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The Demography of *Clethrionomys rufocanus*: from Mathematical and Statistical Models to Further Field Studies

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Abstract. Until recently, most studies on microtines have focused on patterns in population dynamics or demography without providing a quantitative assessment of the robustness of the inferred patterns as well as a link between demography and population dynamics. Developments in statistical time-series analysis on the one hand and in capture-recapture statistical modelling on the other hand, now allow for improved analyses. We review some of the recent developments in the capture-recapture statistical methodology – restricting ourselves to methods most relevant to the demography of small mammals. A 5-years study of the gray-sided vole *Clethrionomys rufocanus* in Hokkaido, Japan was used as an example to explore some models. We then provided a framework for further demographic analysis of microtine populations, including *C. rufocanus*. Investigating the relative importance of the different demographic parameters (e.g. survival, maturation, dispersal) will require studies done on larger scale than is commonly done today, with more effort devoted to the low density phase. Special emphasis is given to study-design, and to experimental designs tailored to the study of specific demographic mechanisms.

Key words: age-structured models, seasonality, survival, capture-recapture, elasticity.

Introduction

Microtines have played an important role in the early development of mathematical and statistical methods for the study of demography and population dynamics. This is particularly true with respect to the work of “George” Leslie (see Crowcroft (1991) for an historical account): beginning in 1940 with his study of the demography of the field vole (*Microtus agrestis*) in the laboratory (Leslie and Ranson 1940), Leslie was among the very first to use statistical methods for analyzing maturation rates with respect to body weights (through the use of logistic regression; Leslie et al. 1945), for estimating population sizes and demographic parameters through capture-mark recap-

ture models (e.g. Leslie and Davis 1939; Leslie et al. 1953) as well as providing the theoretical framework for assessing the relative importance of demographic parameters (Leslie 1945, 1948) and deriving relevant demographic summaries (such as generation time; Leslie 1966). Despite this early emphasis on quantitative methods, the empirical study of population dynamics and demography in microtines has for several decades suffered from too much reliance on *ad hoc* methods (cf. Nichols and Pollock 1983; Nichols 1986; Yoccoz et al. 1993a). While it is correct to emphasize that all models are nothing more than tools used to explore relationships in a given problem or dataset, and that they will sooner or later be shown to be wrong, they are nevertheless based on explicit assumptions: their robustness may therefore be assessed, which is not always the case of *ad hoc* methods. This is true of capture-recapture models (used for estimating demographic parameters; Lebreton et al. 1992) and of demographic models (such as the Leslie or Lefkovich matrix models;

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Caswell 1989a). A noteworthy part of the literature on capture-recapture modelling, for example, focuses on the consequences for survival rate estimation (that is, the bias and variance of the survival estimates) of the failure of the homogeneity assumption stating that all individuals within a group (e.g. sex or age) have the same survival and recapture probabilities (e.g. Carothers 1973; Burnham and Rexstad 1993; Pradel et al. 1997a). All models are indeed based on "unrealistic" simplifying assumptions, collapsing the total variation to a few dimensions, such as time or age. The main problem of statistical modelling is to extract as much information as possible from the data, separating structure (or patterns) from "noise". Similarly, mathematical population models are tools for understanding the dynamical consequences of specific assumptions about ecological mechanisms; their validity does not go beyond the validity of their assumptions. Indeed, "all models are wrong, but some are useful" (G.E.P. Box in Kanji 1986).

Excellent introductions and reviews of both capture-mark-recapture (CMR) methods and demographic analysis are available. (For CMR studies, see, e.g. Pollock et al. 1990; Clobert and Lebreton 1991; Pollock 1991; Lebreton et al. 1992; Nichols 1992; Lebreton and North 1993 and special issues of *Journal of Applied Statistics* in 1995 and *Bird Study* in 1998. For demographic analysis, see, e.g. Caswell 1989b; McDonald and Caswell 1993; Charlesworth 1994; Tuljapurkar and Caswell 1996). However, most of the literature on CMR-studies focuses on birds and large mammals (see references above), and demographic analysis has furthermore often been restricted to species with annual reproduction. Microtines pose specific problems, due to their short life expectancy, large fluctuations in population sizes, and the importance of seasonality in determining their demographic patterns. Age at first reproduction may vary, for example, between one month for the young females born in the spring and nine to twelve months for young females born later in the season or at high densities (Kalela 1957; see also Ota 1984). Densities may vary by a factor of 25 or 50 within a year (Krebs 1993). These large and rapid changes are made possible by both the large reproductive output of microtines (a female may give birth every three weeks to five or six young) and the fact that up to three to four generations can follow each other in a given summer (e.g. Myllymäki 1977). Survival rates may also drop dramatically, in any season, resulting in extensive crashes (e.g. Mihok et al. 1985). Such large and rapid changes necessitate specifically tailored approaches.

During the last decade or so, there has been a tremendous increase in the sophistication of statistical and mathematical models used for analyzing population dynamics patterns and demographic variability. While in the past analysis was often limited by a small number of

possible models (e.g. the Jolly-Seber model restricted to temporal variation) and simplistic software (most of the recent software originated around 1985), the flexibility is now as great for modelling survival and recruitment rates as it is for the usual linear models (see, e.g. Pradel et al. 1997a). These highly welcomed developments have exposed the limitation of available data, small data-sets supporting only the more simplistic models, without sufficient precision for a reliable estimation of relevant biological effects. In fact, field biologists should be aware that while it is now possible to estimate, for example, dispersal or recruitment rates, such models may, to be realistic, need to include hundreds of parameters (see Brownie et al. 1993). This is the consequence of having each demographic rate varying with time, age or populations, as well as on the previous history for each individual. We will later on, for example, consider a demographic model with four age-classes: assuming that the survival rates and the recapture rates vary according to age and time of the year, an unconstrained model (i.e. a model where we do not assume the rates to be function of variables such as density or phase) has eight parameters for each trapping session (excluding the first one), and therefore a study involving 30 sessions (such as the one used here) implies a model with 240 parameters. Specific field study designs are therefore required, both in order to obtain sufficient sample sizes, and to restrict the biologically plausible models empirically (Ims and Yoccoz 1997).

Here, we will first re-analyze a capture-mark-recapture study of the gray-sided vole (*Clethrionomys rufocanus* (Sundevall, 1846)) in Hokkaido, Japan (Nakata 1989). We will then proceed by exploring some of the possible approaches and questions related to demographic analysis and population dynamics, focusing on the same population of gray-sided vole. However, the small sample size of the gray-sided vole study originally reported by Nakata (1989) prevents any statistically firm conclusions. The latter part of the paper is therefore meant to suggest what might be done, given a more extensive study and how such a study should be conducted.

