

Spatial population dynamics of small mammals: some methodological and practical issues

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Yoccoz, N. G. & Ims, R. A., 2004. Spatial population dynamics of small mammals: some methodological and practical issues. *Animal Biodiversity and Conservation*, 27.1: 427–435.

Abstract

Spatial population dynamics of small mammals: some methodological and practical issues.— Small mammals have been widely used to further our understanding of spatial and temporal population dynamical patterns, because their dynamics exhibit large variations, both in time (multi-annual cycles vs. seasonal variation only) and space (regional synchrony, travelling waves). Small mammals have therefore been the focus of a large number of empirical and statistical (analysis of time-series) studies, mostly based on trapping indices. These studies did not take into account sampling variability associated with the use of counts or estimates of population size. In this paper, we use our field study focusing on population dynamics and demography of small mammals in North Norway at three spatial scales (0.1, 10 and 100 km) to illustrate some methodological and practical issues. We first investigate the empirical patterns of spatial population dynamics, focusing on correlation among time-series of population abundance at increasing spatial scales. We then assess using simulated data the bias of estimates of spatial correlation induced by using either population indices such as the number of individuals captured (i.e., raw counts) or estimates of population size derived from statistical modeling of capture-recapture data. The problems encountered are similar to those described when assessing density-dependence in time-series—a special case of the consequence of measurement error for estimates of regression coefficients—but are to our knowledge ignored in the ecological literature. We suggest some empirical solutions as well as more rigorous approaches.

Key words: Spatial autocorrelation, Measurement error, Voles, Norway.

Resumen

Dinámica poblacional espacial de pequeños mamíferos: algunas cuestiones metodológicas y prácticas.— Los pequeños mamíferos se han utilizado ampliamente para ayudarnos a comprender mejor las pautas dinámicas espaciales y temporales de las poblaciones. Ello obedece a que sus dinámicas presentan importantes variaciones, tanto por lo que respecta al tiempo (ciclos multianuales frente a una única variación estacional) como al espacio (sincronía regional, ondas progresivas). Por consiguiente, los pequeños mamíferos han sido objeto de gran número de estudios empíricos y estadísticos (análisis de series temporales), basados principalmente en índices de capturas por trampa. Dichos estudios no tomaban en consideración la variabilidad del muestreo asociada al empleo de recuentos o de estimaciones del tamaño poblacional. En el presente artículo utilizamos nuestro estudio de campo para analizar la dinámica poblacional y la demografía de los pequeños mamíferos del norte de Noruega en tres escalas espaciales (0,1, 10 y 100 km), además de ilustrar algunas cuestiones prácticas y metodológicas. En primer lugar, investigamos las pautas empíricas de la dinámica poblacional espacial, centrándonos en la correlación existente entre las series temporales de la abundancia poblacional en escalas espaciales cada vez mayores. Seguidamente, utilizamos datos simulados para evaluar el sesgo de las estimaciones de la correlación espacial inducida mediante el empleo, bien de índices poblacionales como el número de individuos capturados (es decir, recuentos brutos) o estimaciones del tamaño poblacional derivadas de la modelación estadística de los datos de captura-recaptura. Los problemas encontrados son similares a los descritos cuando se evalúa la dependencia de la densidad en las series temporales—un caso especial de la consecuencia del error de medición con respecto a las estimaciones de coeficientes de regresión—, pese a que, según parece, se han ignorado en la literatura ecológica. Por último, sugerimos algunas soluciones empíricas, así como planteamientos más rigurosos.

Palabras clave: Autocorrelación espacial, Error de medición, Ratón de campo, Noruega.

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Introduction

Small mammals, and in particular voles and lemmings, are well known for their large multi-annual population fluctuations (Stenseth, 1999). Most interestingly, populations of the same species (e.g., the Field vole, *Microtus agrestis*) can exhibit different temporal and spatial dynamical patterns (Henttonen & Hansson, 1986). In Fennoscandia, southern populations show mainly seasonal changes, while northern populations are characterized by 3 to 5 year cycles. Spatial synchrony, meaning that populations in different locations exhibit correlated fluctuations, is also a variable phenomenon, with large-scale (over hundreds of km) synchrony as well as traveling waves having been described (Lambin et al., 1998; Steen et al., 1990). Populations of different species at the same location are often synchronous too (Henttonen & Hansson, 1986). However, most studies of synchrony have used population indices, and did not account for sampling error (e.g. Bjørnstad et al., 1999, Steen et al., 1996).

Accurate estimation of the quantitative patterns of population synchrony, and in particular of the relationship between correlation and distance among populations, is of interest because it can shed light on the mechanisms driving the population dynamics (Bjørnstad et al., 2002; Bolker & Grenfell, 1996, Ranta et al., 1997; Ripa, 2000). The Moran effect (e.g., Bjørnstad et al., 1999) describes a situation where the correlation for the environmental noise is expected to be identical to the correlation observed for the population dynamics. Climate, predation and dispersal are three factors that are important for the population dynamics of small mammals (Hansson & Henttonen, 1985, 1988), but their consequences in terms of population synchrony are likely to be scale-dependent. Climate will generally result in large scale synchrony (e.g., over distances larger than 100 km Krebs et al., 2002), predation by small mustelids (weasel *Mustela nivalis*, stoat *M. erminea*) will be characterized by synchrony at intermediate (10 km) scale, whereas vole dispersal may influence small (1–5 km) scale synchrony (Lambin et al., 1998). Depending on the relative importance and extent of these factors, we would expect spatial correlation patterns with a characteristic scale (Engen et al., 2002).

