. to feed frequently throughout the 24 hr day (Daan and Aschoff 1981). Kenagy and Vleck (1982) found a relatively uniform metabolic level between day and night for *M. longicaudus* and *M. townsendii*.

The preponderance of the subadults (45%) and adults (35%) in the captured population in this

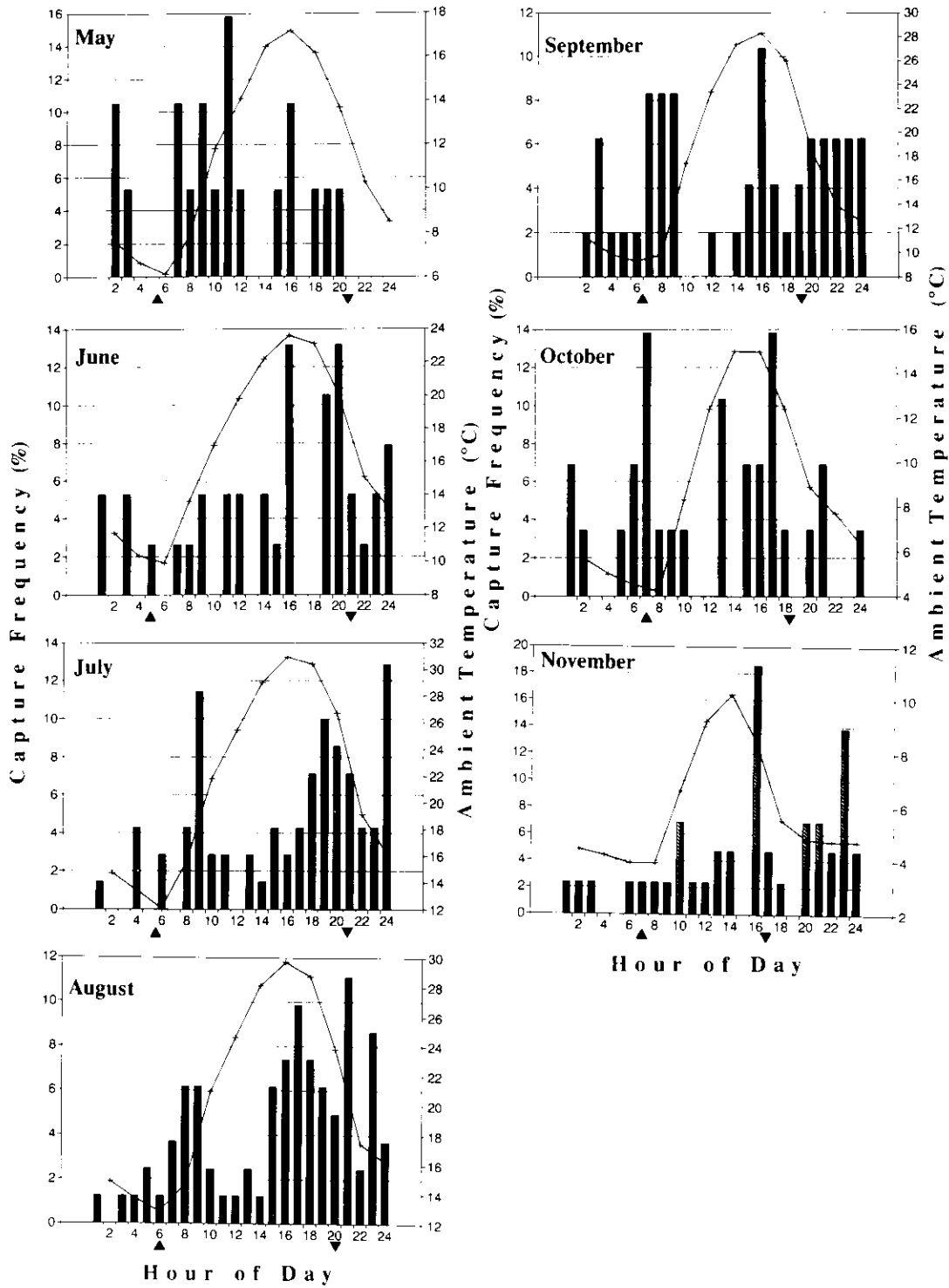


Figure 4. Capture frequencies and mean ambient temperature line through the hours of the day for each month of 1990. Upward and downward arrows at hours of day indicate the mid-month time of sunrise and sunset.

study may account for the diurnal activity pattern seen in the population as a whole. Nocturnal captures of juveniles equalled or exceeded diurnal captures during four months. The distribution of adult activity did not differ from that of the juvenile *M. montanus* reported by Claypool (1984). Juvenile *M. arvalis* and *M. agrestis*, however, were found to be more nocturnal than adults by Hoogenboom *et al.* (1984) and Baumler (1975). Baumler suggested the juveniles might avoid the daytime competition presented by the adults.

Parasitism, predation, and competition are three kinds of interspecific interactions that Madison (1985) suggested correlated with temporal activity in microtines. Parasites have been shown to change the rhythmic behavior of *M. montanus* (Seed and Khalili 1971).

Predatory pressures might induce a predominately diurnal or nocturnal pattern in prey species such as microtines. Hamilton (1937) interpreted the crepuscular peaks of activity in *M. pennsylvanicus* as a strategy to avoid both nocturnal and diurnal predators. The diurnal activity of *M. pennsylvanicus*, in areas where the predatory short-tailed shrew, *Blarina brevicauda*, occurred, was suggested as predation avoidance by Fulk (1972). Another survival strategy of prey species could be to synchronize activity periods with others in the population for exposure to predators in order to benefit from safety in numbers. The activity pattern of a population of *M. arvalis*, preyed on by kestrels, was hypothesized to reflect this strategy (Daan and Slopsema 1978, Rijnsdorp *et al.* 1981), although Lehmann and Sommersberg (1980) interpret the synchronous locomotor behavior of *M. arvalis* differently. They feel it is more important for intraspecific communication while defending a family territory.

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The activity of the vole population in this study was more strongly diurnal in 1989 than in 1990. Hawks and kestrels are often observed in this study site. Perhaps there was a difference in the population densities of both voles and diurnal aerial predators (e.g. hawks) between 1989 and 1990. This might have influenced the vole activity and accounted for the significantly greater number of diurnal occurrences by voles.

Finally, interspecific competition for space with other small mammals might have influenced the temporal activity of this vole population. *Sorex vagrans*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Mus musculus* are known to be present in the study site. Interspecific use of shared runways could be accomplished by temporal avoidance. This behavior was interpreted in the interactions of cotton rats and prairie voles by Glass and Slade (1980). Carley *et al.* (1970) found in their field study, peaks of diurnal activity of *Microtus ochrogaster* to be exclusive from the peaks of nocturnal activity of *P. maniculatus* and *R. megalotis*.

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