A Capture-Mark-Recapture study of *Clethrionomys rufocanus*

Trapping program and statistical modelling

The gray-sided vole fluctuates seasonally in the southern and western part of Hokkaido, but multiannually in northern and eastern parts of the island (Bjørnstad et al. 1996; Stenseth et al. 1996a; Saitoh et al. 1998). The field-study was conducted in a natural mixed forest at Mizuho (43°42' N, 142°39' E), Asahikawa, central Hokkaido, Japan (Fig. 1a). This area is in the transition zone

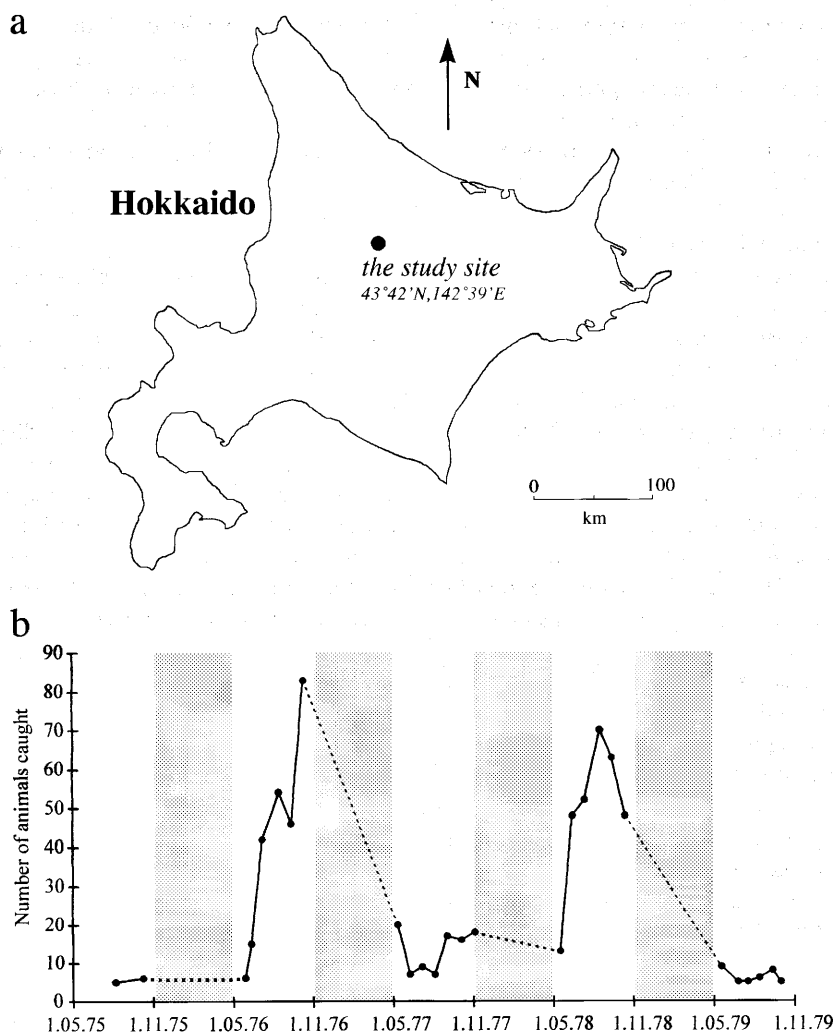


Fig. 1. (a) Map of Hokkaido with the localization of the study. (b) Population dynamics of the grey-sided vole: Numbers of animals caught at each trapping session in different years. Winter periods (November to April) are shaded.

between seasonally and multiannually fluctuating populations, and the observed dynamics appear to be cyclic with a two years period (see below). The climate is cool-temperate, with snow present for about six months (Nakata 1989). A 1-ha grid was used throughout the study, with two Sherman live-traps located at each point in a 10 m by 10 m grid. Trapping was done approximately every month from May to October in 1975 to 1979; each trapping period lasted for three consecutive days. Each individual was individually marked by toe-clipping upon capture. Data from the summer of 1975 were excluded in the following analyses as the study then was rather preliminary and the entire grid was not used. The whole dataset included 27 trapping sessions, with intervals between trapping sessions varying between 19 and 234 days. The dynamics of the population during the five years of the study were characterized by two increase-peak years (1976

and 1978) and three low-density years (1975, 1977 and 1979; see Fig. 1b). Further description of the study area are available in Nakata (1984a, 1989).

Litter size was estimated by using trap lines 250–500 m away from the live-trapping grid (Nakata 1984a). Trap lines and the live-trapping grid were operated using the same schedule. The average litter size based on embryo counts was 5.31 (placental scars gave similar values: 5.56). Litter size varied according to the phase of the population dynamics, with lower litter size being associated with the decrease phase. Moreover, density was negatively correlated with litter size in overwintered females. However, these changes were quantitatively small (Nakata 1984a), and age and parity were also important in determining the variability in litter sizes (older and multiparous females giving birth to larger litters). Nakata (1989), based on the same material as above, focused his analysis on changes in

the reproductive rates: sex ratios, weight at sexual maturity, length of the breeding season and maturation rates. Sex ratio was unbiased in most years, particularly for current year's individuals. The proportion of females amongst overwintered individuals was lower in 1976 and 1977 than in 1978 and 1979, but these changes were not related to the changes in population density. There were, however, consistent changes in reproductive rates with respect to phase and density: at peak phase and high densities, voles matured later and in smaller proportion than at increase and low densities, and pregnancy rates were much lower when densities were high than when densities were low. These changes were of a much larger amplitude than those observed with litter sizes: for example the percentage of pregnant females dropped to less than 10% at "peak" densities, compared to more than 50% during all other periods. Similarly, the proportion of individuals being mature above some given weight (16 g for females and 24 g for males; Nakata 1989) decreased much earlier in high density years than in low density years. No analysis was provided for survival rates.

