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Population Ecology of the Gray-Tailed Vole, *Microtus canicaudus*

Abstract

Voles of the genus *Microtus* play a major role as primary consumers of vegetation and as a prey base for many predators in grassland communities throughout the world. We present demographic and reproductive data from a 2-yr field study of the gray-tailed vole, *Microtus canicaudus*, a little-known microtine species endemic to the Willamette Valley of western Oregon, U.S.A. Population data were recorded on two live-trapping grids from October 1991 through September 1993. Population densities peaked between 1 June and 20 July 1992 at 54 voles/ha. Peak breeding with approximately 80% of adult females pregnant or lactating occurred between May and June with lesser activity in November and December. Very little breeding occurred during late summer and mid-winter months. Recruitment rate averaged 1.6 voles/litter/adult female. Mean home range sizes were twice as large for males (253 m²) as they were for females (135 m²). We compare the results from this field study with those obtained from enclosed populations of *Microtus canicaudus* and with those of "cycling" *Microtus* species. We suggest that agricultural practices, fragmentation of habitat, seasonal flooding of grasslands, and predation work in consort to regulate vole population numbers throughout the Willamette Valley of Oregon.

Introduction

Voles of the genus *Microtus* have been studied extensively with respect to their demography, behavior, and general ecology (Tamarin 1985). These voles occur in a variety of grassland habitats, are primary consumers of green vegetation, and are a prey source for numerous predators. Seventeen species of *Microtus* have been recognized in North America (Jones et al. 1992), eight of which have been well-studied. Although interspecific variation occurs among species, the general characteristics of *Microtus* species are that they have high reproductive potential (Keller 1985), exhibit marked population fluctuations often leading to annual or multi-annual (3-5 yr) cycles (Krebs and Myers 1974, Taitt and Krebs 1985, Batzli 1992), utilize a variety of breeding systems typified by polygynous or promiscuous mating (Wolff 1985, Tamarin et al. 1990) and female territoriality (Ostfeld 1985, Wolff 1985), and have male-biased juvenile dispersal (Boonstra et al. 1987, Wolff 1993, Lambin 1994). Voles are used as ecological model species (Ims and Stenseth 1989) to test hypotheses and construct conceptual and mathematical models addressing questions in population regulation (Hanski and Korpimäki 1995, Krebs 1996), behavioral systems (Tamarin

et al. 1990), and ecological problems such as habitat fragmentation (Ims et al. 1993). Information on additional species contributes to this data base for comparative analyses addressing related questions in population ecology. We present population data from a 2-yr live-trapping study of the little-studied gray-tailed vole, *Microtus canicaudus*. Specifically we ask if gray-tailed voles possess demographic characteristics associated with rapid population growth and resultant high densities typical of cycling *Microtus* species. In multi-annual cycling voles, densities frequently fluctuate from <5 to >200 voles/ha over a 3-5 yr period (Taitt and Krebs 1985). We also compare the demography of field populations of gray-tailed voles with that of enclosed populations (Manning et al. 1995, Edge et al. 1996, Wolff et al. in press).

Gray-tailed voles are a grass-eating *Microtus* occupying the grasslands of the Willamette Valley of western Oregon and southern Washington (Verts and Carraway 1987). Other than a brief description of the habits and general biology of gray-tailed voles (Verts and Carraway 1987), and laboratory studies on sibling recognition (Boyd and Blaustein 1985), copulatory behavior (Dewsbury and Hartung 1982), and reproduction (McDonald and Forslund 1978, Hagen and

Forslund 1979), little is known about the ecology of this species. In one open field, enclosure, and laboratory study, Wolff et al. (1994) found that breeding occurred from March through November with a breeding lull in late summer and mid-winter, adult body size ranged from 30-50 g, mean litter size was 4.4, the mating system was polygynous or promiscuous, home ranges of males were twice as large as those of females, and juvenile dispersal was male-biased.

Study Area and Methods

Gray-tailed voles were live-trapped on two 0.5 ha open trap grids at the E. E. Wilson Wildlife Area, 15 km north of Corvallis, in the central Willamette Valley, Oregon (44° 38' N, 123° 12' W). These grids were situated in open grassland habitat dominated by dense growth of perennial grasses, *Festuca arundinacea*, *Holcus lanatus*, and *Agrostis tenuis*. Each grid consisted of 100 traps in a 10 x 10 array with 7.6 m between stations. One Sherman large-size live trap was placed within 1 m of each station with the front door of the trap intersecting an active vole runway. The two grids were separated by 20 m of untrapped habitat.

