

**A Reanalysis of the Occurrence, Size and Composition of Communal Groups of Prairie
Voles (*Microtus ochrogaster*)**

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Abstract

In our previous analyses of occurrence, size, and composition of communal groups of prairie voles (*Microtus ochrogaster*), we treated population density as a categorical variable ($< 100/\text{ha}$ and $\geq 100/\text{h}$) and used spring through early autumn and late autumn through winter as seasonal categories. To determine if these broad groupings biased our results, we reanalyzed the data treating density as a continuous variable and using a finer seasonal scale. We also conducted new analyses regarding composition of communal groups (specifically, proportion of adult male residents in relation to season and population density) and compared sex ratios of residents of communal groups, residents of all social groups and non-residents. The results confirm our earlier conclusions that variation in occurrence and size of communal groups results primarily from changes in nestling survival and resulting changes in population density, and not responses to weather conditions associated with season. Proportion of adult male residents of communal groups increased with population density and varied by season, being higher during periods of little or no breeding as compared to seasons within the main breeding period. Although raw data suggested that sex ratios of residents of communal groups and residents of all social groups were both female-biased and that of non-residents was male-biased, this difference was not statistically significant. Population density did not influence sex ratios.

Introduction

Prairie voles (*Microtus ochrogaster*) live in communal groups formed when philopatric offspring remain at the nests of either male-female pairs or single females; once offspring have reached adulthood, unrelated adults typically join communal groups (Getz et al., 1993). Communal groups are less common during spring through early autumn than during late autumn through winter. Most groups in spring-early autumn remain as pairs or single female units because snake predation results in low nestling survival. In late autumn, when snakes hibernate, nestling survival increases, leading to increases in population density, size of social groups, and prevalence of communal groups in the population (Getz et al., 1993; McGuire and Getz, 1995; Getz and McGuire 1997). Reproduction in the study population stops or remains very low in winter, and social group size gradually declines through mortality. In addition to seasonal changes in social organization, there are effects of population density: communal groups are more prevalent at high densities ($\geq 100/\text{ha}$) than low densities ($< 100/\text{ha}$; Getz et al., 1993).

The purpose of this account is to reexamine how occurrence, size and composition of communal groups change with season and population density using a finer scale for seasonal categories and treating population density as a continuous variable. We also examine season by population density interactions. Finally, we include three new analyses: (1) season and density effects on proportion of adult male residents of communal groups; (2) proportion of total population (adult males and adult females) that were residents of communal groups; and (3) comparison of sex ratio of communal groups, with that of all residents of social groups (communal, pair and single female) and non-residents.

Methods

Study sites

We monitored prairie voles in two adjacent 1 ha fields at the University of Illinois Biological Research Area, 6 km NE of Urbana, Illinois, USA (40° 15' N, 88° 28' W). The fields, planted with alfalfa (*Medicago sativa*), also contained ragweed (*Ambrosia* spp.), goldenrod (*Solidago* spp.), wild parsnip (*Pastinaca sativa*), and bluegrass (*Poa pratensis*). We trapped one field from October 1980 through July 1984 and the other from June 1983 through May 1987. We analyzed data from January 1983 through May 1987. During this time period, we used multiple methods to find nests (see below); we were confident that we had located all social groups in each study area.

Field methods

To identify members of prairie vole social groups, we placed four to five wooden multiple capture live traps (6.5 x 6.5 x 20 cm—Burt, 1940) baited with cracked corn directly at surface and underground nests (Getz et al., 1993). We found some nests by following radio-collared voles (Hofmann et al., 1984), some by conducting visual searches, and most by dusting voles with ultraviolet powder and tracking them back to their nests (Lemen and Freeman, 1985). We set traps at 0630 h on Monday and checked them at 3–4 h intervals through 2400 h. We checked traps again at 0630 and 0930 h on Tuesday. This 2-d schedule was repeated Thursday morning through Friday morning each week. We categorized social groups as single female units

(an adult female with or without young), male-female pairs (one adult male and one adult female with or without young), and communal groups (at least two adults of the same sex with or without young).

At first capture we weighed each vole to the nearest gram and toe-clipped it for individual identification. At each capture we recorded location, individual identification, sex, and reproductive condition. We assigned age classes based on body mass: juvenile (≤ 20 g), subadult (21-29 g), and adult (≥ 30 g). All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet guidelines of the American Society of Mammalogists (Sikes et al., 2011). For further details of field methods see Getz et al. (1993).