Three general covariates are often considered when analyzing survival rates: time, age and cohort. As is well known in epidemiological studies (Clayton and Schifflers 1987a), for example, it is not possible to consider simultaneously these sources of variation without restricting how they relate to each other (e.g. by assuming additive effects between age and time on a specific scale, usually logarithmic or logit, or by considering that variation associated with, for example, age is adequately summarized by 2 or 3 age-classes; e.g. Gaillard et al. 1993). Statistical analysis aims at finding a compromise between too complex models which may suffer from a lack of precision of the estimated effects as well as from difficult interpretation of the model parameters, and too simple models which may miss some of the main patterns and result in biased estimates (e.g. Burnham and Anderson 1992). Additive models for age and cohort or age and time are typical compromises (see Clayton and Schifflers 1987b). Temporal variation may similarly be constrained to be a function of climatic variables, density or phase (see Clobert and Lebreton 1985; Lebreton et al. 1992). In this study, temporal variation was assumed to be a function of season, distinguishing between winter (October to May), spring or early summer (May-June) and summer-fall (June to October). As trapping dates were approximately the same in different years and as any precise definition of seasons should be based on biological criteria such as phenology of the vegetation, we assigned every trapping interval to a specific season (winter, spring, summer). Age is generally not known in this study. Marking young shortly after birth has very rarely been done in microtines; this may, however, be a fruitful area for future studies, given the importance of early survival in determining population

dynamics (see below and Lambin and Yoccoz 1998). We will here consider only two groups of individuals (in addition to males and females): those caught for the first time below 25 g ("small"), and those with a first weight above 25 g ("large"). Previous analyses have shown that 25 g was an adequate weight limit for separating adults on one hand from juveniles and subadults on the other (Ota 1984). Animals weighing less than 25 g may be maturing individuals, and may therefore profoundly differ in their behavior (e.g. w.r.t. dispersal) from mature, breeding individuals (Saitoh 1995). For survival, we used for the later group a specific model with two "age"-classes: the survival just after capture being lower if some of the smaller individuals are indeed dispersers (Pradel et al. 1997b). These "age"-classes are not related to real age but are convenient ways of handling possible differences in behavior between newly marked and resident individuals. To assess whether 25 g was an appropriate limit, we also used a limit of 30 g, as the large-size group would then only include mature individuals. We finally explored a class of model where survival just after capture was a function of body weight, and not just different between small and large individuals as in the previous models. If indeed smaller, dispersing, individuals are present in the data-set in significant proportions, we would expect animals with lower body weight at first capture to be recaptured less often than animals with larger body weight (residents), and this survival to increase with body weight as the proportion of dispersing individuals decreases.

Most analyses were done using MARK (White and Burnham 1998; RELEASE which is used for testing goodness of fit (see below) is now included in MARK), while some complex models were first fitted in SURGE 5.1 (Reboulet et al. 1998). The current version of SURGE does not allow for unequal sampling intervals and is therefore of limited use for many small mammals studies.

Statistical analysis

A full model including four groups and temporal variation for both survival and recapture rates has 208 parameters (four groups and 26 capture and survival parameters for each group). Given that fewer than 400 individuals were caught in our field study, resulting in an effective sample size of slightly more than 600 (the effective sample size is the total number of releases), such a model is not applicable. Moreover, most of the individuals were naturally caught during periods of high densities, and therefore parameters associated with low densities were typically nonestimable. Similarly, the goodness-of-fit of a general model cannot be thoroughly assessed, and this is another important weakness of small data set. This was the case when using the two goodness-of-fit tests provided by RELEASE (see Burnham et al. (1987) and Cooch et al.

(1996) for the interpretations of these tests and of their components; these two tests assess the goodness of fit of the model with temporal variation only, i.e. the classical Jolly-Seber model): none of the tests was significant. (We give here the sum of the two tests, Test 2 and Test 3, for groups defined by the size at first capture: Male-large: $\chi^2 = 6.13$, $df = 16$; Females-large: $\chi^2 = 7.39$, $df = 7$; Male-small: $\chi^2 = 8.75$, $df = 17$; Females-small: $\chi^2 = 13.94$, $df = 15$; for the four groups combined, the total value of the goodness of fit test was $\chi^2 = 36.21$, $df = 55$, $P = 0.98$.) Most of the contingency tables involved in the two goodness-of-fit tests were too sparse to be reliable. The few tables with large enough expected values did not show any evidence for lack of fit. Note that the usual diagnostics for lack of fit of a statistical model are based on various definitions of residuals (e.g. for generalized linear models, see McCullagh and Nelder 1989). The observations for capture-recapture models are capture histories and not the individuals themselves. As expected numbers are generally very low, pooling of observations is necessary but is not yet satisfactorily implemented (White and Burnham 1998).

Low sample size results in low precision (or equivalently low power) for the parameters of interest. On the basis of statistical criterion such a trade-off between bias and variance, simple models will be selected because the data contain too little information for estimating many biological effects (Burnham and Anderson 1992). However, the

resulting model might just be biologically worthless (e.g. a model with constant survival does not provide any information on possible sources of variability). The alternative is to consider only simple models based on biologically specified assumptions regarding what could be the important ecological factors, and to use model selection criteria as a guide for choosing a compromise between biologically meaningful models and statistical support. Using this pragmatic model selection strategy, we ignored differences in recapture rates between groups (males/females or small/large; models including such difference were never selected in terms of AIC_c) and analyzed survival rates with respect to year (high density, 1976 and 1978, vs low density, 1977 and 1979, years, respectively), seasonal variation (winter, spring and summer-autumn), and interaction between these factors. To consider differences between the four groups (males-females and small-large at first capture) is the same as having an interaction between sex and size in the statistical model for the survival rates. We therefore also implemented simpler models without interaction for these two factors.

Table 1 gives the Akaike's Information Criteria (AIC_c ; Akaike 1985; it is corrected for small sample sizes in the program MARK: see Hurvich and Tsai 1989) for some of the models fitted. Differences of the order of 1 or 2 in the AIC_c -values are, customarily, not considered significant (e.g. Lebreton et al. 1992). We used therefore the models

Table 1. Akaike's Information Criterion corrected for small sample size (AIC_c) for some Capture-Recapture models fitted to the gray-sided vole data (other models with higher values for AIC_c not shown). The AIC_c indicates which model represents a good compromise between simple, biased, models and complicated, unprecise, models. Models are ordered according to increasing value of the AIC_c . The parameter Φ is the apparent survival, p is the recapture rate. The notations for different models are as follows: (.) : constant parameter; 2-age: survival just after capture different and constant in time; year: low and high-density years; spring: first trapping period in May-June; size: small (<25 or <30) vs large (>25 or >30 g) individuals at first capture. For models including seasonal variation, summer survival (from June to October) was taken as the reference value.

