

Testing Sign Indices to Monitor Voles in Grasslands and Agriculture

Abstract

I evaluated the use of sign indices as indicators of relative vole population abundances in grasslands and agricultural systems in western Oregon grasslands. The development of a reliable index based on vole sign that does not rely on the repeated use of traps would greatly aid rapid assessment of relative population densities, and allow greater flexibility in both research and management. I tested the presence and number of burrows, runways, droppings, and damaged vegetation along transects and in quadrats to evaluate each metric's correlation to estimated population size. Vole population size was estimated with mark-recapture techniques. None of the indices performed well, particularly in situations where plots were mowed. The number of animals captured on the first trapping occasion was most correlated with estimated population size. Indices for vole abundance should be tested in the system and with the species of interest prior to their use in research or management.

Introduction

The use of mark-recapture techniques with live trapping is a well-established method to estimate population size and density of small mammals (Williams et al. 2002). However, live trapping requires traps, trained personnel, and a significant investment of time and funding. For researchers interested in estimating relative densities of small mammals, an easy-to-use and relatively precise index would be far more efficient. Likewise, indices can be a valuable tool for land managers whose decisions may require knowledge of relative population density but not necessarily absolute numbers (McComb et al. 2010). Furthermore, avoiding handling animals reduces risk of human infection by diseases such as leptospirosis, Hanta virus, and tularemia.

Sign indices have been used widely in studying mammals for research and management. Droppings or pellets have been used for species ranging from snowshoe hares to elephants (Walsh et al. 2001, Hodges and Mills 2008). Camera traps that photograph their subjects have been used for numerous species, including ungulates, wallabies, and maras (Rowcliffe et al. 2008, Rovero and Marshall 2009). Rodents have been indexed using counts of runways or estimates of grazing intensity (Hansson 1979). Other indices that have been developed for rodents include chew blocks and track plates (Engeman 2005, Whisson et al. 2005).

Grassland voles are species for which indices could be very useful for research and management. Vole population dynamics have major impacts on predator populations (Korpimaki and Norrdahl 1991, Sundell et al. 2004, Gervais et al. 2006), plant communities (Howe et al. 2006), and they may even influence soil properties (Gervais et al. 2010). Voles thus influence their ecological communities in ways that are still not well understood, and much work remains to be done. In agricultural systems, voles are well-known crop pests in many regions of the globe. The damage caused by voles might be limited if the populations were checked early in high density population cycles, as demonstrated by field studies that manipulated predation rates on vole and rabbit populations (Pech et al. 1992, Korpimaki et al. 2002, Korpimaki et al. 2005). This would also require knowledge of the status of the vole population through time, in order to determine when rapid, sustained population growth was beginning to occur. An efficient and reliable index would be of great value in agricultural field scouting to determine when vole numbers reached critical thresholds requiring control.

Although trapping small mammals is a highly effective method of estimating population density, provided that the animals have some reasonable probability of being caught, the use of live traps is essentially limited to use by wildlife professionals. The repeated trapping sessions needed for population estimation can be expensive. Snap traps are easier to use, but still are time-consuming, requiring at least two visits. Killing animals is often not ethically acceptable, and may affect the

¹Author to whom correspondence should be addressed.
Email: jennifer.gervais@oregonstate.edu

population under study enough to interfere with the research question. Snap traps also require handling of carcasses, thus posing some risk of disease transmission to field workers. Cost, training requirements, equipment, mortality in the subject population and disease transmission risk may be minimized with an effective sign index method. In addition, simple enumeration of captured individuals may provide a more precise indicator of population size than estimators of population size if model assumptions regarding underlying process variation do not fit the data (McKelvey and Pearson 2001). Determining which model to use for estimating population size with mark-recapture data can be problematic when capture probabilities are low and numbers of captured animals small (White et al. 1982)

In order to be effective, sign indices must meet certain criteria. The underlying assumption is that the index is consistently proportional to the population density over the range of densities that will be encountered (Caughley and Sinclair 1994). A useful index will be practical to apply, sensitive to changes in density at a scale appropriate to the problem or question, precise and at least consistently biased, and entail as few assumptions as possible (Caughley and Sinclair 1994, Williams et al. 2002, Engeman 2005). Ideally, indices should be validated against known population sizes or at the very least evaluated across varying densities (Engeman 2005, Witmer 2005). Indices may perform differently in different habitats or for different population densities such that the underlying relationship is nonlinear (Williams et al. 2002). These potential issues need to be explored before an index can be confidently used.