The consequences of ignoring the uncertainty in population indices or estimates have been emphasized for at least three decades when analyzing density-dependence (Ito, 1972; Lebreton, 1990; Solow, 2001). It is related to the more general issue of the effect of measurement error on regression coefficients estimates (Fuller, 1987): when the predictor variable is measured with some error (and assuming a simple measurement error model, i.e. additivity and independence), the regression coefficient is biased towards 0 (so-called attenuation). The issue has not been explicitly addressed when analyzing spatial correlation (but see e.g. Moilanen [2002] when one is interested in estimat-

ing parameters of metapopulation models), even if it has been mentioned by Lande et al. (2003), and some statistical analytical models have incorporated measurement error (Viljugrein, 2000). The correlation between two time series of population indices or estimates $\hat{N}_{1,t}$ and $\hat{N}_{2,t}$ is given by:

$$\text{Corr}(\hat{N}_{1,t}, \hat{N}_{2,t}) = \frac{\text{Cov}(\hat{N}_{1,t}, \hat{N}_{2,t})}{\sigma_{\hat{N}_1} \sigma_{\hat{N}_2}}.$$

If the measurement error process is additive and independent for the two populations, the covariance will not be affected, but the two standard deviations will be inflated by the measurement error (Link & Nichols, 1994), and therefore the correlation will be attenuated (biased towards 0).

Viljugrein and her colleagues modeled the measurement error assuming a Poisson distribution. This is likely to underestimate the impact of measurement error as for example heterogeneity of capture, a common problem in most field studies of small mammals (Yoccoz et al., 1993), will lead to variability larger than Poisson. Assessing the size of the bias will therefore depend on having an accurate knowledge of the measurement error process. Dennis et al. (1998) considered a model for analyzing joint density-dependence and suggested using state-space models for taking into account sampling variance but did not implement such models to our knowledge.

In this paper, we investigate how sampling variance due to the population size estimation process affects estimates of spatial autocorrelation. We first describe the empirical patterns of spatial autocorrelation in a multi-scale study of population dynamics of voles in north Norway. The sampling variance associated to raw counts or closed capture-recapture models incorporating heterogeneity of capture is not analytically known, and we therefore used simulated data including both process and sampling variance to investigate the effects on bias of correlation estimates. Finally, we suggest approaches to correct for the observed bias.

Field study design and empirical estimation of spatial correlation patterns

The empirical study is based on trapping 122 0.5 ha grids, twice a year (June and September) during 5 years (1998–2002). The sampling design was hierarchical, with three spatial scales: 1 km, 10 km and 100 km (fig. 1). Each grid covered an area of 0.5 ha, with 16 Ugglan live traps. Each primary trapping session included three secondary sessions (days). We had more than 12,000 captures of > 7,300 individuals belonging to four vole species, the Grey-sided Vole (*Clethrionomys rufocanus*; 3,300 ind., 5,600 capt.), the Red Vole (*C. rutilus*; 2,900 ind., 4,900 capt.), the Bank Vole (*C. glareolus*; 440 ind., 750 capt.) and the Field Vole (640 ind., 950 capt.). In this paper, we only consider the Grey-sided Vole. In addition, more than 5,000 shrews (mostly Common

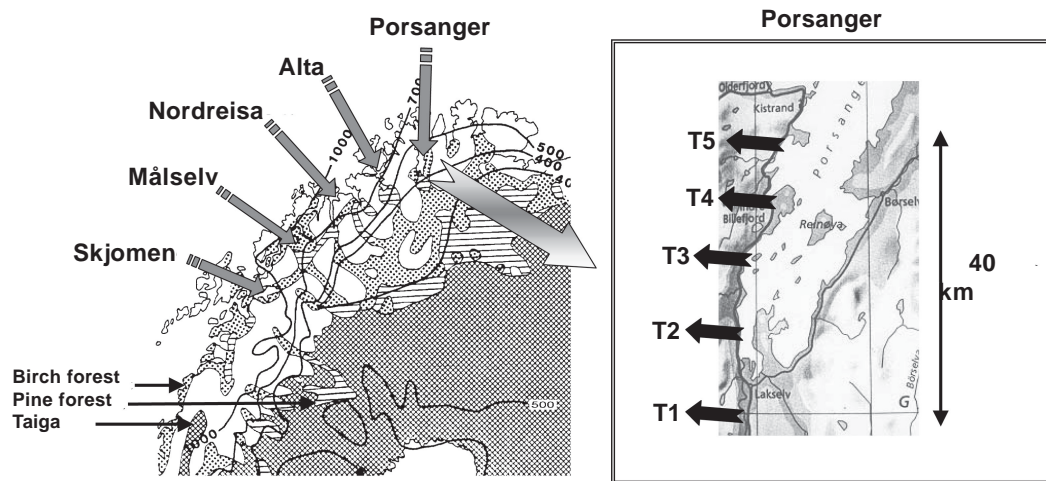


Fig. 1. Map of study area (north Norway) with detailed study design for one fjord region (Porsanger). Each transect (T1 to T5) had five trapping grids from the sea level/valley bottom to the treeline. In two areas, a slightly different design was used: Skjomen (three transects with eight trapping grids each) and Målselv (four transects with six, six, six and five grids respectively).