Model	AIC_c	Number of estimated parameters
$\Phi(\text{spring}^* \text{year}) p(.)$	837.77	4 ^a
$\Phi(\text{spring}^* \text{year} + \text{winter}) p(.)$	839.78	5 ^a
$\Phi(2\text{-age}(<25 \text{ g}) + \text{spring}^* \text{year}) p(.)$	841.35	7
$\Phi(\text{year} + \text{spring}^* \text{year} + \text{winter}^* \text{year}) p(.)$	842.49	7 ^a
$\Phi(.) p(t)$	842.64	17
$\Phi(2\text{-age}(<30 \text{ g}) + \text{spring}^* \text{year}) p(.)$	842.73	7
$\Phi(\text{spring}^* \text{year} + \text{winter}^* \text{year}) p(.)$	842.97	6 ^a
$\Phi(2\text{-age}(<25 \text{ g}) + \text{spring}^* \text{year} + \text{sex}) p(.)$	842.99	8
$\Phi(2\text{-age}(<30 \text{ g}) + \text{spring}^* \text{year} + \text{sex}) p(.)$	844.02	8
$\Phi(.) p(.)$	845.81	2
$\Phi(2\text{-age}(<30 \text{ g})^* \text{weight} + \text{spring}^* \text{year}) p(.)$	845.91	7
$\Phi(2\text{-age}(<30 \text{ g}) + \text{winter}^* \text{year} + \text{spring}^* \text{year}) p(.)$	846.60	9
$\Phi(.) p(\text{sex}^* \text{size})$	848.28	5
$\Phi(t) p(.)$	855.45	27
$\Phi(t) p(t)$	877.98	46

^a spring survival in high density years was estimated as 1 for these models and was considered as estimable.

with constant capture rates but with variability in survival rates according to season and years (Models $\Phi(\text{spring} \cdot \text{year}) p(\cdot)$ and $\Phi(\text{spring} \cdot \text{year} + \text{winter} \cdot \text{year}) p(\cdot)$ in Table 2) to estimate some of the relevant biological differences (see Table 3 for estimates). We discuss first some of the models fitted, but not retained in the final analysis.

Including two age-classes with a specific survival rate just after capture did not result in better models. However, considering for example the model with two groups (large vs small), there was a tendency for females and for males to have a lower survival right after capture (on a logit scale and with 25 g as a cutpoint, the difference for females was -0.35 with $SE=0.30$; for males it was -0.10 with $SE=0.28$. The difference was somewhat larger when the cutpoint 30 g was used). The same tendency was found when using weight as an individual covariate (positive effect of weight for females and for males). This could suggest there are, as would be expected, dispersers ("transients") among the individuals with smaller body weight. The large uncertainty does not allow for any meaningful estimation of the actual proportions (Pradel et al. 1997b), or for comparison of male and female dispersal patterns (Ims 1989; Ishibashi et al. 1998). It may, however, be a fruitful approach for understanding the relative roles of dispersal vs. mortality.

The results do not provide clear evidence for any difference between summer and winter survival, nor between years of low and high density for these seasons, nor for differences between sexes; there is, however, rather strong evidence for a reduced survival in the spring of low-density years (Table 2). While the latter difference is significant, it should be noted that the confidence intervals are very large (see Table 2): any difference in survival between 20 and 80% (the estimated one is 65%) would be consistent at the 5% level with the data. This is also true, but to a lesser extent, for the "absence" of difference between years in

Table 2. Estimated 28-days survival rates according to seasons and years, for the model $\Phi(\text{year} + \text{spring} \cdot \text{year} + \text{winter} \cdot \text{year}) p(\cdot)$. The recapture rate was 0.860 (0.802–0.903)

Period-Year	Estimate	95% C.I.
Winter-Low	0.760	(0.624–0.853)
Winter-High	0.695	(0.625–0.754)
Spring-Low	0.358	(0.183–0.538)
Spring-High	1 (0.847) ^a	1 (0.488–0.962)
Summer-Low	0.679	(0.562–0.771)
Summer-High	0.720	(0.668–0.765)

^a the spring survival is estimated as 1 for this model. We provide in parenthesis the estimate for the model with two age-classes for small individuals. The latter model resulted in similar estimate for survival in low-density years (0.368 vs 0.358).

Table 3. Asymptotic population growth rates for combinations of demographic parameters ($\times 100$; S0 to S4+ : survival and Prep: proportion breeding females) in summer (S), fall (F) and winter (W). See text for explanations. Litter Size and Sex ratio were assumed to be constant (5.3 and 0.5 respectively).

S(S1 to S4+)	F(S1 to S4+)	W(S1 to S4+)	S(S0)	F(S0)	S{Prep 2 to 4}	F{Prep 2 to 4}	Lambda	Basic assumption
75	75	80	70	70	50 100 100	0 50 50	2.08	lower breeding proportions in fall
75	75	80	70	70	100 100 100	50 100 100	5.07	high survival and breeding intensity
75	75	80	70	70	100 100 100	0 0 0	1.36	no reproduction in fall
75	75	80	70	50	100 100 100	50 100 100	4.01	intermediate S0 in fall
75	75	80	70	50	50 100 100	50 100 100	3.22	delay in the age at first reproduction
75	75	80	50	50	100 100 100	50 100 100	2.50	intermediate S0 in summer and fall
75	75	80	30	30	100 100 100	50 100 100	0.95	low S0 in summer and fall
75	75	80	50	50	100 100 100	0 0 0	0.81	intermediate S0 and no reproduction in fall
75	75	70	70	70	100 100 100	50 100 100	2.28	intermediate winter survival
75	75	60	70	70	100 100 100	50 100 100	0.90	low winter survival
65	65	80	60	60	100 100 100	50 100 100	2.10	intermediate survival in summer and fall
55	55	80	50	50	100 100 100	50 100 100	0.75	low survival in summer and fall
55	55	80	80	80	100 100 100	50 100 100	2.18	low adult survival and high S0
60	60	70	40	40	100 100 100	50 100 100	0.29	very low S0
75	75	80	70	70	70 70 70	30 60 60	2.17	low breeding proportions
75	75	80	70	70	0 50 100	0 0 100	1.74	delayed age at first reproduction

summer or winter survival. A difference in real survival of 10% in monthly winter survival rate would not be large enough to be detected. The estimated difference indicates lower survival in high-density years, but the evidence is very weak. This means that demographically large differences (large being defined on the basis of consequences for population dynamics: see below) are "not" inconsistent with the data. We need larger sample sizes to narrow down the possible demographic mechanisms.