Trapping was conducted at 2-wk intervals from 7 October 1991 through 16 September 1993. During a trap week, traps were baited with oats, set each evening and examined the following morning for four consecutive nights. Traps were propped open and pre-baited once during non-trapping days. All captured voles were ear-tagged for identification, and body mass, sex, reproductive condition, and trap location were recorded at each capture. Females were considered in reproductive condition if they were obviously pregnant, lactating, or had widely parted pubic symphyses. Voles were considered adult if they were ≥ 30 g (Wolff et al. 1994). Testes of mature gray-tailed voles are relatively small (~ 8 mm long; Wolff et al. 1994) and often retracted abdominally and not detectable externally in adult animals. Recruits were defined as any newly marked, <30 g animals caught after the initial population was marked.

Population sizes were estimated using the program CAPTURE and the jack-knife estimator (Rextad and Burnham 1992). Trappability was the percent of marked animals caught each trap week. Population growth rate was estimated by dividing the change in $\ln(\text{density} + 1)$ between

successive trap periods by the number of weeks between trap periods. Mean longevity (not accounting for dispersal) was estimated by subtracting the first from the last week of capture for animals first caught when they weighed <30 g. The ratio of recruits to adult reproductive females was computed by dividing the number of recruits captured each month by the number of reproductive females captured 4 wks earlier. This 4-wk period provided time for juveniles to be weaned, suffer mortality, and be recruited into the population.

Home range area was estimated using the minimum area polygon method (Hayne 1949) for adults that were caught 7-9 times over a 4-6-wk period. Home ranges were not calculated for animals with more than one capture in perimeter traps. Animals caught in perimeter traps often have home ranges that extend beyond the grid and therefore home range sizes would have been underestimated.

From 3 April to 18 May 1995, we trapped and removed voles for 46 consecutive days in one 0.5 ha pen enclosed on the sides and top with chicken wire. This pen excluded all avian and larger terrestrial predators, but allowed for movement of voles. The enclosed pen was located adjacent to our two open-field live-trapping grids. We used these data to get a population estimate of a high density population in the absence of predators.

Results

During the 2-yr study, 579 gray-tailed voles were trapped 3,117 times on the two grids. In addition, 60 Townsend's voles (*Microtus townsendii*), 55 deer mice (*Peromyscus maniculatus*), 87 wild house mice (*Mus musculus*), and 109 vagrant shrews (*Sorex vagrans*) were captured. Only the results from gray-tailed voles are presented in this paper.

Only eight voles (1.4 % of the population) moved between the two grids during the 2 yrs so we treated the grids as independent samples and present the data as means and standard errors of the two grids with an $n = 2$. The sex ratio did not differ from 1 on either grid (M:F, 166:151 and 125:130, both $X^2 < 0.18$, $P > 0.50$; sex of seven animals was not determined). Mean trappability (Krebs and Boonstra 1984) over the two years of the study was 84% (se = 0.32%) for males and 74% (se = 0.21%) for females.

Mean population size of voles ranged from 5 to 27 voles/0.5 ha during the 2-yr study (Fig. 1).

Population densities were highest in December 1991, June 1992, and January 1993. The population remained relatively low throughout the remainder of 1993 even during the spring breeding season. The mean weekly population growth rate from April through August 1992 and 1993 was -0.11 (se = 0.283) and 0.00 (se = 0.200), respectively.

Some adult females were in reproductive condition every month except for January 1992 (Fig. 2). Peak breeding activity for females occurred during May-June, with a secondary peak in October. Breeding activity declined considerably in February-March and August-September of both years. Peaks in recruitment followed peaks in female reproductive activity in autumn 1991, summer 1992 and autumn 1992, although relatively low recruitment followed a major peak of female reproductive activity in the summer of 1993. Mean juvenile recruitment/reproductive female was 1.6 (se = 0.25). Fifty-four percent of the animals caught were caught just once. Mean minimum longev-

ity differed significantly between males (3.9 wks, $n = 96$, $se = 0.50$) and females (5.8 wks, $n = 128$, $se = 0.65$; $F = 4.45$, $P < 0.05$).

Due to small sample sizes on each grid, mean home range sizes were estimated for the two grids combined. Mean home range size for males (253 m^2 , $sd = 138$, $n = 11$) was significantly larger than it was for females (135 m^2 , $sd = 82$, $n = 26$; $F_{1,35} = 9.689$, $P = 0.004$).