Fig. 1. Mapa del área de estudio (norte de Noruega), que incluye el diseño de un estudio detallado para una región de fiordos (Porsanger). Cada transecto (T1 a T5) presentaba cinco rejillas de captura, desde el nivel del mar/fondo del valle hasta la línea de árboles. En dos áreas se utilizó un diseño ligeramente distinto: Skjomen (tres transectos con ocho rejillas de captura cada una) y Målselv (cuatro transectos con seis, seis, seis y cinco rejillas, respectivamente).

Shrews, *Sorex araneus*) were caught but most were killed by the trapping.

Numbers of individuals captured per grid varied between 0 and 40. We estimated population size using models for closed populations (Pollock et al., 1990; Borchers et al., 2002). We considered two models: M_0 (identical capture rate for all individuals) and M_{h2} (2nd order jackknife estimator [Burnham & Overton, 1979], a non-parametric estimator incorporating heterogeneity of capture). These two models were used to estimate population size independently for each grid and species. We investigated further the sources of variability in capture rates, both within and among grids using the Huggins' conditional likelihood approach (Huggins, 1989; Alho, 1990; Borchers et al., 2002). We used grid, sex and body weight as covariates, and applying Horvitz-Thompson-like estimator for each grid:

$$\hat{N} = \sum_{i=1}^n \frac{1}{\hat{p}_i}$$

where \hat{p}_i is the estimated probability that the individual i is caught at least once. The \hat{p}_i are given by:

$$\hat{p}_i = 1 - \prod_{k=1}^3 [1 - p_{ki}]$$

where the probabilities p_{ki} of catching individual i in session k are modeled as function of the covariates using a logit link. We used the value of the conditional likelihood to calculate the AIC values and select an appropriate model.

Simulations and estimation of spatial correlations

Data were simulated according to two processes: a population dynamic process mimicking multiannual population cycles, and a sampling process describing the capture of individuals.

Population dynamics differed among regions and among species. For the Grey-sided Vole, they were consistent with 5-years cycles in the NE and somewhat shorter cycles in the SW (Hansson & Henttonen, 1985). For the Red Vole, some populations had only seasonal fluctuations with no indication of cycles. However, the time-series are too short to estimate adequately the periodicity. We simulated the true population dynamics using a second-order autoregressive model, with two case-studies (cyclic populations and stable populations; see Stenseth, 1999 for general discussion of parameter values in autoregressive models):

$$\text{AR2: } \log(N_{t+1}) = 4.5 + 0.2 * \log(N_t) - 0.5 * \log(N_{t-1}) + \lambda_t$$

$$\text{AR1: } \log(N_{t+1}) = 3.5 + 0.2 * \log(N_t) + \lambda_t$$

where λ_t , the stochastic component of population growth, is assumed to follow a normal distribution with mean 0 and variance σ^2 . The first case-study, AR2, mimics a 5-years cycle, whereas the second, AR1, mimics stable

