Measurement error in a burrow index to monitor relative population size in the common vole

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A b s t r a c t . Various population indices are widely used to monitor relative population size of many pest and game species to aid their management. However, information on the level of uncertainty associated with their estimates is rarely available. Here we explore sampling and systematic error associated with the index of re-opened burrow entrances which is used extensively in central Europe for surveying common vole populations. We found that relative sampling errors were enormous for low-density populations, attaining almost 400%. However, in high-density populations and for large sample sizes, the relative error dropped below 10% and the estimate is quite reliable. The dispersion of burrow entrances became more clumped at low population densities enhancing further the sampling variation. We demonstrated that the index is related to population size in a non-linear fashion, overestimating the population change at high densities. Consequently, population dynamics of the common vole described by the untransformed burrow index appear more variable than they are in reality.

Introduction

Typically, most population dynamics analyses in current ecology rely upon population indices collected for various agricultural and forest pests and many game animals at broad spatial and temporal scales to aid their management. Indices represent simpler and cheaper alternatives to more expensive and laborious capture-recapture methods. However, they also produce weaker inferences because they are not based on true estimation of detection probabilities as other formal estimation methods. In fact, detectability is assumed to be constant over time and space (Y o c c o z et al. 2001). Therefore, developing a sampling design that optimizes the trade off between the cost and inferential strength for informed management decisions is highly desirable.

Voles are typically among small mammals for which several indices to monitor their relative population densities have been proposed (e.g., H a n s s o n 1979, G i r a u d o u x et al. 1995, H u b b s et al. 2000, Q u é r é et al. 2000). In the management of the common vole (*Microtus arvalis* Pallas, 1778), the most abundant mammal in central Europe regularly damaging crops in high-density years (T r u s z k o w s k i 1982, B a b i n s k a - W e r k a 1979, J a c o b 2003, H e r o l d o v á et al. 2004), counts of re-opened burrow entrances per unit area have been used extensively from the '60s of the 20th century (P o l y a k o v 1961,

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L i r o 1974, B u k e r 1984, R o m a n k o w - Ż m u d o w s k a & G r a l a 1994). As a consequence, long-term datasets are now available for modern population analyses aimed at describing negative feedback structure which serves a basis for drawing ecological inferences on a pattern of population dynamics (T k a d l e c & S t e n s e t h 2001, T k a d l e c et al. 2006). However, there is only marginal information on an error with which the index measures a change in vole population numbers (L i r o 1974). If the error is important, then the ecological inferences about the pattern of population dynamics may be flawed.

As with any other measurement, the inferential strength of burrow indices depends on the accuracy with which the population size is measured, combining both precision (repeatability) and systematic error (bias) (W i l l i a m s et al. 2002). The precision is high when the sampling variance due to the inexactness of the process of counting and spatial variance of counts is low (M ö n k k ö n e n & A s p i 1998). Because the variance of a sample mean is inversely proportional to the sample size, it declines asymptotically to 0 as the total sample size of the area sampled increases. However, increasing the area size increases the cost of the monitoring programme as well, urging a design that is optimized using either perspective. The sampling variance can be affected by the dispersion pattern of burrow entrances in space (e.g., M ö n k k ö n e n & A s p i 1998). Clumped distributions are always associated with the sampling variance much higher than the mean. These distributions are often approximated by the negative binomial characterised by the presence of one frequency mode or by the Neyman type A distribution characterised by several frequency modes (A n s c o m b e 1950). Identifying the proper distribution might help in modelling the spatial processes during vole colonisation events.

Systematic error is a bias in measurements which leads to the measured values being systematically too high or too low. Contrary to the random variation, which arises from random fluctuations in measurements, the bias is consistent and repeatable. Constant systematic error is very difficult to deal with, because its effect is only observable if it can be removed. Such an error cannot be removed by repeating measurements or averaging large numbers of results. A common means to remove the systematic error is a calibration, i.e., a relationship between the true density and index values. If the bias is ignored it may lead to inaccurate or wrong inferences.