Statistical analyses

In our previous analyses of factors influencing the occurrence and composition of communal groups (Getz et al., 1993; Getz and McGuire, 1997; McGuire and Getz, 1995), we examined seasonal effects using two categories: spring through early autumn and late autumn through winter. In this paper we analyzed seasonal effects on a finer scale: winter (December through February), spring (March through May), summer (June through August), and autumn (September through November). As in our previous studies (Getz et al., 1993; Getz and McGuire 1997; McGuire and Getz, 1995), we used minimum number known to be alive (MNA; Krebs, 1999) to estimate population density of prairie voles for each trapping session; however, rather than categorizing population density as $< 100/\text{ha}$ and $\geq 100/\text{ha}$, in this paper we treated population density as a continuous variable.

We used generalized linear models with a Poisson distribution and log link function to test for the effects of population density and season on number of communal groups and average number of adult residents of communal groups. We standardized population density to mean of zero and standard deviation of one to improve convergence. We used generalized linear models with a binomial distribution and logit link function to test for the effects of population density and season on the following: proportion of communal groups (number of communal groups/total number of social groups); proportion of adult male residents of communal groups (number of adult male residents of communal groups/total number of adult residents of communal groups); proportion of adult males in the population that were residents of communal groups (number of adult male residents of communal groups/total number of adult males in the population); and proportion of adult females in the population that were residents of communal groups (number of adult female residents of communal groups/total number of adult females in the population). The initial models for each analysis included the fixed factors population density and season; when possible, we included a population density by season interaction. If the interaction was not significant, then we dropped it from the model. We used generalized linear models with a binomial distribution and logit link function to test for the effects of population density and “sample population” on sex ratio (males/females). The “sample populations” included residents of communal groups, residents of all social groups and non-residents. In all analyses, we used an autocorrelated error structure because data were arranged by week and a given communal group could be present for several weeks (number of observations = number of weeks = 268). For the sex ratio analysis, only those weeks with at least 10 communal groups were included to avoid small sample size bias. Contrasts were carried out on least squares means with P values adjusted for multiple comparisons (Tukey-Kramer). All analyses were performed using GLIMMIX procedure in SAS version 9.4.

Results

Descriptive statistics for response variables and population density are presented in Table 1. Means in Table 1 are actual means; unless otherwise stated, means reported below represent least squares means.

Table 1. Descriptive statistics by season for some response variables related to communal groups and population density of prairie voles. Data are actual means ($\pm SE$); n represents number of weeks monitored in each season.

Variable	Season			
	Winter ($n = 72$)	Spring ($n = 78$)	Summer ($n = 56$)	Autumn ($n = 61$)
Number ^a	13.3 \pm 1.3	2.7 \pm 0.4	2.0 \pm 0.5	10.1 \pm 1.8
Proportion ^b	0.55 \pm 0.03	0.21 \pm 0.02	0.10 \pm 0.02	0.26 \pm 0.03
Adult residents ^c	4.6 \pm 0.2	3.3 \pm 0.1	2.8 \pm 0.1	3.4 \pm 0.1
Population density	150.2 \pm 14.1	56.3 \pm 4.6	84.0 \pm 9.0	169.3 \pm 19.8

^aNumber of communal groups present

^bProportion of communal groups = number of communal groups/total number of social groups

^cNumber of adult residents of communal groups

Occurrence of communal groups

Number of communal groups increased with population density ($F = 109.37$; $df = 1$, 12.08; $P < 0.0001$; Table 2). There was a tendency for number of communal groups to vary by season ($F = 2.48$, $df = 3$, 256.2, $P = 0.06$; Table 2), with number in winter (7.9 ± 1.8) higher than number in either spring (6.2 ± 1.6 ; $P = 0.07$) or summer (6.2 ± 1.6 ; $P = 0.13$). Number of communal groups in winter was similar to number in autumn (7.2 ± 1.6).

Table 2. Effects of population density and season on number of social groups that were communal in a population of prairie voles.

Predictors	Beta	SE Beta	df	t	P
Intercept	1.979	0.230	3.6	8.62	0.0017
Population density	0.456	0.044	12.1	10.46	<0.0001
Winter ^a	0.089	0.071	265.7	1.26	0.210
Spring	-0.153	0.109	249.8	-1.40	0.163
Summer	-0.149	0.010	260.0	-1.49	0.136

^aAutumn is the reference

We found that proportion of communal groups increased with population density ($F = 59.61$, $df = 1$, 262, $P < 0.0001$) and varied by season ($F = 4.05$, $df = 3$, 262, $P = 0.0077$; Table 3). Proportion of communal groups was higher in winter (0.34 ± 0.04) than in either summer (0.22 ± 0.04) or autumn (0.25 ± 0.04); proportion in winter did not differ from that in spring (0.29 ± 0.04). The population density by season interaction was not significant for proportion of communal groups ($F = 0.47$, $df = 3$, 259, $P = 0.70$).