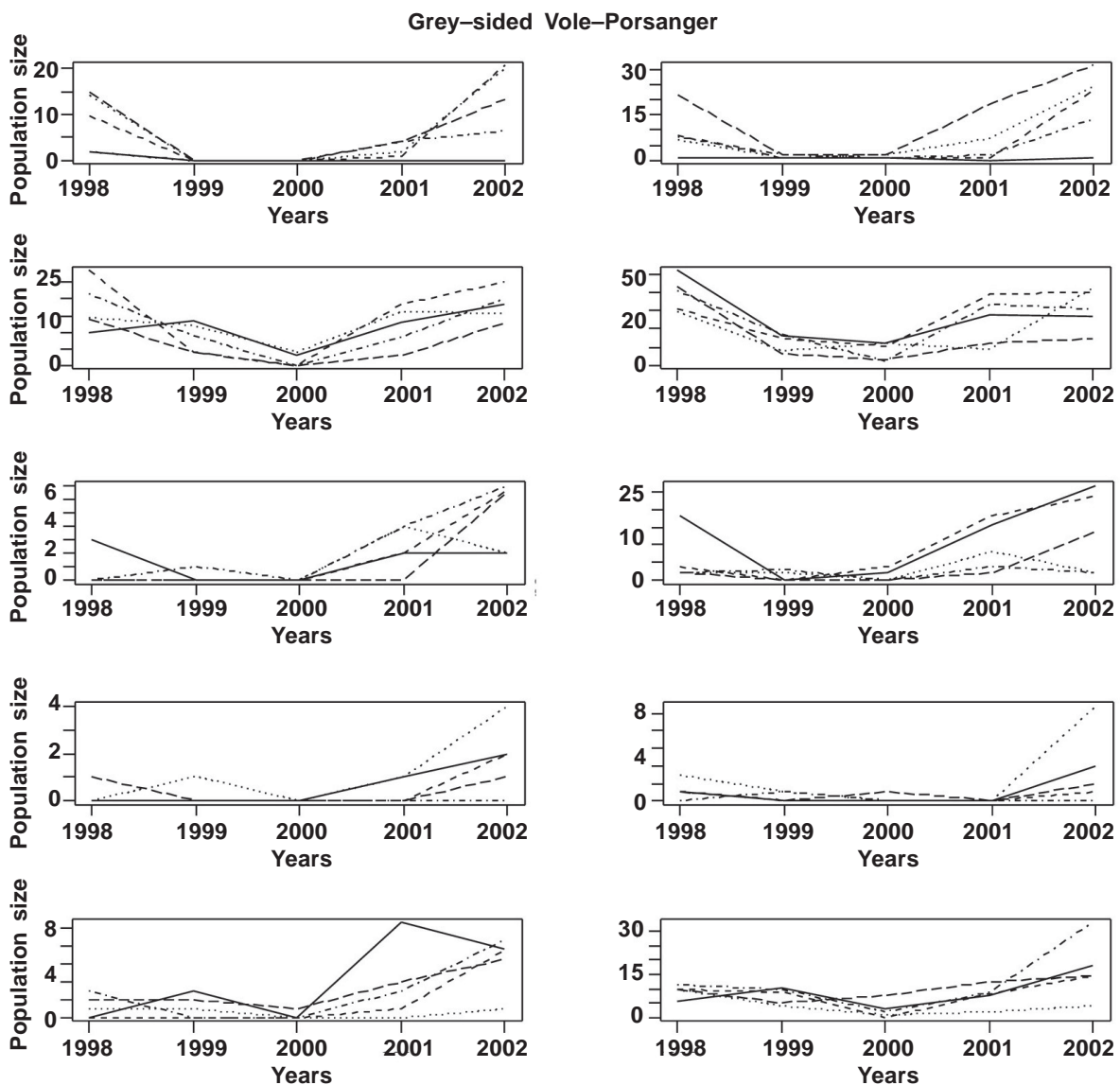


Fig. 2. Population dynamics of the Grey-sided Vole in Porsanger (A) and Alta (B), 1998–2002. The spring (left) and fall (right) population sizes are given for the five transects and the five trapping grids in each transect. Population size is estimated using the second-order jackknife estimator, M_{h2} . The populations in Porsanger and Alta show multi-annual (5-years cycle) fluctuations, in addition to the seasonal fluctuations associated with the reproductive period (June to September). Even if the five transects are located in the same habitat type (birch forest), there is large variation in population abundance, within and among transects.

populations. The variance σ^2 was set equal to 0.04 in order to get fluctuations with amplitude similar to the one observed.

The capture–recapture data were simulated using WiSP (Borchers et al., 2002), assuming three secondary capture sessions, random variation in capture probabilities among the two populations and in time, and individual heterogeneity. The parameters describing capture prob-

abilities and heterogeneity were chosen in order to give capture probabilities similar to those observed in the actual vole data: secondary session capture probabilities were assumed to vary between the average values 0.18 and 0.5 (i.e., the probability of being caught at least once is then between 0.45 and 0.875; see fig. 3), with a random variation among sessions equal to 0.1 on the logit scale.