Here, we focus on both components of measurement error incorporated in the index – sampling variance and systematic bias. The sampling variance is measured as a sampling error (standard error of the mean). We describe how it varies with (1) sample size (the number of quadrates sampled) and (2) relative population density. We also analyse the dispersion pattern relative to the population density and attempt to discriminate between the unimodal negative binomial and Neyman type A distribution with several frequency modes. We measure the systematic error by identifying a functional relationship between the Jolly-Seber estimate of population size, as representing the true density, and the index.

Study Area and Methods

We collected data on a burrow index in two natural populations of the common vole in the Czech Republic, one in the outskirts of Olomouc city (49° 34' N, 17° 13' E) in central Moravia between 2002 and 2005, another in Drnholec (48°53' N, 13 16°27' E), southern Moravia between 1998 and 2003. Both populations were alfalfa fields situated in lowland about 200 m above sea level and were regularly monitored using intensive capture-recapture sampling programme, with trapping sessions occurring at intervals of 2–4 wks. In Olomouc,

the study plot of 40 × 70 m (0.28 ha) was divided to a grid of 150 squares (hereafter squares) 4 × 4 m (16 m²) each. The plot in Drnholec was 35 × 75 m (0.2625 ha) in size and consisted of 105 squares 5 × 5 m each. The soil in Drholec was a mollisol type (chernozem) with a much finer texture than that in Olomouc (fluvisol). Population densities over the period of study ranged from zero to 11 000 burrow entrances per hectare.

We measured the relative population density using a modified index of re-opened burrow entrances during intervals between the trapping sessions. As proposed originally for use in alfalfa fields, all burrow entrances are closed on 4 to 5 quadrats (hereafter quadrats) 10×10 m chosen at random and the counts of re-opened burrow entrances are taken next day (EPPO 1975, Z a p l e t a l et al. 2000). We modified the method by recording the counts for at least 90 squares of the plot and then subjecting these counts to resampling in computer simulations. For instance, to obtain the number of burrow entrances per one quadrat (100 m²) in the Olomouc population, we sampled randomly counts for 6 squares (6 × 16 = 96 m²) with replacement. The sum was multiplied by 1.0417 to remove the discrepancy between 96 and 100 m². An estimate of index was obtained by repeating this procedure 5 times to receive counts for 5 quadrats and then computing the mean per quadrat. Sizes of small squares on both plots are large enough to harbour more than one colony of voles (see Mackin-Rogalska et al. 1986). This modified method assumes that the distribution of burrow entrances in a plot represents adequately the distribution in a population at large. Furthermore, resampling of data from the same plot may introduce a problem of pseudoreplication which can lead to the underestimation of variance parameters.

To measure the sampling variance in the index, we performed 10 000 simulations and then estimated the sampling error as a standard deviation of the mean (= standard error) according to the formula:

$$\text{sampling error} = \sqrt{\text{var}\,(\overline{x}_i)}$$

where $\overline{x}_i$ is the estimate of index for each of the 10 000 runs ($i = 1, 2, \ldots, 10\,000$). In addition, we estimated a relative sampling error as a coefficient of variation of the sampling error (W h i t e et al. 1982):

$$\text{relative sampling error} = (\text{sampling error})/\text{mean}$$

where the mean is estimated from the sum of all counts per plot. This measure is useful if we want to express the amount of uncertainty to be proportional to the relative population size. All simulations were done using R (R Development Core Team 2006).

The relationship between the sampling error and sample size (the number of quadrats) was modelled as a linear regression taking logs of both variables. The dependence of sampling error on relative population size was described with the quadratic log-log model:

$$\log (\text{sampling error}) = b_0 + b_1\log (\text{mean}) + b_2\log^2(\text{mean}),$$

the untransformed version of which corresponds to the equation:

$$\text{sampling error} = a_0\,\text{mean}^{\,b_1 + b_2 \log (\text{mean})}.$$

The pattern of spatial distribution of burrow entrances in the study plot was analysed using the exponent k of the negative binomial distribution for small square counts. We used maximum likelihood estimation as implemented in package MASS of R and linear regression

model to describe its relationship to index. We fitted a nonlinear regression through the origin to describe the relationship between the Jolly-Seber estimate (JS) of population size (program Jolly) and the index. The parameters of equation

$$JS = b_1 \text{index}^{b_2}$$

were estimated by non-linear least squares. We used AICc to decide whether nonlinear or linear version (without exponent) of the regression is to be applied (B u r n h a m & A n d e r s o n 1998).