Table 3. Effects of population density and season on proportion of communal groups (number of communal groups/total number of social groups) in a population of prairie voles.

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	-1.758	0.251	262	-7.00	<0.0001
Population density	0.006	0.001	262	7.72	<0.0001
Winter ^a	0.395	0.138	262	2.86	0.005
Spring	0.171	0.185	262	0.92	0.356
Summer	-0.184	0.139	262	-1.32	0.188

^aAutumn is the reference

Size and composition of communal groups

Average number of adult residents of communal groups increased with population density ($F = 39.58$, $df = 1$, 198 , $P < 0.0001$) and varied by season ($F = 11.43$, $df = 3$, 198 , $P < 0.0001$; Table 4). Average number of adult residents in winter (4.1 ± 0.2) was higher than in either summer (3.0 ± 0.2) or autumn (3.2 ± 0.2), but did not differ from spring (3.7 ± 0.2). Average number of adult residents in spring was higher than summer, and tended to be higher than autumn ($P = 0.08$).

Table 4. Effects of population density and season on the average number of adult residents of communal groups in a population of prairie voles.

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	1.138	0.050	198	22.74	<0.0001
Population density	0.145	0.023	198	6.29	<0.0001
Winter ^a	0.237	0.048	198	4.95	<0.0001
Spring	0.149	0.061	198	2.43	0.016
Summer	-0.074	0.063	198	-1.17	0.245

^aAutumn is the reference

Proportion of adult male residents of communal groups increased with population density ($F = 12.12$, $df = 1$, 262 , $P = 0.0006$) and varied by season ($F = 7.75$, $df = 3$, 262 , $P < 0.0001$; Table 5). The general pattern was for proportion of adult male residents to be higher during periods of little or no breeding (winter, 0.45 ± 0.01) as compared to seasons within the main breeding period (spring, 0.42 ± 0.02 ; summer, 0.39 ± 0.02 ; and autumn, 0.41 ± 0.01). More specifically, proportion of adult males in communal groups in winter was significantly higher than the proportion in either summer or autumn, and tended to be higher than that in spring ($P = 0.13$). The population density by season interaction was not significant for proportion of adult male residents of communal groups ($F = 0.68$, $df = 3$, 259 , $P = 0.56$).

Table 5. Effects of population density and season on proportion of adult male residents of communal groups (number of adult male residents of communal groups/total number of adult residents of communal groups) in a population of prairie voles.

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	-0.435	0.069	262	-6.29	<0.0001
Population density	0.0006	0.0002	262	3.48	0.0006
Winter ^a	0.160	0.040	262	4.04	<0.0001
Spring	0.034	0.065	262	0.51	0.608
Summer	-0.091	0.060	262	-1.52	0.130

^aAutumn is the reference

Proportion of adult males in the population that were residents of communal groups increased with population density ($F = 60.83$, $df = 1, 256$, $P < 0.0001$) and varied by season ($F = 9.88$, $df = 3, 256$, $P < 0.0001$; Table 6). Proportion of adult males in the population that were residents of communal groups was higher in winter (0.25 ± 0.03) than in either summer (0.12 ± 0.03) or autumn (0.15 ± 0.03), and tended to be higher than the proportion in spring (0.18 ± 0.04 , $P = 0.11$). The population density by season interaction was not significant for proportion of adult males in the population that were residents of communal groups ($F = 0.34$, $df = 3, 253$, $P = 0.80$).

Table 6. Effects of population density and season on proportion of adult males that were residents of communal groups in a population of prairie voles (number of adult male residents of communal groups/total number of adult males in the population).

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	-2.257	0.265	256	-8.51	<0.0001
Population density	0.005	0.0006	256	7.80	0.0001
Winter ^a	0.636	0.132	256	4.83	<0.0001
Spring	0.190	0.228	256	0.83	0.406
Summer	-0.292	0.224	256	-1.31	0.193

^aAutumn is the reference

Similarly, proportion of adult females in the population that were residents of communal groups increased with population density ($F = 43.35$, $df = 1, 261$, $P < 0.0001$) and varied by season ($F = 4.44$, $df = 3, 261$, $P < 0.005$; Table 7). Proportion of adult females in the population that were residents of communal groups was higher in winter (0.31 ± 0.04) than in either summer (0.18 ± 0.04) or autumn (0.24 ± 0.04), but did not differ from the proportion in spring (0.28 ± 0.05). Proportion of adult females in the population that were residents of communal groups was higher in spring than summer. Finally, the population density by season interaction was not significant for proportion of adult females in the population that were residents of communal groups ($F = 0.34$, $df = 3, 253$, $P = 0.80$).