Sign indices have been developed for voles in Europe and successfully used in research (Hansson 1979, Lambin et al. 2000). The goal of this project was to evaluate whether sign indices could be used without trapping by land managers and others interested in tracking the relative densities of vole populations in western Oregon's grassland habitats.

Specifically, my objectives were to explore the ability of various vole sign indices and a single trapping event to reflect densities of voles across two grassland habitats, agricultural fields in grass seed production and unmanaged grassland. Do number of burrows, occurrence of runways, droppings, evidence of herbivory, or first night's

trap captures correlate to actual vole numbers? I addressed this question by estimating vole population density with mark-recapture techniques. I then measured sign indices and examined their relative performance in reflecting population size.

Methods

Field Methods

Vole populations were studied at the Hyslop Agronomy Station of Oregon State University, 15 km south of Corvallis, Oregon USA. The primary rodent on the study site is the gray-tailed vole, *Microtus canicaudus*. Deer mice (*Peromyscus maniculatus*) are also present in much lower numbers, as are shrews (*Sorex vagrans*). Twenty-four enclosures, 0.2 ha each, were created out of sheet metal buried 90 cm into the soil and extending 90 cm above ground in the early-mid 1990s. The enclosures were used extensively in previous research on voles (Manning et al. 1995, Schauber et al. 1997, Wang et al. 2001). Originally these enclosures were vole-proof, but damage by flooding, wind, and accidents with farm equipment have torn small gaps in some walls, and the 2.5 m wide gates no longer shut tightly. However, I assumed geographic closure for the four-day trapping intervals because the enclosures were still largely intact.

Vegetation consisted of pasture grasses and weeds, including some thistle, blackberry, and composite annuals. Eight enclosures were mowed to a height of approximately 10 cm in April 2007, whereas 16 were left unmowed. Mowed enclosures had not been randomly selected. Grass seed head heights reached over 1 m in these enclosures, although the majority of the vegetation was 30 cm high. I used all 8 mowed enclosures and 8 of the 16 unmowed enclosures with the least amount of fence and gate damage in this study. Although there was some variation in density of vegetation in the unmowed enclosures, I did not quantify the vegetation's characteristics.

Trapping and handling protocols were approved by the Oregon State University Institutional Animal Care and Use Committee. Trapping was conducted in four sessions held over the course of late spring through summer 2007. I began trapping sessions on May 21, July 2, August 9, and August 22. Four enclosures were selected in each session, representing a mix of mowed and

unmowed enclosures. An 8x8 trapping grid was set up in each enclosure with five meter spacing between Sherman live-traps. The traps were propped open and pre-baited with oatmeal at least five nights before trapping was begun. For each trapping period, the oatmeal was replenished and the traps set in the evening beginning an hour before dusk, and checked the following morning at dawn. If night time temperatures were expected to fall below 10° C, polyester batting was also added to the traps. Trapping was conducted for four consecutive nights, as this was determined to be adequate for estimation of population size in earlier work (Manning et al. 1995). Captured voles were outfitted with a numbered ear tag and weighed.

Five sign indices were measured in each enclosure immediately prior to trapping except for the first session, when indices were measured immediately after trapping was completed. The sign indices consisted of counts of burrow entrances that were not collapsed, presence of droppings, presence of grazed plants, clipped green vegetation that had not yet dried out, and presence of runways. I examined both quadrats and strip transects for vole sign. Quadrats measured 0.25 m on a side and were systematically placed at 7.5 m intervals on a 5x5 grid in each enclosure. Quadrat size was based on other studies using similar indices of vole abundance (Hansson 1979, Lambin et al. 2000). The strip transects were conducted on the first, third, and fifth line of the quadrat grid. Vole sign was examined on a zero-width transect, a 0.5 m wide transect, and a 1 m wide transect. Transects were considered subsamples of the enclosure and the mean value was used for analysis.

Statistical Methods

Manning et al. (1995) used Program CAPTURE (White et al. 1982) to evaluate the relative precision and bias of 11 probabilistic estimators using known populations of gray-tailed voles consisting of 30, 60, or 90 individuals in a replicated trial. They reported that individual heterogeneity in capture probability was the main source of variation in capture probabilities, such that the jackknife and Chao's M_h (Chao 1989) estimators were most appropriate for this system. The performance of Chao's M_h and the jackknife M_h improved with population size. Of those two, however, the jackknife estimator was most stable in its ability to perform with 4 versus 10 capture occasions.