Results

Increasing a sample size from 2 to 8 quadrats (10 × 10 m) reduced both relative and absolute sampling error of estimates substantially (Fig. 1a,b). At low population densities just above zero, relative sampling error for only two quadrats was enormous, reaching almost 400%. It remained high even for 8 quadrats (200%). In contrast, at the maximum density of about 11 000 re-opened burrow entrances, the relative sampling error for 2 and 8 quadrats dropped to 13 and 6%, respectively. The decrease appears to be less pronounced for sample size higher than 5 quadrats. Sampling error at low population densities (<10 entrances per hectare) varies from 29 to 14 for 2 and 8 quadrats, respectively. However, it is from about 1400 to 700 entrances per hectare at maximum densities. Relative sampling error drops dramatically for increasing population densities up to about 1000 burrow entrances (Fig. 1c). For sample sizes of 5 and more quadrats and densities above 1200 burrow entrances, it falls below 25%. At the maximum of about 11 000 entrances, relative sampling errors become small even for a sample size of 2 quadrats, attaining 10%. Increasing sample size to 8 quadrats, relative sampling error declines to 135 and 5% for the minimum and maximum population size, respectively. The corresponding absolute sampling errors for 2 quadrats are 22 and 1700 entrances for the minimum and maximum population size, respectively. For 8 quadrats, the sampling errors are about 10 and 800 entrances, respectively.

Sampling variation is known to depend on the degree of aggregation in space. The most clumped dispersions were observed at low densities when the parameter k of the negative binomial distribution attained values below 0.1 in both of the populations studied (Fig. 2a,b).
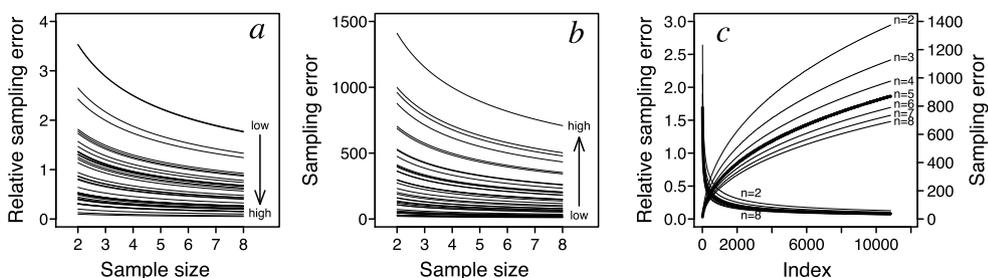

Fig. 1. Relative sampling error (*a*) and sampling error (*b*) as regressed on a sample size (the number of 10 × 10 m quadrats) for data from Olomouc and Drnholec. The relationship was modelled by linear regression using log-transformed values of both variables. The arrows indicate the direction along which the relative population densities increase. (*c*) The dependence of relative sampling error and sampling error on the mean index for various sample size (*n* = 1–8) for both locations. The lines for a sample size of 5 are in bold to indicate a design employed in practice. All curves are corrected for a bias introduced by log-transformation (S p r u g e l 1983).
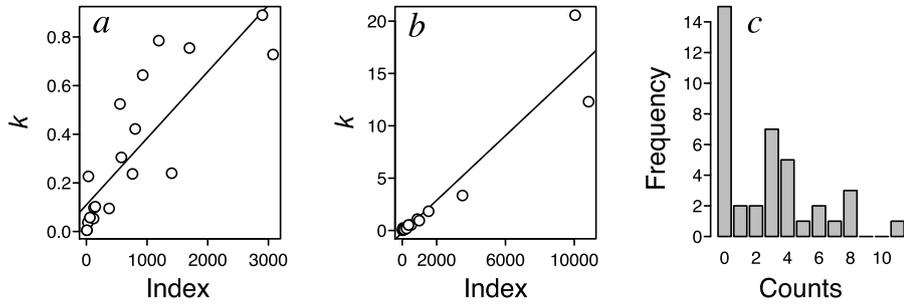
Fig. 2. The relationship between the parameter k of the negative binomial distribution and the index for locations Olomouc (*a*) and Drnholec (*b*) and an example of frequency distribution of burrow entrances counts per small square (c) from location Olomouc in July 2005.

