Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence

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Using long-term data on two forest rodent species [the bank vole *Clethrionomys glareolus* (Schreber, 1780) and the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834)] from the Białowieża Primeval Forest (E Poland), we decompose the annual density-dependent and density-independent structures into their seasonal components. For this purpose we adopt a state-space modelling approach explicitly incorporating sampling stochasticity. As density-independent factors we use the North Atlantic Oscillation (NAO) – a proxy variable for the overall climatic condition – and data on annual seed production. We find a weak effect of the NAO in the annual models for both species as well as during the winter in the seasonal model for *C. glareolus*. The effect of the NAO disappears, however, when seed-crops are incorporated into the models (for both the annual and the seasonal – suggesting that NAO primarily affects seed production). Seed production enters the models with a positive effect during the winter only, suggesting that the among-year variation in rodent density is primarily accounted for by differences in seed-production, particularly oak seeds. For *A. flavicollis*, a slightly positive effect of hornbeam also appears in the summer dynamics. The obtained results are discussed on the basis of earlier studies on the same populations, on the same species studied elsewhere as well as on the basis of general ecological insight.

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Introduction

Ecologists studying temporal variation in the size of animal populations (ie population dynamics) have entertained a long-lasting discussion regarding the importance of intrinsic, density-dependent factors (eg Nicholson 1933) versus extrinsic, density-independent factors (eg Andrewartha and Birch 1954); for a

recent review, see Turchin (1995). Although insects initially provided an important focus for this debate (eg Uvarov 1931), small rodents have later played a more central role (Turchin 1995, Leirs *et al*. 1997, Lima *et al*. 1999, 2001a, b, Berryman 1999, Stenseth 1999, Berryman and Turchin 2001), not the least due to their extensive multiannual and often cyclic variation in population size (Batzli 1992, Krebs 1993, Stenseth 1999). Much of this work on the influence of intrinsic and extrinsic factors in the regulation of the dynamics of small rodents links directly back to the pioneers in the field (Elton 1924, 1942, 1956, Kalela 1957, 1962, Chitty 1960, 1967, Andrzejewski 1963, 1975, Andrzejewski and Olszewski 1963, Petrusewicz 1963, 1966, 1983a, b, Buchalczyk and Pucek 1968, Pucek *et al*. 1968, Pucek and Olszewski 1971, Pucek and Lowe 1975, Krebs 1978, 1996; see also Bujalska and Hansson 2000). Based on these studies on rodent populations (as well as on the basis of studies on other groups of organisms; Turchin 1995), we have learned that both intrinsic and extrinsic factors play an important role in the determination of their dynamics, as well as their interactions (eg Leirs *et al*. 1997).

Although less emphasized in the more general literature on population dynamics, essentially all populations live in some sort of seasonally varying environment (Boyce 1979, Boyce *et al*. 1999): the importance of both the density-dependent and the density-independent factors may vary considerably between seasons. However, very few empirically based seasonal models for rodents are available (but see Hansen *et al*. 1999). Most of the recent work on small rodent population dynamics has, for example, focused on among-year variation (Turchin 1993, 1999, Bjørnstad *et al*. 1995, Falck *et al*. 1995a, b, Stenseth *et al*. 1996a, b, 1998a, b, Saitoh *et al*. 1997, 1998, 1999, Stenseth 1999). Even though both the within-year (ie seasonal) and the among-year variation in demography are important components in shaping the population dynamics patterns observed on a multiannual scale, these two sources of variation have rarely been studied simultaneously. Decomposing the among-year variation in density into its seasonal components (Stenseth *et al*. 1998b, Hansen *et al*. 1999) is important since different ecological mechanisms (such as social processes, food or predation) are likely to be acting differently on animal populations in different seasons (Gliwicz 1983, Boutin 1990, Krebs 1994, Jędrzejewski *et al*. 1996, Jędrzejewska and Jędrzejewski 1998, Newton 1998). Populations of small rodents are indeed likely to be good model systems for studying the seasonal decomposition of the between-year annual variation in the population dynamics. This is so because they invest heavily in reproduction by having relatively large litters and sometimes early age at first reproduction (Bujalska 1971, Yoccoz *et al*. 1993), and because they typically have different generations within a year exhibiting markedly different reproductive strategies (Adamczewska 1961, Schwarz *et al*. 1964, Gliwicz *et al*. 1968, Prévot-Julliard *et al*. 1999, Yoccoz and Stenseth 2000). One major objective of this study is, therefore, to decompose the annual variation in density (and the model describing this variation) into its seasonal components.