Percent relative bias was estimated to be 9.83 for populations of 30 voles, -2.26 for populations of 60 voles, and -1.90 for populations of 90 voles. Manning et al. (1995) concluded that the jackknife estimator offered the best compromise between trapping effort and estimator performance.

This work was performed in the same system of enclosures on the same species as Manning and colleagues' earlier work (Manning et al. 1995). Therefore, I estimated population size with mark-recapture techniques using Program CAPTURE and the jackknife estimator. Voles that died in traps were removed from the data prior to analysis, and their numbers were added to the estimated population size and confidence intervals.

Sign indices were then compared to estimated population sizes of voles in the enclosures using a regression procedure in Proc GENMOD in SAS (SAS Institute, Cary, NC). Main effects were each sign index and mowing treatment. All effects were considered fixed. Initial models included interaction terms of mowing treatment by sign index to examine if interactions existed that could preclude combining data across all enclosures regardless of mowing treatment. Wald chi-square test output in the GENMOD procedure was used to evaluate the statistical significance of interactive effects and appropriateness of combining data. Lack of significance in the Wald chi-square test indicated that there was no evidence that the regression coefficient of the interaction term was different than zero. I then ran models without interaction terms to generate correlation coefficients for each index separately for each mowing treatment. I examined only single-index models because the objective was to determine which, if any, sign index could serve as a surrogate for live trapping in estimating population density.

Results

Although some movement among enclosures was possible because the walls were not entirely vole-proof, it was not likely to occur during the short time frame of the trapping session, and no tagged animal was recovered outside its original enclosure. A total of 385 individual voles were captured over the course of the study. Of these, 46 died in traps, with mortalities spread among the sessions (Table 1). Very few traps (<5) were ever sprung without catching a vole, so this was disregarded in the analysis. Traps were never found

TABLE 1. Mean population sizes (\hat{N}) and 95% CIs for gray-tailed voles in 16 enclosures used to compare sign index performance at Hyslop Agricultural Station, Oregon State University, Corvallis. Start dates are May 21 for Group 1, July 2 for Group 2, August 12 for Group 3, and August 22 for Group 4. Enclosures 1-8 were mowed prior to the start of the study. The jackknife estimator of Program CAPTURE was used to estimate population size. Animals that died during capture have been added to the means and confidence intervals.

Grid	Mow	Start	Count	First Day Capture	Died	\hat{N}	SE	95% CI
1	Y	2	12	4	0	23	5.6	17-40
2	Y	3	13	3	5	20	4.4	16-34
3	Y	4	6	1	0	9	2.9	7-21
4	Y	4	12	4	0	14	2.6	13-26
5	Y	2	12	4	0	20	4.4	15-34
6	Y	3	25	8	6	42	6.9	33-61
7	Y	3	31	7	4	54	8.3	43-76
8	Y	4	12	3	1	23	5.5	17-39
9	N	1	13	3	3	21	4.4	16-34
10	N	1	12	3	2	15	3.1	13-27
11	N	4	55	19	2	110	12.2	92-139
12	N	2	50	19	3	94	11.1	78-121
13	N	1	27	15	11	35	4.5	30-49
14	N	3	45	18	5	73	9.3	60-98
15	N	2	53	18	3	99	11.5	82-127
16	N	1	7	1	1	9	1.7	8-15

open but stripped of bait, and triggers were tested each time the traps were set.

Populations of voles in the enclosures varied widely, with low numbers occurring in both mowed and unmowed enclosures. The greatest numbers were associated with the unmowed enclosures, however (Table 1). Densities were generally comparable to those tested by Manning et al. (1995) although both lower and higher densities were estimated in the present study.

Interactions between sign indices and mowing treatment were particularly prevalent in the widest

strip transect data, although almost non-existent in the line-intercept transect data (Table 2). This result suggests that sign indices cannot be compared across habitat types, or even across habitat types with dissimilar characteristics such as structure, although the potential bias introduced by doing so will vary depending on the index type. In this study, line intercept transects were least likely to produce index data that were affected by habitat.