Demographic analysis: seasonal matrix models

A population dynamics model

The demography of small mammals is first of all influenced by seasonality (e.g. Kalela 1957; Schaffer and Tamarin 1973; Krebs and Myers 1974; Ota 1984): reproductive rates vary with time of the year (both the percentage of breeding females for a given age and the maturation rate), but survival rates may also vary: there is, for example, some evidence that winter survival rates are higher than summer survival rates in the bank vole (*Clethrionomys glareolus*) in Central Europe, Fennoscandia and the European Alps (Gliwicz 1983; Steen 1994; Yoccoz and Mesnager 1998; A.-C. Julliard, H. Henttonen et al. unpublished results) as well as in the gray-sided vole (Dewa 1975). It is therefore necessary in discrete time models to consider time-steps shorter than one year, for example one month. A time-step of one month fits approximately the gestation length of voles (three weeks), and the interval between trapping periods. The length of the breeding season (defined as the period when 50% or more individuals matured) was approximately 6 months in the studied population (from mid-April to mid-October; Nakata 1989). The breeding season was shorter in high density years, by one to two months.

A convenient way of describing and analyzing demography and population dynamics is based on matrix models (see Caswell 1989a for a review). In such models, demographic parameters during a given time step vary according to age (Leslie 1945; see Fig. 2) or to size/stage (Lefkovich 1965; see Sauer and Slade 1986 for an example of size-structured models for voles). Leslie matrix models are furthermore based usually only on the female component of the population (see Charlesworth 1994 for modeling males and females).

Microtines may start breeding (giving birth) at the age of one month old (e.g. Keller 1985; Yoccoz et al. 1993b), and reproductive and survival rates may be assumed to stabilize after 4 months of age. There is hardly any reliable empirical estimation of senescence rate in any wild population of small mammals (Boonstra 1994; Gaillard et

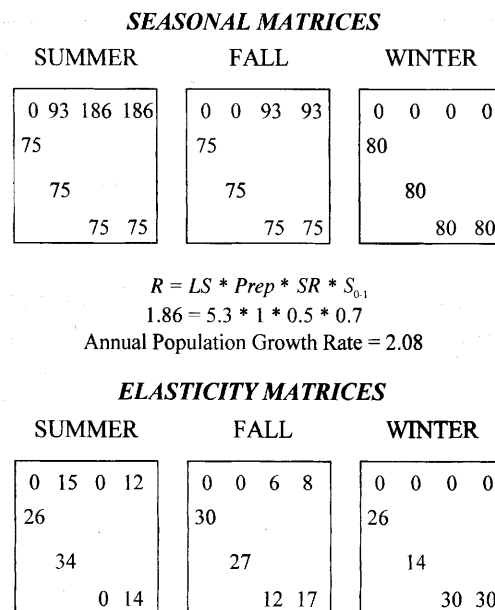


Fig. 2. Seasonal matrices ($\times 100$) used to model population dynamics of the gray-sided vole. We used a litter size (LS) of 5.3, as estimated from embryo counts (Nakata 1989). Percentage of breeding females ($Prep$) was assumed to be age- and season-dependent, with all females more than three month old reproducing during the summer, and only 50% reproducing in the fall. The values of sex ratio (SR) and survival of newborn (S_{0-1}) were taken as 0.5. We assumed the summer to last four months, the fall two months and the winter six months. The annual population growth rate is given by the dominant eigenvalue of annual matrix. Elasticity matrices ($\times 100$) are those associated respectively with the middle of the summer, the beginning of the fall, and the beginning of the winter (see text). The elasticities of each matrix sum to one.

al. 1994; Slade 1995). Each monthly matrix may then reasonably be assumed to have the following form:

$$B = \begin{bmatrix} R_1 & R_2 & R_3 & R_{4+} \\ S_{1-2} & 0 & 0 & 0 \\ 0 & S_{2-3} & 0 & 0 \\ 0 & 0 & S_{3-4} & S_{4+} \end{bmatrix}$$

where $R_i = (\text{Breeding Female Percent}) * (\text{Litter Size at birth}) * (\text{Sex Ratio at birth}) * (\text{1st Month Survival})$, for a vole aged i months ($i \geq 1$). For gray-sided voles, we can assume that females give birth for the first time when two months-old (i.e. $R_1 = 0$). Furthermore, sex-ratio is set to 0.5. (Nakata (1989) showed that the sex ratio in the population varied significantly between years and age-classes, but no data are available for sex ratio at birth; Lambin (1994) showed that sex ratio at birth could vary with density and season - more females than males being produced at low densities in the spring, but the generality of such a

phenomenon has not been evaluated.) Litter size is also assumed to be constant, this parameter being usually the least variable among reproductive rates in a given population (see Nakata 1984a and above). Survival rate during the first month of life is unknown; this value must therefore be assumed on the basis of other studies and on the numbers of young per lactating females produced. Survival rates before breeding (i.e. before an age of two months) are confounded with dispersal in nearly all empirical studies (assuming most dispersal occurs before or around the first breeding attempt; see Saitoh 1995; Lambin 1997), and the small size of trapping grids makes the distinction between apparent survival (i.e. survival - dispersal) and real survival difficult to make in practice.

To account for the variable length of the breeding season, we used three Leslie matrices: one for the winter when there is no reproduction, B_W , one for the spring-summer, B_S , when most individuals reproduce and/or mature, and one for the late summer-early autumn, B_F , with possibly no or low intensity of reproduction in high-density years. We assume the winter lasts six months, the summer four months and the fall two months. Yearly dynamics may be given by the Leslie matrix $A_{F \rightarrow F}$ (assuming we count the population right before the winter as done in the time-series data discussed by Stenseth et al. 1996a and Saitoh et al. 1998):

$$A_{F \rightarrow F} = B_F^2 * B_S^4 * B_W^6.$$

The different matrices and resulting population growth rate are given in Fig. 2. Note that the annual growth rate means that the population would double each year. In fact, the observed growth rates (see Fig. 1) varied between approximately 0.2 and 5: this growth rate is therefore well within the actual range. The next step is to understand what kinds of changes in demographic rates may account for the observed variability of the population growth rate.

Sensitivity and elasticity

Assessing the importance of any given parameter in A may be done on the basis of the change in the population growth rate as a consequence of a change in this parameter. Sensitivity (s_{ij}) is defined with respect to absolute change, whereas elasticity (e_{ij} , or relative sensitivity) is defined with respect to relative change. That is, for a given parameter a_{ij} :

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}},$$

$$e_{ij} = \frac{\partial \text{Log}(\lambda)}{\partial \text{Log}(a_{ij})} = s_{ij} \cdot \frac{a_{ij}}{\lambda}.$$

Sensitivities and elasticities may be calculated directly on the basis of the left and right eigenvectors of the Leslie matrix (Caswell 1978; de Kroon et al. 1986; the population growth rate is given by the dominant eigenvalue). They have been rather extensively used for analyzing the demography of annually reproducing species, in particular plants, birds and large mammals (see Caswell 1989a; Gaillard et al. 1998 for examples). In particular, demographic analysis is used to assess whether a demographic parameter - for example, adult survival rate - has a disproportionate impact on population growth rate. Research or management should then focus on such a parameter (see Gaillard et al. 1998 for a discussion).