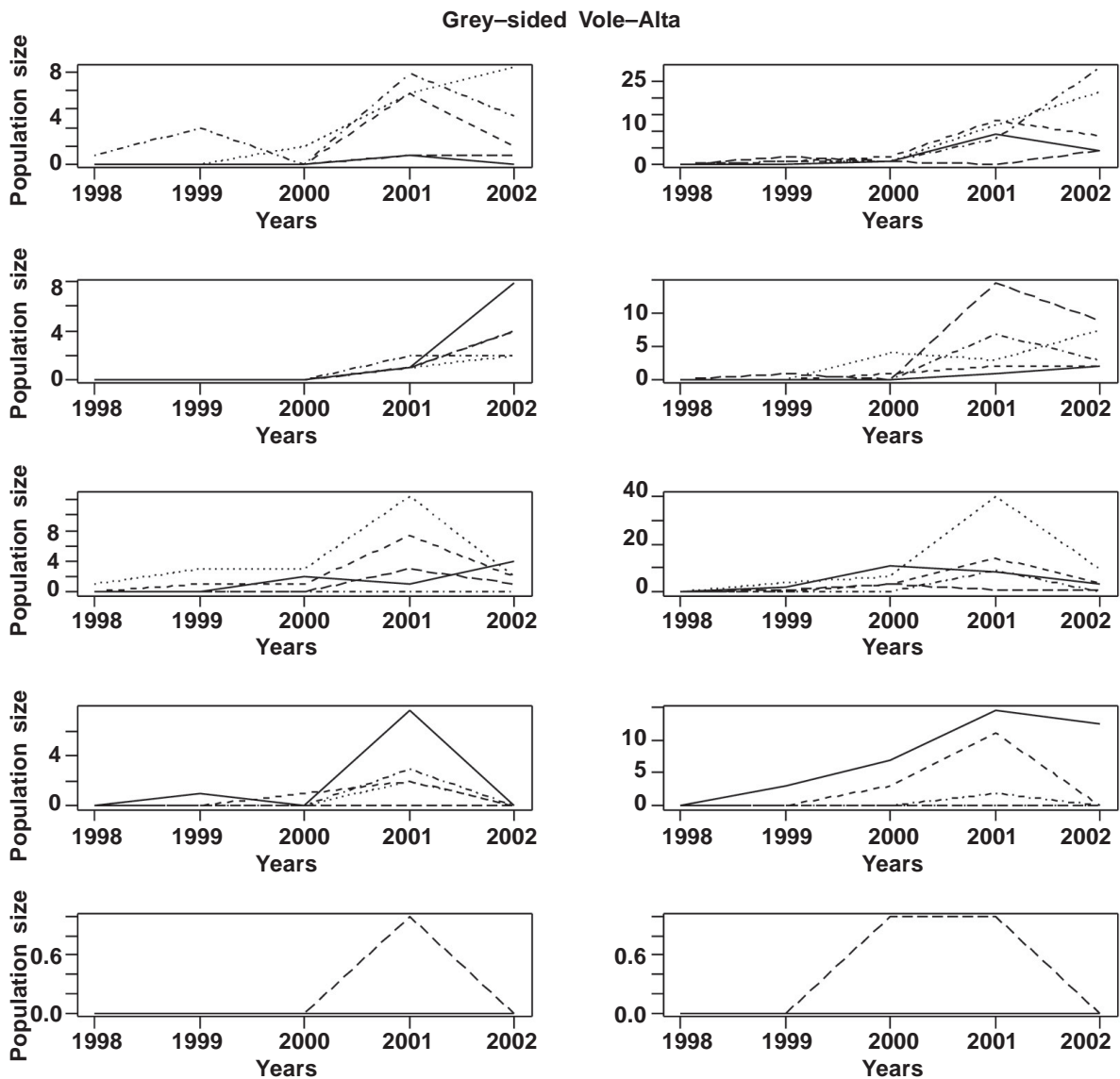


Fig. 2. Dinámica poblacional del ratón de campo de flancos grisáceos en Porsanger y Alta, 1998–2002. Se indican los tamaños poblacionales durante la primavera (izquierda) y el otoño (derecha) para los cinco transectos y las cinco rejillas de cada transecto. El tamaño poblacional se calcula utilizando el estimador jackknife de segundo orden, M_{h2} . Las poblaciones en Porsanger y Alta presentan fluctuaciones multianuales (ciclo de 5 años), así como fluctuaciones estacionales asociadas con el período reproductor (de junio a septiembre). Aunque los cinco transectos estén situados en el mismo tipo de hábitat, bosque de abedules, existe una amplia variación en la abundancia poblacional, tanto en cada uno de los transectos como entre ellos.

Two synchronous populations were simulated by assuming that the stochastic components for the two population growth rates were correlated, that is the λ_t were assumed to follow a binormal distribution with identical variance for the two populations and a correlation $r\delta$. We estimated the correlations using the logarithm of number of animals caught (raw counts) as well as population size estimated using model M_0 and M_{h2} .

Results

Empirical correlation patterns

The dynamics of populations differed among species and regions. In Porsanger (NE), the Grey-sided Vole experienced a synchronous decline in 1998–99, followed by a synchronous increase and peak in 2002 (fig. 2). In Alta (ca. 150 km from

Porsanger), the Grey-sided Vole had very low population levels in 1998–1999, experienced a synchronous increase in 2000–01, but had already crashed in 2002 (fig. 2). The spatial synchrony at a large scale is therefore phase-dependent, being most pronounced in the increase phase 2000–2001. Given this difference in the dynamics, we will restrict the discussion below to the intermediate (among transects: 10 km) and small (within transect: 1 km) scale spatial patterns in Porsanger.

The correlations within and among transects were highly variable, for population size and population growth rates (table 1). They were in general higher within transects than among transects indicating stronger correlations at small spatial scales, but the pattern was not consistent. As population sizes were variable and sometimes quite low (e.g. transect 4; fig. 2), part of the variability results at least in part from sampling variability.

One component of the sampling variability is linked to the population size estimation process. Given that we estimate population size of the same species, in the same habitat type, with the same trappers, and with trapping sessions occurring on the same days, we would assume that capture rates may vary little among trapping grids, even if this has not been assessed in most studies. To explore this possibility, we used the Huggins/Alho's model with different sets of covariates (table 2). There was no evidence for variation among grids, but evidence for heterogeneity in capture rates linked to body weight: large, reproducing (adult) animals have a higher capture rate than small (juvenile/subadult) individuals (fig. 3). This implies that populations with different age structure would have different average probabilities of capture. The overall estimate for population size in the five grids was lower than the M_{h2} estimate (table 2), either because body weight is only one source of heterogeneity of capture and/or the second-order jackknife estimator is biased high. Heterogeneity of capture is therefore likely to be one of the main sources of sampling variability in population size estimates.