Some indices showed limited promise in the unmowed enclosures. Counts of runways and droppings produced correlation coefficients of 0.44

TABLE 2. Evaluating the presence of interactive effects between sign indices and mowing treatment. Populations of voles were estimated in 16 enclosures using mark-recapture methods and each enclosure was surveyed for vole sign to examine the relationship between the index and estimated population size. Eight enclosures were mowed and 8 were not mowed. The table values are the Wald chi-square values for the interaction term of index by mowing treatment, indicating if the regression coefficient for the parameter estimate is not zero. *P* values are given in parentheses. Wald chi-squares and probabilities were obtained using Proc GENMOD in SAS. Firstday is the number of voles captured in the first trapping event, clipped is number of plants damaged by grazing, and droppings are counts of fecal deposits. Degrees of freedom equal 1 in all cases.

Interaction Terms	0 m width	0.5 m width	1.0 m width
Grazed x Mowed	2.78 (0.01)	3.67 (0.06)	5.2 (0.02)
Clipped x Mowed	0.68 (0.41)	0.44 (0.51)	3.2 (0.07)
Droppings x Mowed	2.24 (0.13)	2.85 (0.09)	4.01 (0.05)
Burrows x Mowed	1.05 (0.31)	4.08 (0.04)	3.24 (0.07)
Runways x Mowed	16.31 (0.00)	8.63 (0.00)	11.7 (0.00)
Firstday x Mowed	0.33 (0.56)	0.33 (0.56)	0.33 (0.56)

TABLE 3. Correlation coefficients for relationships between vole sign indices and total numbers of voles estimated by mark-recapture techniques and Program CAPTURE using the jackknife estimator. Correlation coefficients given in the table are the adjusted r^2 values generated by Proc GENMOD in SAS. Firstday is the number of voles captured in the first trapping event per enclosure. Clippings are the frequency of bits of cut vegetation, and grazed is the frequency of vole-damaged plants. Droppings is the frequency of fecal piles. Asterisks indicate statistical significance at the $P=0.05$ level.

Transect Width	Mowed			Unmowed		
	0.0 m	0.5 m	1.0 m	0.0 m	0.5 m	1.0 m
Clippings	0.14	0.30	0.28	0.26	0	0.03
<i>F</i>	2.17	4.01	3.67	3.56	0.00	1.21
<i>P</i>	0.19	0.09	0.10	0.11	0.96	0.32
Runways	0	0	0	0.74	0.54	0.70
<i>F</i>	0.10	0.33	0.67	21.37	9.13	15.02
<i>P</i>	0.76	0.59	0.44	0.00*	0.02*	0.01*
Droppings	0	0.09	0	0.44	0.63	0.59
<i>F</i>	0.50	1.70	0.86	6.39	13.09	9.70
<i>P</i>	0.51	0.24	0.39	0.05*	0.01*	0.03*
Burrows	0	0	0	0.08	0.24	0.12
<i>F</i>	0.11	0.46	0.88	1.63	3.22	1.85
<i>P</i>	0.75	0.52	0.39	0.25	0.12	0.23
Grazed	0	0.02	0	0.22	0.26	0.45
<i>F</i>	0.43	1.13	0.47	3.00	3.47	5.96
<i>P</i>	0.54	0.33	0.52	0.13	0.11	0.06
Firstday	0.75					0.79
<i>F</i>	22.03					28.17
<i>P</i>	0.00*					0.00*

to 0.74 with no trends regarding transect widths (Table 3). In contrast, none of the sign indices I used were very effective at indicating the number of voles present in the mowed enclosures (Table 3). Holes were generally poor to very poor indicators of vole numbers in either mowing treatment.

Quadrat-based sampling performed very poorly, with the number of quadrats in which vole sign was detected showing essentially no relationship to the number of voles estimated to be present in the mowed enclosures. Results were slightly

better in the unmowed habitat but the strongest relationship, between number of quadrats with grazed vegetation and total number of voles, still had an adjusted r^2 of only 0.33 (Table 4).