However, for multivoltine species such as voles, successive generations may experience different environmental conditions, particularly with respect to seasonal variation. We should then use the approach proposed by Caswell and Trevisan (1994) in order to evaluate the sensitivities (absolute and relative) for the demographic parameters of each B -matrix. The annual matrix A is indeed not directly tractable: each of its components is the product of parameters in the different seasonal B -matrices, and has no straightforward biological interpretation. Only the matrices B correspond to estimates of demographic rates (survival and reproductive rates) and therefore ecological mechanisms. The elasticities for each seasonal matrix B are given in Fig. 2. Note that even within a season, the elements of the different matrices B will not have the same elasticities.

With only a few parameters estimated from field data, many combinations of other demographic parameters could be used to "explain" the observed population dynamics, and in particular the large differences observed between years with increase and years with stable population sizes during the breeding season. The winter decrease is, however, only related to survival in this subspecies since winter reproduction is negligible, and one startling aspect is the absence of increase in three summers out of the five summers of this study (Fig. 1b). The fall-to-fall dynamics are therefore clearly bimodal, with either a large decrease or a large increase, while the spring densities are rather similar, even if the low numbers do not warrant any firm conclusion in the latter case.

This apparent alternation between two regimes - increase and decrease (Framstad et al. 1997) - would imply that any approach based on asymptotic arguments (and constant parameters) may fail as a description of the observed population dynamics. However, we argue that 1) the approach is still relevant for answering questions about possible dynamical consequences of a change in a demographic parameter; and 2) the apparent delay in population rate of increase (e.g. low rate of increase after a high density year) necessitates that we incorporate a delayed-density effect. However, this would add to the complexity

of the present model which is already too detailed "relative" to the available field data. We will below emphasize the data requirements for further analysis.

One further difficulty in evaluating the impact of different demographic factors results from their (probably) different sensitivities to any given ecological factor. While demographic sensitivities and elasticities measure the consequence of changing one single demographic parameter by an absolute or relative amount, any factor (e.g. kinship, phase or density) will affect different demographic parameters to different degrees (Wisdom and Mills 1997; Gaillard et al. 1998). It is, for example, quite reasonable that lower kinship may influence negatively adult female survival and survival of newborns (Kawata 1990; Lambin and Krebs 1993; Lambin and Yoccoz 1998; see Ishibashi et al. 1997, 1998), but may probably not affect survival of subadults, or proportion of breeding females. One way of expressing this is to consider that any change $\Delta\lambda$ in the population growth rate due to a change in a given ecological factor can be written as (Levin et al. 1987; Caswell 1989b; Levin and Huggett 1990; Brault and Caswell 1993):

$$\Delta\lambda = \sum \Delta a_{ij} \cdot \frac{\partial\lambda}{\partial a_{ij}},$$

where the sensitivities $\frac{\partial\lambda}{\partial a_{ij}}$ are evaluated for the average Leslie matrix (i.e. average values are used for each demographic parameter). In the case of seasonal Leslie matrices, this expression becomes more complicated since a given change in the environment may affect different parameters in a given matrix, but also different matrices. The population growth rates given in Table 3 results from systematic changes in one parameter in all matrices for a given season. It is obvious that winter survival rate will have a greater importance when the winter is longer: a 5% decrease in monthly winter survival from 0.80 to 0.75 results in a population halved if the winter is nine months long (the overall survival dropping from 13.4% to 7.5%), and only reduced by one quarter if the winter is only 4 months long (41% vs. 32%). Moreover, as the age structure changes throughout the year (in the case of seasonal matrices, there is an asymptotic age structure for each time period in the year, and this structure changes within a year), the "same" matrix will translate to different sensitivities depending on the time of the year. For example, for the case corresponding to the first line in Table 3, the sensitivities (or equivalently here, the elasticities) for the different age-specific winter survival rates will exactly reflect the age structure of the population at the end of the breeding season, which is for the four age-classes: 0.26, 0.14, 0.30, 0.30, respectively (Fig. 2). Similarly, two months after reproduction started, there are no three month-old females, and the corresponding sensitivities and elasticities are zero (Fig. 2). The fact that a given demographic parameter such as, for example, adult sur-

vival has a time-varying elasticity complicates the demographic analysis.

Generation time (defined as the mean age of females when they give birth; Leslie 1966) and elasticity for reproductive parameters (which include the survival of the newborn) are inversely related in annually reproducing species: species with a generation time larger than two years are more sensitive to a relative change in adult survival rates than to a relative change in reproductive rates (Lebreton and Clobert 1991). We would therefore conclude that reproductive parameters are much more important than adult survival rates in microtines, because of their short generation time, usually of the order of a few months. However, this is not the case because of the change in time scale involved in microtines, months instead of years. With a monthly survival rates of 0.75 or 0.80, microtines have the same kind of demography as much larger mammals (such as wolves or white-tailed deer; see Gaillard et al. 1989) but on a different scale. Consequently, adult survival rates may be as important as reproductive parameters for determining the increase of population size during the summer (see elasticity matrices given in Fig. 2). An additional factor may be the relationship between adult female survival rate and survival of newborn: it seems likely that death of the mother will imply death of the litter, and therefore the two survival rates may better be considered as related parameters.

In Table 3, we provide annual population growth rates for demographic rates consistent with the values estimated in the field study. Taking the upper limit for all parameters (including a six months long reproductive season) results in a population increasing by a factor of five from one year to another. As proportion of breeding females, sex ratio, litter size and survival from birth to weaning (S_0) appear as a product in the definition of the R_i terms, these parameters will have the same elasticity. However, it is likely that, for example, a 20% relative change in S_0 is more likely to occur than the same relative change in litter size or sex ratio (Keller 1985; Innes and Millar 1994). Changes in S_0 or in proportion of breeding females (due either to a change in age at first reproduction or a change in pregnancy rates) are therefore expected to play a larger role in population dynamics than changes in litter size.

The different combinations of demographic rates shown in Table 3 could be taken as those observed in low and high density years, and the fact that the population growth rate may then vary between 0.29 and 5.07 is consistent with the population dynamics (Nakata 1989; see Fig. 1b). Moreover, different combinations of demographic rates may result in similar annual population growth rates, and the available data do not allow to distinguish between these scenarios. It seems likely that a large increase or decrease in population size would require changes in more

than one parameter.