Simulations

Correlations based on estimated population size or number of animals caught were biased low, and the bias was relatively large (up to 30% for model M_{01} , tables 3, 4). The bias was due to the increased variance of population size, as the covariances were not biased. The worst case resulted from using the model M_{01} , whereas M_{h2} and raw counts did give similar biases. The simple estimator (M_{01}) was both biased (because of the presence of heterogeneity of capture) and relatively imprecise, resulting in an overall larger measurement error than the jackknife estimator which was not biased (results not shown). The raw counts were of course biased, but did not include any estimation uncertainty. Using proper estimates for the process variance (Link & Nichols, 1994; Link et al., 1994; Burnham & White, 2002) would correct for most of

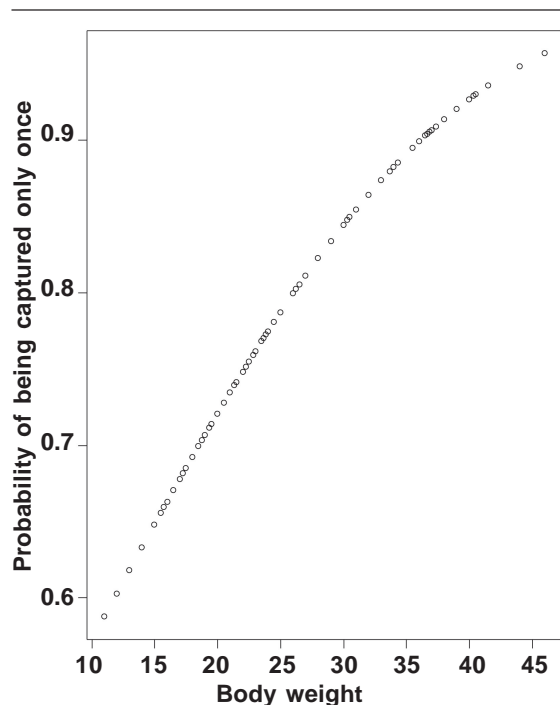


Fig. 3. Probability of being captured at least once as a function of body weight for the Grey-sided Vole, transect 2, Porsanger, Fall 1998. Most breeding individuals weight more than 25 g, and their probability of being captured is higher than 0.8. Individuals with a body weight as low as 10 g have just been weaned and are caught only if the trap is close to their nest.

Fig. 3. Probabilidad de ser capturado, como mínimo una vez, expresada como una función del peso corporal para el ratón de campo de flancos grisáceos, transecto 2, Porsanger, otoño de 1998. La mayoría de los individuos en edad reproductora pesan más de 25 g, y la probabilidad de que sean capturados es superior a 0,8. Los individuos con peso corporal de sólo 10 g han sido destetados recientemente y sólo resultan capturados si la trampa se halla cerca de su nido.

the bias, but assuming a Poisson distributed error would correct only for suggest that some population indices such as raw counts may result in similarly biased correlations compared to those obtained using estimated population size, and that using an inadequate model for capture rates is in fact worse than using raw counts. The main difficulty is that most trapping indices have unknown measurement error and therefore the biases are difficult to remove (i.e., by estimating the measurement error and the true process variance). This is indeed a general problem in

Table 1. Empirical patterns for the correlations of population size and population growth rates within (average pairwise correlations among trapping grids within a transect) and among transects (average pairwise correlations among trapping grids between two transects) for the Grey-sided Vole in Porsanger region in autumn. Transect 1 (T1) is south, transect 5 (T5) is north (see fig. 1).

Tabla 1. Patrones empíricos para las correlaciones del tamaño poblacional y de las tasas de crecimiento poblacional en cada uno de los transectos (correlaciones promedio entre pares con relación a las rejillas de captura en un transecto) y entre varios transectos (correlaciones promedio entre pares con relación a las rejillas de captura entre dos transectos) para el ratón de campo de flancos grisáceos en la región de Porsanger. El transecto 1 (T1) está en el sur, mientras que el transecto 5 (T5) está en el norte (ver fig. 1).

Population size (Log(N _t))					
	T1	T2	T3	T4	T5
T1	0.54				
T2	0.42	0.72			
T3	0.20	0.55	0.52		
T4	0.39	0.25	0.12	0.35	
T5	0.45	0.61	0.45	0.48	0.55
Population growth rates (Log(N _{t+1}) – Log(N _t))					
	T1	T2	T3	T4	T5
T1	0.55	–	–	–	–
T2	0.32	0.64	–	–	–
T3	0.10	0.56	0.38	–	–
T4	0.40	0.13	0.02	0.36	–
T5	0.37	0.60	0.33	0.38	0.55

Table 2. Huggins/Alho's model applied to the Grey-sided Vole and the five stations of transect 2, fall 1998, Porsanger: A. Conditional likelihood values (CL) and conditional AIC (CAIC) (N. Number of parameters; *Best model, include on the covariate body weight, see fig. 2); B. Parameter and population size estimates for model including only body weight as a covariate (E. Estimates; SE. Standard error). The resulting estimate is compared to the jackknife estimate (Model M_{h2}).