The two populations seem to differ in dependencies of clumping on a relative population size (slope$_{Olomouc}$ = 0.00027, slope$_{Drnholec}$ = 0.013), with the Drnholec population being less clumped at high density than the population in Olomouc (interaction population×population size: $F_{1,31}$ = 7.39, p = 0.011). Typically, the frequency distributions of counts per square exhibited several periodic modes at frequencies around the mean number of burrow entrances and their multiples. This suggests that the Neyman type A distribution may be more appropriate for description of a vole colonisation process than the binomial one (Fig. 2c).

The relationship between index and Jolly-Seber estimate of population size was obviously nonlinear in either location, indicating the presence of a systematic error (Olomouc: the difference in AICc = 9.3; Drnholec: the difference in AICc = 13; Fig. 3). The index increases more rapidly than the Jolly-Seber estimates, overestimating population change especially at high densities.
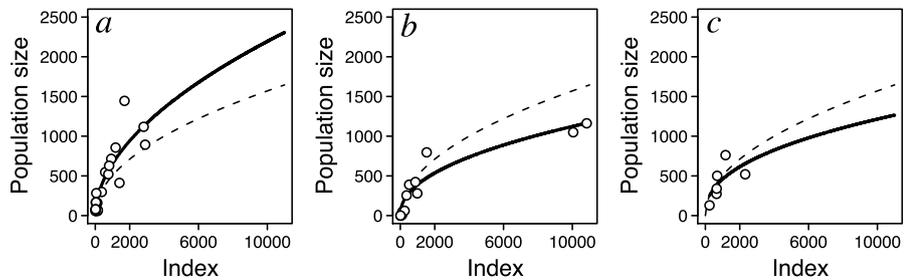
Fig. 3. The non-linear relationship between population size (Jolly-Seber estimate) and index for Olomouc (*a*) and Drnholec (*b*). The dashed curve depicts prediction from a model with averaged parameters over both locations. For the sake of a direct comparison, we fitted a model with the same structure to published data from Łomna (*c*) near Warsaw, Poland (L i r o 1974). Equations for the three populations were as follows: Olomouc JS = 17.277index $^{0.526}$, Drnholec JS = 16.395index $^{0.459}$, Łomna JS = 24.618index $^{0.423}$.

Discussion

We explored sampling and systematic error associated with the index of re-opened burrow entrances which has been used extensively in central Europe to monitor common vole populations. We found that relative sampling error is enormous for low-density populations, attaining almost 400%. This is partly because the dispersion of burrow entrances becomes more clumped at low population densities. However, for high-density populations and

large sample sizes, it drops below 10% and the estimate is therefore quite reliable. We further demonstrated that the index is related to population size in a non-linear fashion, systematically overestimating the size of population change, especially at high density. These findings suggest that sample size of 5 quadrats 10×10 m is a reasonable compromise between the required level of uncertainty and the cost but that further optimization is still possible by lowering the number of quadrats sampled at high density without any substantial reduction in the precision of estimates. The observation that index systematically overestimates variation in population numbers indicates that the inferences that have been drawn on the pattern of population dynamics from time series analyses based on raw indices may be affected.