Linking up with the time series modeling

One main focus of time series analysis of population abundances is the existence and strength of direct and delayed density-dependence (Stenseth et al. 1996b; Saitoh et al. 1997). Saitoh et al. (1998) emphasize how the patterns in population dynamics are related to patterns in density-dependencies: delayed density-dependence for multiannual fluctuations in the north and east of Hokkaido direct for seasonal fluctuations in the south and west (see also Bjørnstad et al. 1996). The apparently cyclic pattern exhibited by the population studied here implies that some delayed density-dependent mechanism(s) affects demographic parameters. The above demographic models, however, did not include density-dependence: the small sample size of the field study precluded any reliable estimation of the shape and strength of density-dependent effects on demographic rates. Density-independent models cannot be used to address specifically the mechanisms behind the density-dependent structure exhibited by the analysis of time series. However, they may provide useful guidelines as to how large the density-dependent changes in demographic parameters must be to reproduce the observed changes in densities. Finally, given more extensive data to estimate density-dependent relationships, they can be used to understand the resulting population dynamics (e.g. Leirs et al. 1997).

There are at the present stage two obvious shortcomings to any detailed demographic modelling: 1) the relatively large number of unknown parameters (e.g. survival during the first month of life, dispersal vs. mortality) and 2) the possibly very large range of uncertainty/variability observed in some parameters (e.g. survival rates in the spring). It is clear from Table 3 that we can build very different scenarios which could account for the large observed increase or decrease. A necessary first step to identifying demographic processes most important for determining the patterns in population dynamics will then be to narrow down most of the parameter values so as to restrict – if possible – the effect of density-related mechanisms to only a few parameters. We may, however, think that for the population of gray-sided voles studied here, the absence of increase in low-density years could be a consequence of low survival of newborn and possibly adults – given that the statistical similarity in summer adult survival is probably due to the small sample sizes. As to the winter period, the lack of evidence for a difference between years in winter survival rates coupled with large differences in population declines may reflect both problems with the low sample sizes (particularly in years with low densities), and increased movements (i.e. lower apparent survival) in low density years.

New models and future field studies: some recommendations

New statistical approaches for capture-recapture studies

Recent years have witnessed an impressive development of capture-recapture models, simultaneously with a development of population dynamics models including age- or stage-structure (e.g. Lebreton 1996; Nichols 1996; Pradel 1996; Tuljapurkar and Caswell 1996). Most of these developments are relevant for studies of microtines, but we doubt that existing data-sets can be used for implementing new capture-recapture models in a satisfactory manner. We will therefore provide some guidelines for future studies.

The study of mechanisms for phase- and density-dependence (see Framstad et al. 1997) is clearly a challenging problem: this requires that we can properly estimate density, or at least estimates of relative changes of density (Skalski and Robson 1992); most importantly, we need to be able to estimate densities for different functional categories if we aim at understanding the mechanisms. The best available approach to estimate densities and at the same time obtain estimates on demographic parameters is based on closed population models (Otis et al. 1978; Pollock et al. 1990). This approach necessitates at least five capture sessions to give statistically reliable estimates. In a dense population of sibling voles (*Microtus epiroticus*) at Svalbard, Yoccoz et al. (1993b) found that up to seven or eight capture sessions were required. This is because some models (e.g. the model including only heterogeneity of capture, M_h) are biased for small numbers of capture sessions (Julliard personal communication; see also Burnham and Overton 1978). Populations of gray-sided voles with high recapture rates may be reliably estimated using less than five trapping sessions (Nakata 1984b), but this may be dependent on the habitat sampled as well as the density (high density populations are more difficult to study, in part because of trap saturation).

Studies using a robust design ("primary" sessions separated by long periods such as one month, and "secondary" sessions separated by less than a day; Pollock 1982) allow the estimation of temporary emigration (individuals which leave the study area for some period; Kendall et al. 1997), as well as a more thorough analysis of capture heterogeneity (e.g. how capture and recapture rates vary with sexes, age or body weight: Pollock et al. 1984; Huggins 1989; Julliard personal communication). This may in particular be useful to investigate edge effects (individuals which do not use the trapping grid continuously; Tanaka 1980), or to reduce heterogeneity by estimating population size for homogeneous categories.

An alternative approach to estimating density is to use open population models to directly estimate population growth rates (Pradel 1996). Such an approach may be more robust than using estimates of density. Capture heterogeneity does not result in large biases in survival estimates if heterogeneity is not too severe (e.g. Carothers 1973), and this may also be true of the estimation of population growth rates (Pradel 1996). The next challenge for statisticians is to incorporate the type of time series models structure used for analyzing data on population abundances (e.g. autoregressive models) in open population models used for estimating survival rates (Burnham 1998; see also Lee and Lin 1996).

One well-known deficiency of studies of open populations based on capture-mark-recapture, is that death and dispersal are not estimated separately (Lebreton et al. 1992). This is also true for recruitment *in situ* and immigration, but the robust design can be used to separate these two components (Nichols and Pollock 1990). Another approach to estimating recruitment based on reversing capture histories may be used to estimate the proportion of the breeding population which has never bred before in the population (Pradel 1996). If we know the age of each individual, this information could be translated into the proportion of individuals which starts breeding at different ages in the population (Pradel et al. 1997a). This would clearly be most useful to investigate how age at first reproduction (or, more importantly, its distribution in a given cohort) changes with density and season.

The study of dispersal or transfer rates between populations (the emphasis depending on the scale of heterogeneity in the habitat; see Ims and Yoccoz 1997 for a review) will continue to be most difficult. Apart from experimental studies where we may assume the exchange rates to be similar or a function of few factors (such as in enclosed populations inhabiting vegetation fragments of similar sizes and compositions; e.g. Ims et al. 1993), models involving survival as well as exchange rates between populations include too many parameters to be estimated. Part of the problem lies in the necessity for any realistic biological approach to include memory (Brownie et al. 1993): in most microtines, dispersal occurs once and is associated with maturation, while most models are Markovian (i.e. a given individual does not remember its history, implying that it can disperse again and again, irrespective of previous dispersal). Moreover, any history such as captured as subadult in one habitat patch, not captured, captured as adult in another habitat patch, could be understood in many different ways (see Fig. 3), and the complexity of capture histories becomes quickly intractable. Finally, dispersal events are usually rare and small probabilities result in large coefficients of variation. We do not see how mechanisms could be evaluated without very large