The best indicator of number of voles present was the number of animals caught the first day of the trapping session. The correlation coefficients were $r^2 = 0.75$ ($n=8$) and $r^2 = 0.80$ ($n=8$) for the mowed and unmowed treatments, respectively and there was no evidence of an interaction with mowing ($P = 0.56$), indicating that this index

TABLE 4. Correlation coefficients for indices of vole sign in 25 cm by 25 cm quadrats and total vole population size as estimated by mark-recapture. Sign was either recorded as present or absent in each quadrat. "Any" refers to the existence of any vole sign in the quadrat. Degrees of freedom equals seven in all cases. Clipping is the presence of bits of clipped vegetation, grazed is the frequency of vole-damaged plants, and droppings are the frequency of fecal piles. Statistical significance at the $P=0.05$ level is indicated with an asterisk.

	Clipping	Droppings	Burrows	Runways	Grazed	Any
Mowed	0	0	0.01	0	0	0
<i>F</i>	0.56	0.64	1.05	0.72	0.26	0.13
<i>P</i>	0.48	0.46	0.35	0.43	0.63	0.73
Unmowed	0	0.26	0.02	0.13	0.33	0.21
<i>F</i>	0.01	3.39	1.11	2.00	4.4	2.90
<i>P</i>	0.94	0.11	0.33	0.21	0.08	0.14

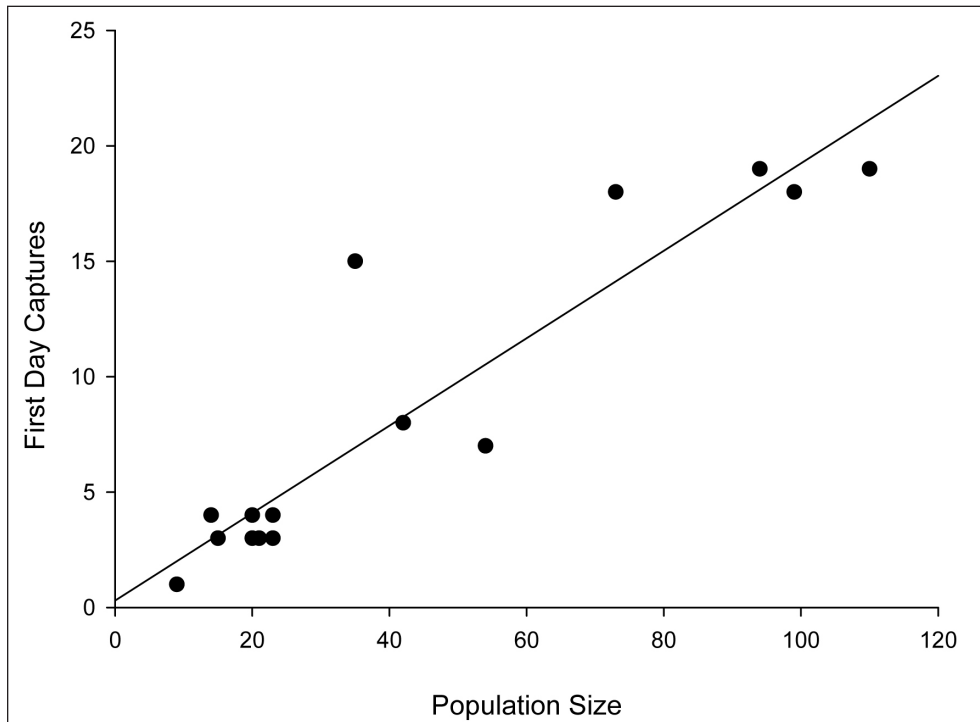


Figure 1. Regression of population size of gray-tailed voles estimated with Program CAPTURE using the jackknife estimator and the number of voles captured on the first trapping event for each of 16 enclosures.

could be robust to differences in habitat among sampling locations (Figure 1). The first night's capture for each enclosure was closely tied to the total number of voles estimated to be present across treatments ($r^2 = 0.85$, $n=16$).

Discussion

Indices rely on the assumption that there is a constant, if unknown, relationship between the index value and the actual population size or density (Williams et al. 2002). This relationship may not be linear in the case of gray-tailed voles because of their flexible territorial behavior. Wolff et al. (1994) found that male voles had estimated home range sizes of 94 m^2 ($\pm 54.3 \text{ m}^2 \text{ SD}$), whereas females' territories were estimated at half that size ($56.0 \pm 30.1 \text{ m}^2$) in the same enclosures. However, they also found that the amount of territorial overlap was related to vole density, with greater numbers of voles sharing the same physical space as density increased (Wolff et al. 1994). The relationship between indices and population abundances of gray-tailed voles may therefore not be linear, making the use of sign indices unreliable without

knowing the underlying relationship (Williams et al. 2002).