A key influence on power of any index to reveal a trend in monitoring programmes for agricultural pests is its variability (G i b b s et al. 1998). Even with robust indices, ecologists developing monitoring designs have to confront complex sampling issues, including how many quadrats to sample and how often to survey the population within any given year. The index of re-opened burrow entrances has been used to survey the common vole populations for many decades. Currently, it presents not only the main tool for management decisions but also the primary source of long-term data for analyzing its population dynamics (e.g., T k a d l e c & S t e n s e t h 2001, T k a d l e c et al. 2006). Considering a sample size in terms of costs and benefits, we conclude that 5 quadrats is a reasonable solution combining the highest efficiency with the lowest possible cost. Extremely high relative sampling errors observed at densities less than 100 do not pose a serious problem for decision-makers, for the upper limits of confidence interval does not exceed 500 entrances even for the largest sampling errors of about 200%. At population densities much above 1000 entrances, the relative error becomes small falling below 10% which is a desired level of precision for most population measurements in general (W h i t e et al. 1982). Thus, the risk of being wrong here by forecasting low densities is relatively small. For managers, estimates from about 500 to 1000 entrances seem to be most critical. Overestimation of the true density may result in wasting resources into unnecessary controlling measurements, whereas underestimation entails losses in a crop yield. Under these circumstances, it pays to invest more in sampling to achieve more precise estimates. These extra-resources spent at critical densities can however be saved at high densities when the sample size can be effectively lowered.

The findings on spatial variance of burrow entrances indicate that the dispersion pattern varies with population density, being less aggregated at high density. This is what can be expected because in a very dense local population, most or all suitable sites may be occupied and no place is left for random or aggregated dispersion (M ö n k k ö n e n & A s p i 1998). Moreover, a multimodal Neyman type A distribution seems to be superior to the negative binomial in describing the spatial pattern of burrow entrances. Unlike the negative binomial distribution, arising from random distribution of colonies in which entrances are distributed independently in a logarithmic series, the type A of Neyman distribution arises from the model of randomly distributed colonies in which both the number of colonies per sample and the number of entrances per sample have a Poisson distribution (A n s c o m b e 1950). This study therefore lends more support to the latter as a better descriptor of the vole colonization pattern. When densities grow, the counts of entrances increase primarily because of increasing numbers of colonies rather than that of the colony size. As a result, the degree of clumping decreases with increasing density. The differences between Drnholec and Olomouc may reflect differences in quadrat size and soil type. Softer soils may allow voles to dig their burrows more regularly in space. Consequently, spatial variation in sampling errors is to be expected among soil types with different textures.

We are the first to demonstrate in an unambiguous way that the relationship between the burrow index for the common vole and its population size is non-linear. This is not at variance with the previous work (L i r o 1974) indicating a linear dependence, for it was obtained at much lower densities and using simple enumeration technique for estimating population size. In fact, applying non-linear regression to data published by Liro, no essential difference in the pattern can be found over the comparable densities (Fig. 3c). Hence, we conclude that the burrow index strongly overestimates population change at high densities. This may have serious implications to ecological analyses of population dynamics patterns in the common vole and small rodents in general. It is obvious that the burrow index magnifies temporal variation in numbers by overestimating peak densities. As population variation is correlated with cyclicity (H e n t t o n e n et al. 1985, T k a d l e c & S t e n s e t h 2001), the population dynamics of the common vole, when depicted using original untransformed index, may appear more cyclic than they are in reality.

Therefore, there are two problems to cope with when inferring the common vole dynamic pattern based on burrow indices. In low-density populations, the estimates are less biased but very noisy, suffering from the huge sampling error. In high-density populations, the relative population sizes measured are more precise but may be biased. However, unlike the former error that can only be dealt with prospectively, through a more elaborate sampling design, the latter error is amenable to retrospective elimination, at least partially. Variability within and among sites will preclude removing this type of error completely. Hence, further research into how much the elimination of systematic error from time series data affects the resulting structure of density dependence in the common vole is clearly warranted.

L I T E R A T U R E

Anscombe F.J. 1950: Sampling theory of the negative binomial and logarithmic series distributions. *Biometrika* *37: 358–382.*

Babinska-Werka J. 1979: Effects of common vole on alfalfa crop. *Acta Theriol. 24: 281–297.*

Buker J.B. 1984: Aantalsschommelingen bij de veldmuis *Microtus arvalis* (Pallas, 1779) in de periode 1978–1981 (Fluctuations in the numbers of common voles *Microtus arvalis* (Pallas, 1779) during the period 1978–1981). *Lutra 27: 304–311 (in Dutch with English summary).*