During the 46-day trap period in the 0.5 ha predator-exclusion pen in 1995, we caught 308 gray-tailed voles. Very little sign of vole activity was seen outside the pen even though suitable habitat was plentiful. We did not trap the grids during this time, but we saw fewer runways, holes, grass clipping and scat piles than at any time during the 2 yrs of trapping.

Discussion

During the 2-yr field study, population density of gray-tailed voles fluctuated between 5 and 27

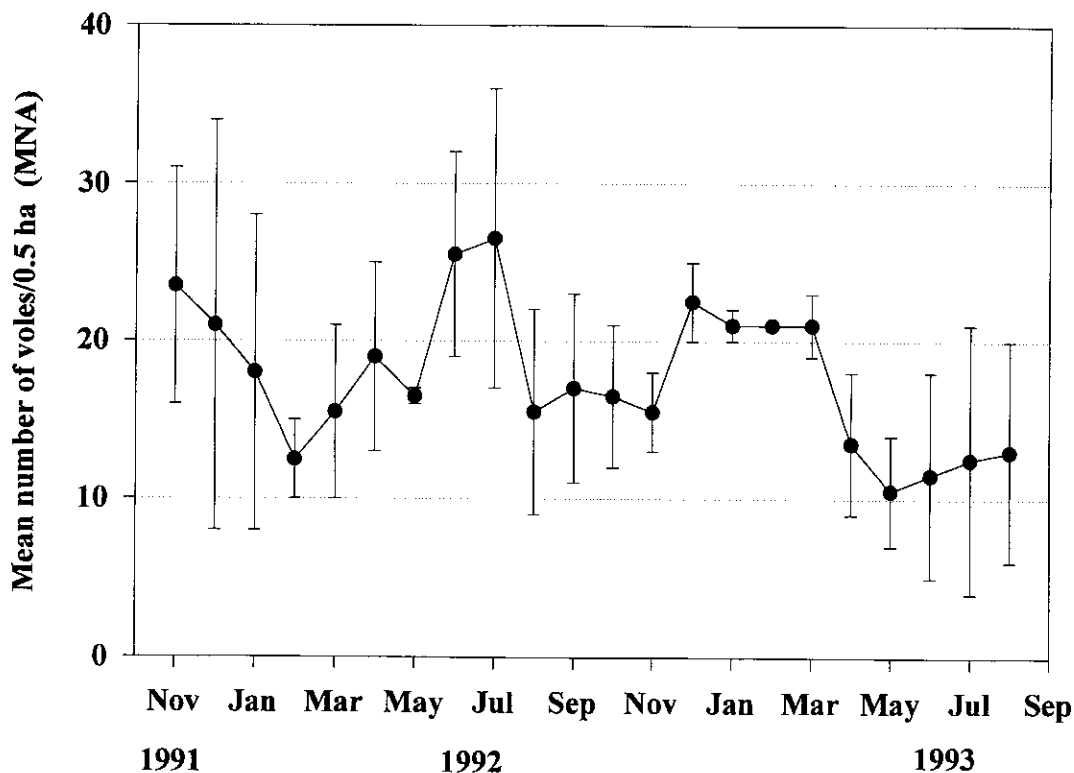


Figure 1. Mean (se) number of gray-tailed voles/0.5 ha from November 1991 to September 1993 at the E. E. Wilson Wildlife Area research site.