Table 7. Effects of population density and season on proportion of adult females that were residents of communal groups in a population of prairie voles (number of adult female residents of communal groups/total number of adult females in the population).

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	-1.629	0.266	261	-6.12	<0.0001
Population density	0.004	0.001	261	6.73	<0.0001
Winter ^a	0.350	0.129	261	2.72	0.007
Spring	0.237	0.202	261	1.18	0.240
Summer	-0.347	0.186	261	-1.86	0.064

^aAutumn is the reference

Comparison of sex ratios of residents of communal groups, residents of all social groups and non-residents

Descriptive statistics (actual means \pm *SE*, range) for sex ratio data were as follows ($n = 57$ weeks): residents of communal groups, 0.87 ± 0.03 , 0.44 - 1.57; residents of all social groups, 0.84 ± 0.03 , 0.78 - 2.00; non-residents, 2.05 ± 0.26 , 0.47 - 13. The generalized linear model revealed that neither population density nor sample type affected sex ratio (population density: $F = 3.49$, $df = 1, 92$, $P < 0.065$; sample type: $F = 2.03$, $df = 2, 92$; $P = 0.13$; Table 8). None of the least squares means differed from one another (residents of communal groups, 0.78 ± 0.04 ; residents of all social groups, 0.75 ± 0.03 ; non-residents, 0.76 ± 0.04).

Table 8. Effects of population density and sample type (residents of communal groups, residents of all social groups, or non-residents) on sex ratios in prairie voles (males/females).

Predictors	<i>Beta</i>	<i>SE Beta</i>	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	0.694	0.368	92	1.88	0.063
Population density	0.002	0.001	92	1.87	0.065
Communal groups ^a	0.154	0.203	92	0.76	0.451
All social groups	-0.046	0.188	92	-0.24	0.810

^aNon-resident is the reference

Discussion

The analyses presented here, using finer scale seasonal categories and treating population density as a continuous rather than categorical variable, support our previous conclusions that once snakes hibernate in autumn and nestling survival increases, communal groups increase in prevalence and size (Getz et al., 1990; Getz et al., 1993; Getz and McGuire 1997; McGuire and Getz, 1995). We found that number and proportion of communal groups in the population, as well as average number of adult residents of communal groups, were highest in winter. Proportions of adult males and adult females in the population that were residents of communal groups also were highest in winter. Consistent with our previous conclusions that increased nestling survival in autumn leads to increases in population density and more and larger communal groups, we found all measures of prevalence and size to increase with population density. In previous analyses, we typically did not test for population density by season

interactions; here, we found no evidence that effects of population density on characteristics of communal groups differed among seasons.

We previously reported that male prairie voles were more likely than female prairie voles to directly transfer into groups with potential mates and without potential competitors (McGuire et al., 2013). One of our new analyses here revealed that the proportion of adult male residents of communal groups was highest in winter; this suggests to us that adult males might be more tolerant of sharing a nest with one another outside the main breeding season. Although raw data indicated that sex ratios of residents of communal groups and residents of all social groups were both female-biased and that of non-residents was male-biased, this difference was not statistically significant. Population density also did not influence sex ratios.

We conclude from these and earlier analyses of the field data that the following scenario best describes changes in communal group prevalence, size and composition. Nestling survival is very low from late spring through early autumn owing to snake predation. As a result, most social groups remain as male-female pairs or single females; those groups that do become communal, are small. In late autumn, following hibernation of snakes, nestling survival increases, with most male-female pair and single female social groups becoming communal and size of communal groups increasing. Increases in the proportion of communal groups and group size continue until reproduction declines or ceases in early winter. Mortality from avian and mammalian predators gradually results in declines in population density and reductions of communal group size during winter and into early spring. Most communal groups are reduced to male-female pairs or single females by late spring, when reproduction begins. But, by late spring, snakes have emerged and nestling mortality is high. Thus, most social groups remain as male-female pairs or single female until snakes hibernate in late autumn, when the sequence of events repeats itself. The magnitude of such changes depends upon the amplitude of population fluctuation in a given year (Getz, et al., 2006).

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