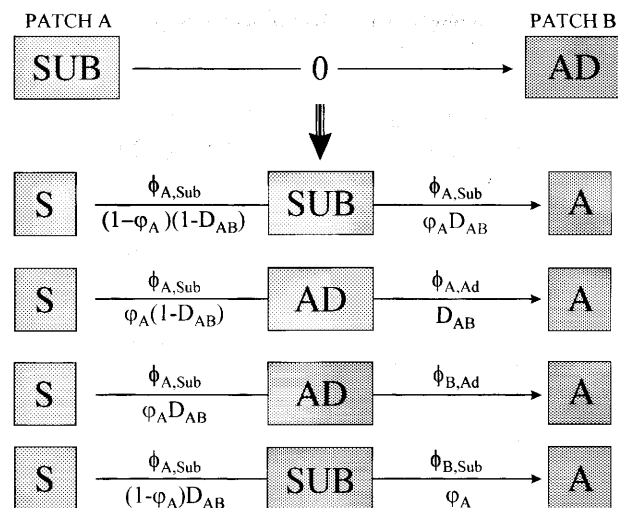


Fig. 3. An illustration of the increased complexity for models involving survival (ϕ), dispersal (D) and maturation (φ). Given two patches, and a capture history with the individual not being caught in the second session, there are at least 4 different paths involving different parameters. This is nevertheless a simplification as we assumed that event such as maturation or dispersal are taking place at the end of each time interval. Assuming they take place at the beginning would result in different capture history probabilities.

amounts of data or simplified experimental designs. However, there is a strong need to understand population dynamics processes occurring at scales larger than most trapping grids (ca. 1-ha), but smaller than the large-scale (larger than 10 km) patterns studied, for example, by Bjørnstad et al. (1998a).

Sample size considerations will also be particularly acute if we want to understand why populations sometimes do not increase (this study or others) for one year or more. The characteristics of such a "phase" is that densities are low, and therefore sample sizes too small for any statistically meaningful comparison. For example, having two groups of 50 individuals marked in the fall, a difference in monthly survival equal to 10% (70 and 80% respectively or 80 and 90%) will be difficult to detect. Our estimate of monthly winter survival was 0.76 with a 95% C.I. of (0.62–0.85) for the low-density years. Clearly we will need to increase dramatically the size of our studies if we aim at analyzing demographic changes occurring when the density is low.

A suggested study design for Clethrionomys rufocanus of Hokkaido

The present analysis does not lead us to any firm conclusions regarding demographic processes which may explain the alternation between low and high density years

(defined on the basis of fall densities; Stenseth et al. 1996a; Saitoh et al. 1997). However, it indicates that a plausible hypothesis would be 1) lower survival during winters following high fall densities, and 2) lower survival of reproducing adults during spring, and possibly summer, during low-density years. The demographic model showed that a difference in monthly winter survival rate of 10% can lead to large difference in dynamics, while the same is only true for larger differences in spring pre-weaning survival rates. Distinguishing between these different processes, and their relative importance and associated biological mechanisms, is an empirical challenge. In particular, we may ask whether longer winters result in larger decreases just because of the direct effect of the winter length, without differential density-dependent effects, or whether longer winters result also in stronger density-dependent effects, for example by reducing to a larger extent the monthly winter and spring survival rates (see also Stenseth et al. 1998).

To distinguish between these hypotheses will require a study design with large populations (in order to obtain large sample sizes in the low phase), properly replicated at the population level (i.e. it is necessary to have at least two or three populations studied in each zone, as defined by the dynamical patterns). Adequate estimation of densities implies that the robust design is used, with probably 7 or 10 secondary trapping sessions at high densities. Studying large populations will result in minimizing edge effects, and also provide adequate sample sizes for estimating the proportion of transients and immigrants (Nichols and Pollock 1990; Pradel et al. 1997b). For the latter, a proper choice for the interval between trapping sessions is important (see Yoccoz et al. 1993a), and this interval depends on the maturation rates of the voles, and may therefore be adjusted according to population dynamics. A reciprocal transplant experiment between populations from different regions should be useful for investigating the long-term effects of density (e.g. through vegetation) on the survival of voles. Finally, controlling as much as possible for the effects of extraneous variables (e.g. vegetation types, local climate) is recommended, and a partial solution is to use populations where the habitat is artificially homogenized. Enclosed populations may be useful for controlling the impact of emigration and immigration, but may result in artefactual dynamics (Krebs et al. 1969). All these requirements make the study large (and expensive!). However, understanding the demographic processes behind the observed dynamics requires such a large study.

To identify the actual mechanisms behind the demographic processes may most efficiently be done using experimental studies (e.g. Krebs 1988). The basic biology of the gray-sided vole is sufficiently known to appropriately design such replicated, manipulative studies (e.g. Ims 1988). The importance of kinship structure for popula-

tion dynamics (Ishibashi et al. 1998) could for example be evaluated using a similar approach as in Lambin and Krebs (1993). Furthermore, such an experiment could be done using animals coming from the different phases of the cycles and/or different areas, and at different initial densities, to investigate the relative importance of kinship, phase and density for the population dynamics in a factorial design. A combination of extensive descriptive studies narrowing the demographic scenarios in field populations and of experimental studies evaluating the relative importance of specific ecological mechanisms for these scenarios is likely to be the most efficient approach in the future.

Conclusion

Until fairly recently, empirical studies of demographic processes were limited by the small number of statistical and demographic models available for assessing the importance of various ecological mechanisms for population dynamics. Recent methodological developments have led to a somewhat inverse situation: models exist but they require large amounts of data to provide reliable estimates. At the same time, empirical studies of the ecological mechanisms have progressed significantly in recent years, at least with respect to the finer social and spatial organization (see Kawata 1987, 1988; Ishibashi et al. 1997, 1998). The large scale temporal and spatial population dynamics patterns have been well described (Saitoh 1987; Bjørnstad et al. 1996, 1998a, b; Stenseth et al. 1996a, 1998; Saitoh et al. 1997, 1998). What individuals do (e.g. social and spatial organization) and consequences of individual behavior in terms of population dynamics is still a largely unexplored field, however (Sutherland 1996). A fruitful approach for empirical field studies would therefore be to address precise hypotheses derived from population dynamics studies done at large scales, and to implement the corresponding appropriate observational or, preferably, experimental designs at smaller scales (Krebs 1988). Our empirical knowledge on the biology of the gray-sided vole, added to the statistical and mathematical tools presented here, should guarantee that we may understand the biological mechanisms behind the observed changes in population dynamics and demography of the gray-sided vole.

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