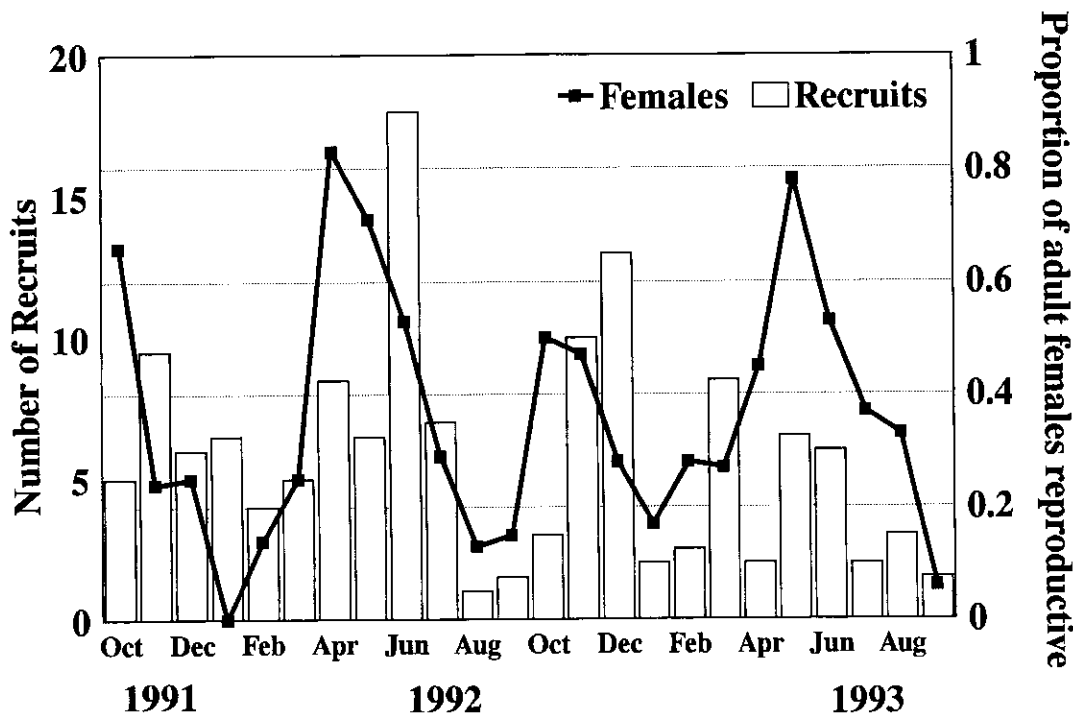


Figure 2. The proportion of adult females that were in reproductive condition and the number of recruits entering the population from October 1991 to September 1993 at the E. E. Wilson Wildlife Area research site.

voles/0.5 ha with no indication of annual or multi-annual cycles. Vole populations that exhibit multi-annual cycles have very distinct changes in density, age ratios, survival, and recruitment from year to year (Krebs and Myers 1974, Taitt and Krebs 1985). We saw none of these characteristics in our population that would indicate a multi-annual cycle was occurring. Reproduction and juvenile recruitment occurred primarily from March-November with a breeding lull in late summer and again in mid winter. This breeding pattern is typical of other microtine rodents at this latitude (Keller 1985). Mean minimum longevity (including survival and emigration) was 3.9 wks for males and 5.8 wks for females and 54% of the animals were caught only once suggesting that animals did not remain long on the study area. With short longevity, an unproductive winter period of 3 months with little recruitment, a subsequent low spring population, and a mean population growth rate during the breeding season near zero or negative, populations did not grow to peak cyclic levels.

The relatively low numbers of voles and lack of evidence for cycling may be related to three

interrelated factors: patchy habitats, predation, and seasonal flooding of habitats. The Willamette Valley consists of a mosaic of habitats characterized by agricultural fields and urban environments with <1% permanent grassland (Oregon GAP Analysis Program, F. Faure, personal communication). Also, much of the Willamette Valley is flooded from December through March when an average of 58 cm of rain falls. During this time, many voles are forced out of some areas and confined to others. Throughout the year, but especially during winter, the Willamette Valley hosts a large resident and migratory population of raptors, primarily red-tailed hawks (*Buteo jamaicensis*) and kestrels (*Falco sparverius*), as well as several other species of hawks and owls. The E. E. Wilson Wildlife Area provides refuge for a very dense population of raptors as well as red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and several species of large snakes, all of which have been sighted on the study area. Foraging on voles by great-blue herons (*Ardea herodias*) on the edge of flooded fields is a common sight in the Willamette Valley during winter (personal observations). Patchy habitats and the presence

of diverse facultative predators that consume animals dispersing from patches have been used to explain the lack of cycles for some other microtine populations (e.g. Hansson and Henttonen 1985, Hanski et al. 1991, Korpimäki and Norrdahl 1991).

Our census of voles in the predator-exclusion pen in spring 1995 demonstrates that gray-tailed voles have the potential to reach high densities that could lead to cycles. We caught 308 voles in a 0.5 ha pen that were designed to exclude all avian and large terrestrial predators. The number of voles caught likely represents the number of voles in the pen rather than immigrants during the 46-day removal period because very little sign of vole activity was seen outside the pens. On our trapping grids adjacent to these pens, we also saw very little sign of active runways, burrows, clippings, or scat piles. These results suggest that in the absence of predators, gray-tailed voles were able to achieve extremely high densities (616 voles/ha), similar to peak densities in cycling *Microtus* species (Krebs and Myers 1974, Hansson and Henttonen 1985, and others).

Very little historical information is available regarding the relative abundance of gray-tailed voles, but in November 1974, voles were reported to be "numerous" and at "peak" or "cyclic" densities near our study site (B. J. Verts, personal communication). Also, Goertz (1964) reported that gray-tailed voles exhibited episodic irruptions, but not with a predictable frequency. It appears that gray-tailed voles have the potential to reach higher densities than those measured on our open grids, but we suggest they may be prevented from reach-

ing this potential by heavy predation and existence in a patchy and fragmented landscape.