The sign indices I tested do not appear to be robust to differences in habitat structure, making it difficult to compare data across sites or possibly even different stages of crop growth in the case of agriculture. However, the number of captures generated by a single night's trapping could be used as an index that is less sensitive to habitat type, which may allow the use of snap traps. This would greatly reduce the labor and expense of data collection, although it would still require handling animals.

Transect counts of runways and droppings correlated somewhat with total gray-tailed vole population size in unmowed pasture enclosures, the correlation between presence of fecal pellets and estimated population size was 0.74. The persistence of old droppings may be a confounding factor, although research exploring this question with snowshoe hare pellets concluded that clearing plots of pellets was not needed for indicating relative abundances (Hodges and Mills 2008). However, western Oregon's highly seasonal weather patterns

and subsequent influence on decomposition rates would suggest that indices using vole fecal pellets should not be compared across time. Removing vole fecal pellets from transects or quadrats before resurveying the area would likely be prohibitively time-consuming even if it did substantially improve index correlations with population size.

In the mowed enclosures, the indices I examined were generally not correlated with estimated population size. The quadrat method of sampling performed poorly in both mowing treatments. This is in contrast to work done by researchers in northern England, upon whose methods the quadrat sampling I employed was based (Lambin et al. 2000).

Vole sign may not be linearly correlated to actual density for a number of reasons. In the case of burrows, the entrances and associated tunnels may remain intact for many months following a population crash in western Oregon (J. A. Gervais, unpublished data). When populations begin to recover, it is likely that the voles make full use of these pre-existing burrows. They may have larger territories when densities are low, producing signs of activity over a larger area than a single individual would at greater densities, thus confounding sign and population size in methods indexing only presence or absence. Alternatively, increasing densities may lead to increasing home range overlap (Wolff et al. 1994). Burrows have been suggested as an indicator of vole activity (Liro 1974, Steiner et al. 2007), but I found that simply counting them is likely to be highly misleading.

Seasonality of behavior or weather patterns will influence the occurrence of sign. Digging by voles in western Oregon also appears to be limited to the fall and spring, when soil is moist but not saturated. Burrows therefore may be maintained through generations, and digging activity will be strongly seasonal. The dry weather during the summer also prevents the quick disintegration of droppings, and these appeared to build up over the course of the study. I did not attempt to remove droppings from along a transect to evaluate recent sign, this may be worth testing although it would require a second field visit and exact placement of the repeat transect, thus increasing cost.

Grazing activity can also leave persistent sign, because blades of grass that have been cropped by voles will retain evidence of the damage. I did not count grazed grass blades whose tips had

turned brown, as those were not recently damaged. However, the damage is still cumulative, and vegetation does not grow rapidly in midsummer in western Oregon due to summer drought. The presence of recently clipped vegetation is more ephemeral, and thus may be a better indicator of recent activity. However, I noted a sharp decline in the presence of cut vegetation from June to late August, although some clipped vegetation was observed in all trapping sessions. It seems probable that voles shift their herbivory underground later in the summer, feeding on roots when above-ground vegetation has declined in quality due to the extended drought. Greater rates of vegetation clipping may occur earlier in the season, when voles appear to be developing stockpiles. Therefore, it seems that comparisons cannot be made through time, but only through space at the same time.

Successful indices will perform over a range of densities and be robust to observer variability, habitat variation, and ideally, seasonal changes in performance. There appears to be no strong and consistent correlation between gray-tailed vole numbers in grassland systems and the occurrence of their burrows, runways, or grazing activity. Droppings in unmanaged systems may give some indication of population size, but this index as used here was not very precise. However, my results suggest that a single night's trapping can provide an index of population size that is robust to differences in habitat structure and density. The possibility that snap trap grids might perform equally well should be explored, particularly when estimates of vole abundance are desired to guide control efforts as this sampling design may also indicate the spatial distribution of voles across the landscape. Given the study or management objectives, a greater investment in indexing vole populations may still be necessary.

Acknowledgements:

D.K. Rosenberg and D. Saunders Rose assisted with fieldwork, and T. Manning provided training in live-trapping techniques and advice on voles in general. B. Glenn, D. K. Rosenberg, and R. Camp provided helpful comments on earlier versions of this manuscript. This research was supported by a grant from USDA CSREES Western Integrated Pest Management Program. Publication of this paper was supported in part by the Thomas G. Scott Publication Fund.