*Tabla 2. Valores de probabilidad condicional (CL), criterio de Información de Akaike Condicional (CAIC), estimaciones de parámetros y de tamaños poblacionales para el modelo de Huggins/Alho aplicado al ratón de campo de flancos grisáceos y las cinco estaciones del transecto 2, otoño de 1998, Porsanger: * Mejor modelo, incluye el peso corporal como covariante (ver fig. 2); B. Estimaciones del peso corporal y del parámetro para el modelo que incluye sólo el peso corporal como covariante (E. Estima; SE. Error estandard). El valor de estima resultante se compara con el valor del transecto estimado mediante jackknife (Modelo M_{h2}).*

A			
Model	N	CL	CAIC
Grids + body weight + sex	7	326.38	666.76
Body weight + sex	3	329.57	665.14
*Body weight	2	329.76	663.52
Intercept	1	335.04	672.08
B			
Parameter	E(SE)	Model M _{h2}	
Intercept	-1.60(0.40)	–	
Body weight	0.048(0.015)	–	
Total population size	229.4(13.8)	264.5(13.8)	

most monitoring programs using field techniques that do not allow for uncertainty estimation (Yoccoz et al., 2001, 2003).

Most of the recent discussion of spatial population dynamics is focusing on analyzing how correlations among populations change as a function of the distance and direction among populations (e.g., Bjørnstad et al., 2002), on comparing these correlations among species and comparing those correlations to those of, e.g., climatic variables such as temperature (in particular the so called "Moran effect" predicting identical spatial correlations for the environmental disturbance and the population abundance; Bjørnstad et al., 1999; Liebhold et al., 2004;

Peltonen et al., 2002). As we have shown here, correlations will in general be biased low and the extent of the bias will depend of the measurement error. Even in our case study with high capture rate, the bias was large (i.e., 20 to 30%), and we would expect much larger biases for studies based on simple indices. On the contrary, variables such as temperature are precisely measured and show little sampling variability and would result in low bias for estimates of spatial correlation. It means that further comparisons among species and variables should include measure-

Table 3. Correlations and covariance matrices estimated using a 5,000 year time-series simulated using an AR1 process (stable population). All covariances and correlations are calculated using log-transformed data: A. Covariance matrix of the true population sizes; B. Covariance matrix of the estimated population size using M_{h2} ; C. Covariance matrix of the population indices (number of animals caught N_c); D. Bias in the estimated correlations (true value for $\rho = 0.7$)

Tabla 3. Correlaciones y matrices de covarianza estimadas utilizando una serie temporal de 5.000 años y un proceso AR1 (población estable). Todas las covariantes y correlaciones se calculan mediante datos transformados logarítmicamente: A. Matriz de covarianza de tamaños poblacionales verdaderos; Matriz de covarianza de tamaños poblacionales estimados con M_{h2} ; C. Matriz de covarianza de índices poblacionales (número de animales capturados N_c); D. Diagonal en las correlaciones estimadas (valor verdadero para $\rho = 0,7$)

	Pop1	Pop2
A		
Pop1	0.213	0.149
Pop2	0.149	0.206
B		
Pop1	0.249	0.150
Pop2	0.150	0.250
C		
Pop1	0.255	0.149
Pop2	0.149	0.25
D		
Estimated population size using model M_0 :	0.54	
Estimated population size using model M_{h2} :	0.60	
Population counts (N_c):	0.59	

Table 4. Correlations and covariance matrices estimated using a 1,000 year time-series and a AR2 process (cyclic population). All covariances and correlations are calculated using log-transformed data: A. Covariance matrix of the true population sizes; B. Covariance matrix of the estimated population size using M_{h2} ; C. Covariance matrix of the population indices (number of animals caught N_c); D. Bias in the estimated correlation (true value for correlation = 0.7).

Tabla 4. Correlaciones y matrices de covariantes estimadas utilizando una serie temporal de 1.000 años y un proceso AR2 (población cíclica). Todas las covariantes y correlaciones se calculan mediante datos transformados logarítmicamente: A. Matriz de covarianza de tamaños poblacionales verdaderos; Matriz de covarianza de tamaños poblacionales estimados con M_{h2} ; C. Matriz de covarianza de índices poblacionales (número de animales capturados N_c); D. Diagonal en las correlaciones estimadas (valor verdadero para correlación = 0,7).

	Pop1	Pop2
A		
Pop1	0.268	0.165
Pop2	0.165	0.235
B		
Pop1	0.312	0.172
Pop2	0.172	0.279
C		
Pop1	0.321	0.172
Pop2	0.172	0.280
D		
Estimated population size using model M_0 :	0.50	
Estimated population size using model M_{h2} :	0.58	
Population counts (N_c):	0.57	

ment error since the extent of measurement error and therefore the bias is likely to differ among species and variables.

Acknowledgements

We thank the Norwegian Research Council (Biodiversity programme) and the Norwegian Institute for Nature Research for financial support, and two anonymous referees for constructive comments.