Burnham K.P. & Anderson D.R. 1998: Model Selection and Inference: A Practical Information–Theoretical Approach. *Springer-Verlag, New York.*

EPPO 1975: Guidelines for the development and biological evaluation of rodenticides. *EPPO Bull. 5: 5–49.*

Gibbs J.P., Droege S. & Eagle P. 1998: Monitoring populations of plants and animals. *BioScience 48: 935–940.*

Giraudoux P., Pradier B., Delattre P., Deblay S., Salvi D. & Default R. 1995: Estimation of water vole abundance by using surface indices. *Acta Theriol. 40: 77–96.*

Hansson L. 1979: Field signs as indicators of vole abundance. *J. Appl. Ecol. 16: 339–347.*

Henttonen H., McGuire A.D. & Hansson L. 1985: Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. *Ann. Zool. Fenn. 22: 221–227.*

Heroldová M., Zejda J., Zapletal M., Obdržálková D., Jánová E., Bryja J. & Tkadlec E. 2004: Importance of winter rape for small rodents. *Plant Soil Environ. 50: 175–181.*

Hubbs A.H., Karels T. & Boonstra R. 2000: Indices of population size for burrowing mammals. *J. Wildl. Manage. 64: 296–301.*

Jacob J. 2003: Short-term effects of farming practices on populations of common voles. *Agric*. *Ecosyst*. *Environ*. *95: 321–325*.

Liro A. 1974: Renewal of burrows by the common vole as the indicator of its numbers. *Acta Theriol*. *19: 259–272*.

Mackin-Rogalska R., Adamczewska-Andrzejewska K. & Nabagło L. 1986: Common vole numbers in relation to the utilization of burrow systems. *Acta Theriol*. *31: 17–44*.

Mönkkönen M. & Aspi J. 1998: Sampling error in measuring temporal density variability in animal populations and communities. *Ann. Zool. Fenn. 35: 47–57*.

Polyakov I.J. 1961: Wrednyje gryzuny i borba s nimi [Pest rodents and their control]. *Moskwa, p. 1–261 (in Russian)*.

Quéré J.-P., Raoul F., Giraudoux P. & Delattre P. 2000: An index method of estimating relative population densities of the Common Vole (*Microtus arvalis*) at landscape scale. *Rev. Ecol.-Terre Vie 55: 25–32*.

R Development Core Team 2005: R. A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.

Romankow-Żmudowska A. & Grala B. 1994: Occurrence and distribution of the common vole, *Microtus arvalis* (Pallas), in legumes and seed grasses in Poland between 1977 and 1992. *Pol. Ecol. Stud. 20: 503–508*.

Sprugel D.G. 1983: Correcting for bias in log-transformed allometric equations. *Ecology 64: 209–210*.

Tkadlec E. & Stenseth N.C. 2001: A new geographical gradient in vole population dynamics. *Proc. R. Soc. Lond. B 268: 1547–1552*.

Tkadlec E., Zbořil J., Losík J., Gregor P. & Lisická L. 2006: Winter climate and plant productivity predict abundances of small herbivores in central Europe. *Clim. Res. 32: 99–108*.

Truszkowski J. 1982: The impact of the common vole on the vegetation of agroecosystems. *Acta Theriol. 27: 305–345*.

White G.C., Anderson D.R., Burnham K.P. & Otis D.L. 1982: Capture-recapture and removal methods for sampling closed populations. *Los Alamos National Laboratory, Los Alamos*.

Williams B.K., Nichols J.D. & Conroy M.J. 2002: Analysis and Management of Animal Populations. Modelling, Estimation, and Decision Making. *Academic Press, San Diego*.

Yoccoz N.G., Nichols J.D. & Boulinier T. 2001: Monitoring of biological diversity in space and time. *Trends Ecol. Evol. 16: 446–453*.

Zapletal M., Obdržálková D., Pikula J., Zejda J., Pikula J. (Jr.), Beklová M. & Heroldová M. 2000: Hraboš polní (*Microtus arvalis*) (The Common Vole (*Microtus arvalis*)). *State Phytosanitary Administration, Brno (in Czech with English summary)*.