Literature Cited

- Caughley, G. and A. R. E. Sinclair. 1994. *Wildlife Ecology and Management*. Blackwell Scientific Publications, Oxford, England.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 45:427-438.
- Engeman, R. M. 2005. Indexing principles and a widely applicable paradigm for indexing animal populations. *Wildlife Research* 32:203-210.
- Gervais, J. A., S. M. Griffith, J. H. Davis, J. R. Cassidy, and M. I. Dragila. 2010. Effects of gray-tailed vole activity on soil properties. *Northwest Science* 84:159-169.
- Gervais, J. A., C. M. Hunter, and R. G. Anthony. 2006. Interactive effects of prey and p,p'DDE on burrowing owl population dynamics. *Ecological Applications* 16:666-677.
- Hansson, L. 1979. Field signs as indicators of vole abundance. *Journal of Applied Ecology* 16:339-347.
- Hodges, K. E., and L. S. Mills. 2008. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256:1918-1926.
- Howe, H. F., B. Zorn-Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* 87:3007-3013.
- Korpimäki, E., and K. Norrdahl. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals? *Oikos* 62:195-208.
- Korpimäki, E., K. Norrdahl, T. Klemola, T. Pettersen, and N. C. Stenseth. 2002. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society B* 269:991-997.
- Korpimäki, E., K. Norrdahl, O. Huitu, and T. Klemola. 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society B* 272:193-202.
- Lambin, X., S. L. Petty, and J. L. MacKinnon. 2000. Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology* 69:106-118.
- Liro, A. 1974. Renewal of burrows by the common vole as the indicator of its numbers. *Acta Theriologica* 19:259-272.
- Manning, T., W. D. Edge, and J. O. Wolff. 1995. Evaluating population-size estimators: an empirical approach. *Journal of Mammalogy* 76:1149-1158.
- McComb, B., B. Zuckerberg, D. Vesely, and C. Jordan. 2010. *Monitoring Animal Populations and Their Habitats: A Practitioner's Guide*. CRC Press, Boca Raton, Florida.
- McKelvey, K., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology* 79:1754-1765.
- Pech, R. P., A. R. E. Sinclair, A. E. Newsome, and P. C. Catling. 1992. Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia* 89:102-112.
- Rovero, F., and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46:1011-1017.
- Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228-1236.
- Schauber, E. M., W. D. Edge, and J. O. Wolff. 1997. Insecticide effects on small mammals: influence of vegetation structure and diet. *Ecological Applications* 7:143-157.
- Steiner, J. J., W. E. Gavin, G. W. Mueller-Warrant, S. M. Griffith, G. W. Whittaker, and G. M. Banowetz. 2007. Conservation practices in western Oregon perennial grass seed systems. II. Impacts on gray-tailed vole activity. *Agronomy Journal* 99:537-542.
- Sundell, J., O. Huitu, H. Henttonen, A. Kiakusalo, E. Korpimäki, H. Pietianen, P. Saurola, and I. Hanski. 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology* 73:167-178.
- Walsh, P. D., L. J. T. White, C. Mbina, D. Idiata, Y. Mihindou, F. Maisels, and M. Thibault. 2001. Estimates of forest elephant abundance: projecting the relationship between precision and effort. *Journal of Applied Ecology* 38:217-228.
- Wang, G., W. D. Edge, and J. O. Wolff. 2001. Rainfall and guthion 2S interactions affect gray-tailed vole demography. *Ecological Applications* 11:928-933.
- Whisson, D. A., R. M. Engeman, and K. Collins. 2005. Developing relative abundance techniques (RATs) for monitoring rodent populations. *Wildlife Research* 32:239-244.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Publication LA-8787-NERP. Los Alamos National Laboratory, Los Alamos, New Mexico.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego, California.
- Witmer, G. C. 2005. Wildlife population monitoring: some practical considerations. *Wildlife Research* 32:259-263.
- Wolff, J. O., W. D. Edge, and R. Bentley. 1994. Reproductive and behavioral biology of the gray-tailed vole. *Journal of Mammalogy* 75:873-879.

Received 16 June 2009

Accepted for publication 27 April 2010