References

- Alho, J. M., 1990. Logistic regression in capture-recapture models. *Biometrics*, 46: 623–635.
- Bjørnstad, O. N., Peltonen, M., Liebhold, A. M. & Baltensweiler, W., 2002. Waves of larch budmoth outbreaks in the European Alps. *Science*, 298: 1020–1023.
- Bjørnstad, O. N., Stenseth, N. C. & Saitoh, T., 1999. Synchrony and scaling in dynamics of voles and mice in northern Japan. *Ecology*, 80: 622–637.
- Bolker, B. M. & Grenfell, B. T., 1996. Impact of

- vaccination on the spatial correlation and persistence of measles dynamics. *Proceedings of the National Academy of Sciences USA*, 93: 12648–12653.
- Borchers, D. L., Buckland, S. T. & Zucchini, W., 2002. *Estimating animal abundance. Closed populations*. Springer-Verlag, London.
- Buckland, S. T., Newman, K. B., Thomas, L. & Koesters, N. B., 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling*, 171: 157–175.
- Burnham, K. P. & Overton W. S., 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology*, 60: 927–936.
- Burnham, K. P. & White, G. C., 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics*, 29: 245–264.
- Dennis, B., Kemp, W. P. & Taper, M. L., 1998. Joint density dependence. *Ecology*, 79: 426–441.
- Engen, S., Lande, R. & Sæther B. E., 2002. The spatial scale of population fluctuations and quasi-extinction risk. *American Naturalist*, 160: 439–451.
- Fuller, W. A., 1987. *Measurement error models*. John Wiley and Sons, New York.
- Hansson, L., & Henttonen, H., 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, 67: 394–402.
- 1988. Rodent dynamics as community processes. *Trends in Ecology and Evolution*, 3: 195–200.
- Henttonen, H. & Hansson, L., 1986. Synchrony and asynchrony between sympatric rodent species with special reference to *Clethrionomys*. In: *Causes and geographic patterns of microtine cycles* (H. Henttonen, Ed.). Ph. D. Thesis, Univ. of Helsinki, Helsinki.
- Huggins, R. M., 1989. On the statistical analysis of capture experiments. *Biometrika*, 76: 133–140.
- Ito, Y., 1972. On the methods for determining density-dependence by means of regression. *Oecologia*, 10: 347–372.
- Krebs, C. J., Kenney, A. J., Gilbert, S., Danell, K., Angerbjörn, A., Erlinge, S., Bromley, R. G., Shank, C. & Carriere, S., 2002. Synchrony in lemming and vole populations in the Canadian Arctic. *Canadian Journal of Zoology*, 80: 1323–1333.
- Lambin, X., Elston, D. A., Petty, S. J. & MacKinnon, J. L., 1998. Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings of the Royal Society, London B*, 265: 1491–1496.
- Lande, R., Engen, S. & Sæther, B.-E., 2003. *Stochastic population dynamics in ecology and conservation*. Oxford University Press, Oxford.
- Lebreton, J.-D., 1990. Modelling density dependence, environmental variability, and demographic stochasticity from population counts: an example using Wytham Wood great tits. In: *Population biology of passerine birds: 89–102* (J. Blondel, A. Gosler, J.-D. Lebreton, & R. H. McCleery, Eds.). Springer-Verlag, Berlin.
- Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjørnstad, O. N., Westfall, R., Elkinton, J., & Knops, J. M. H., 2004. Within-population spatial synchrony in mast seeding of North American oaks. *Oikos*, 104: 156–164.
- Link, W. A. & Nichols, J. D., 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos*, 69: 539–544.
- Link, W. A., Barker, R. J., Sauer, J. R. & Droege, S., 1994. Within-site variability in surveys of wildlife populations. *Ecology*, 75: 1097–1108.
- Moilanen, A., 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos*, 96: 516–530.
- Peltonen, M., Liebhold, A. M., Bjørnstad, O. N. & Williams, D. W., 2002. Spatial synchrony in forest insect outbreaks: Roles of regional stochasticity and dispersal. *Ecology*, 83: 3120–3129.
- Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E., 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107: 1–97.
- Ranta, E., Kaitala, V. & Lundberg, P., 1997. The spatial dimension in population fluctuations. *Science*, 278: 1621–1623.
- Ripa, J., 2000. Analysing the Moran effect and dispersal: their significance and interaction in synchronous population dynamics. *Oikos*, 89: 175–187.
- Solow, A. R., 2001. Observation error and the detection of delayed density dependence. *Ecology*, 82: 3263–3264.
- Steen, H., Ims, R. A. & Sonerud, G. A., 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology*, 77: 2365–2372.
- Steen, H., Yoccoz, N. G. & Ims, R. A., 1990. Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations. *Oikos*, 59: 115–120.
- Stenseth, N. C., 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, 87: 427–461.
- Viljugrein, H., 2000. Spatio-temporal patterns of population fluctuations in waterfowl and small mammals. Ph. D. Thesis, Oslo Univ.
- Yoccoz, N. G., Nichols, J. D. & Boulinier, T., 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16: 446–453.
- 2003. Monitoring of biological diversity – a response to Danielsen et al. *Oryx*, 37: 410.
- Yoccoz, N. G., Steen, H., Ims, R. A. & Stenseth, N. C., 1993. Estimating demographic parameters and the population size: an updated methodological survey. In: *The biology of lemmings: 565–587* (N. C. Stenseth & R. A. Ims, Eds.). Academic Press, London.