For the last 3 yrs, our research group has conducted experiments with gray-tailed voles in 0.2 ha enclosures that have been planted with alfalfa (*Medicago sativa*; Manning et al. 1995, Edge et al. 1995, in press, Schaubert et al. in press, Wolff et al. in litt.). We present some comparisons of the demography and behavior of voles in the two study sites. All analyses were conducted using the same methods. Population densities in the enclosures frequently reached an equivalent of 350 to 500 voles/ha (Edge et al. in press, Schaubert et al. in press) and >2,000 voles/ha in habitat fragmentation studies (Wolff et al. in litt.) which is considerably higher than the 54 voles/ha recorded from our field site. The proportion of females in the population that were in reproductive condition during the breeding season averaged about 80% at both sites and juvenile recruitment rates were comparable at about 1.6 juveniles/adult female (Edge et al. in press, Schaubert et al. in press). Minimum longevity of voles was greater in the enclosures than on the open grids for both males and females (Table 1). However, longevity of voles on open grids is confounded by emigration, so is not directly comparable to longevity in the enclosed populations where emigration was not possible. Mean weekly population growth rates throughout the spring and summer on open grids was -0.11 in 1992 and zero in 1993 (mean -0.054 for the two years) compared to 0.09 and 0.14, respectively, in the enclosed grids (mean of 0.11) and 54% of the voles were caught only once on

TABLE 1. Comparison of demographic features of gray-tailed voles on the open grids at the field site and enclosed grids at Hyslop Farm; mean (se). Data from enclosed grids are from Edge et al. (in press) and Schaubert et al. (in press).

	Open grids	Enclosed grids	P
Maximum density, voles/ha	54	350-500	
Animals caught only once	54%	24%	
Population growth/week*	-0.054 (0.229)	0.11 (0.028)	Mann-Whitney _{1,14} , P = 0.093
Longevity, wks			
males	3.9 (1.24)	6.4 (0.62)	F _{1,8} = 3.141, P = 0.114
females	5.9 (1.38)	8.7 (0.69)	F _{1,8} = 3.315, P = 0.106
Home range size, m ²			
males	253	93	F _{1,44} = 31.7, P < 0.001
females	135	56	F _{1,8} = 17.3, P < 0.001

*mean population growth/week during the May-August breeding season for the two years combined.

open grids compared to 24% in the enclosures (Table 1; Edge et al. in press, Schaubert et al. in press). Growth rates near or below zero and higher mortality (and/or dispersal of animals off the open grids) could have kept the open populations at relatively low numbers. The relatively high population growth rates and lack of dispersal in the enclosed population may all have contributed to the high densities (Krebs et al. 1969, Boonstra and Krebs 1977, Ostfeld 1994). Our two sites consisted of different vegetation (alfalfa in enclosed habitat and mixed pasture grasses in the open habitat) however voles apparently do equally well in both habitats and may even prefer grasses (e.g. *Microtus ochrogaster* and *M. pennsylvanicus*, L. Getz, pers. comm.). The fact that densities in the enclosed populations often reached >350 voles/ha compared to a maximum of 54 voles/ha in the field suggests that any intrinsic or self-regulating mechanisms were not effective in limiting population growth in the enclosures (Wolff and Schaubert 1996, see also Heske and Bondrup-Nielsen 1990).

At both sites, home ranges of males were twice as large as those of females, but home ranges at the field site were twice as large as they were in enclosures for both sexes (Wolff et al. 1994; Table 1). Home range size in small mammals is quite flexible and subject to variations in habitat quality and population density (Ostfeld 1985, Wolff 1985, Boutin 1990). In one experiment in our enclosures, densities approached 3,000 voles/ha and we recorded home range sizes of ~25 m² with

as many as 9-12 voles sharing a home range (Wolff and Schaubert 1996).

We conclude that gray-tailed voles possess attributes common of other *Microtus* species. The high reproductive potential can lead to high densities, however, population size and/or multi-annual cycles seem to be limited by extrinsic constraints. Gray-tailed voles are flexible in their behavior and social structure as evidenced by the comparisons of home range size and overlap in open and confined populations. We suggest that habitat fragmentation in conjunction with winter flooding that further limits habitat occupancy increases vulnerability of voles to predators which prevents populations from reaching cyclic densities. Occasional population irruptions potentially can occur under an appropriate set of extrinsic conditions.

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