The extensive annual variations in population size of seed-eating rodents are profoundly influenced by seed-crop production (Jensen 1982, Pucek *et al*. 1993, Ostfeld *et al*. 1996, McCracken *et al*. 1999, Hansson *et al*. 2000). This phenomenon was documented for a variety of European forest rodents (the wood mice *Apodemus sylvaticus* – Watts 1969, Gurnell 1993; yellow-necked mice *Apodemus flavicollis* – Pucek *et al*. 1993) as well as for several American species (*Peromyscus leucopus* and *P. maniculatus* – Gashwiler 1979, Ostfeld *et al*. 1996, Wolff 1996a, b). Densities are typically at their peak one year after a heavy seed crop, usually in the next autumn, but they decline rapidly over the winter. Throughout the next year they most often remain much below the long-term average and return to 'normal levels' as late as on the third year after a heavy seed crop (Jensen 1982, Pucek *et al*. 1993, Hansson *et al*. 2000). As seeds of various tree species (oak and beech) are known to provide excellent food for the rodents (see Hansson 1998), it is likely that the rodents' survival is improved for some time following a mast crop. It was also shown experimentally by the effect of supplementary food (cf Watts 1970, Andrzejewski 1975, Bujalska 1975, Löfgren *et al*. 1996). Similar effects of mast crop on vertebrate demography have been demonstrated in various seed-eating bird species, such as tits in Europe (Van Balen and Hage 1989, Verhulst 1992, Newton 1998), jays and woodpeckers in America (Smith 1986), and large mammals such as wild boar in Europe (Okarma *et al*. 1995, Jędrzejewska *et al*. 1997). Again, due to their extensive within- and among-year variation in density, rodents are ideal study systems for this purpose.

We know, however, very little about how the variability in extrinsic factors (such as food availability and climatic factors determining the weather conditions) determines the within-year and among-year dynamics of seed-eating rodents. Typically, weather is considered a density-independent external factor (Andrewartha and Birch 1954, Leirs *et al*. 1997). Recently, there has been much interest in how large-scale climatic variability (related, eg, to the North Atlantic Oscillation, NAO; Hurrell 1995) affects the dynamics of populations – particularly of large herbivores (Post *et al*. 1997, Mysterud *et al*. 2001) and carnivores (Stenseth *et al*. 1999, Post *et al*. 1999). For southern-hemisphere rodents, such large-scale climatic processes have been incorporated into population models (eg Lima *et al*. 1999, 2001a, b). No study on northern hemisphere has yet related variation in the NAO to population ecology of rodents. Thus, the second major objective of this study is to evaluate the importance of such large-scale climatic processes in shaping the dynamics of forest rodents. This we do by asking to what extent large-scale climatic factors have a direct or indirect (eg through seed-production and/or snow conditions) effect on the rodent dynamics. This objective of our study is then linked directly to the decomposition of the annual dynamics into its seasonal components described above. In this paper, we address the dichotomy of density dependence and density independence empirically on the basis of general phenomenological population dynamics models.

As our empirical basis, we use the long-term data on two rodent species from the Białowieża Primeval Forest (eastern Poland) – bank voles *Clethrionomys glareolus* (Schreber, 1780) and yellow-necked mice *Apodemus flavicollis* (Melchior, 1834) (Aulak 1970, Pucek *et al*. 1993, Jędrzejewska and Jędrzejewski 1998, Hansson *et al*. 2000; for a general discussion of the importance of long-term data, see Stenseth 1995). These rodent populations serve as ideal bases for studying the density--dependent and density-independent structure for the two main seasons, the summer and the winter. For this purpose we use a state-space modelling approach (eg Fahrmeir and Tutz 1994); that is, our data are linked to the ecological process model through an observation model describing sampling error.

Not only do seasonal long-term population data exist for this system, but also good data on the environmental factors – both climate and food – are available (Pucek *et al*. 1993, Jędrzejewska and Jędrzejewski 1998). Analysing such data within a general phenomenological model-structure may provide a basis for obtaining a better understanding of the underlying population processes.

We furthermore take this opportunity to implicitly review much of the recent literature on small rodent population dynamics in the light of our new findings – not the least by trying to integrate the central and eastern European literature on small rodents with the corresponding Fennoscandian and North American literature and by so doing extending earlier reviews (Petrusewicz 1983a, Flowerdew *et al*. 1985, Stenseth 1985c, Stenseth and Saitoh 1998a, Bujalska and Hansson 2000, see also Grüm and Bujalska 2000).

The Białowieża Primeval Forest

The Białowieża Primeval Forest (about 1500 km²) on the Polish-Belarusian border is one of the best preserved deciduous and mixed forest of European lowland (Fig. 1). This forest is protected to different levels on the two sides of the state border, but its central part – Białowieża National Park (BNP) located in Poland – has been strictly protected during the last 80 years. The oldest part of BNP (of 47.5 km^2) was recently (1996) enlarged to 105 km^2 (Fig. 1). The strict reserve of BNP has preserved the pristine mature forests unaltered by forest management, tourism, transportation, timber exploitation and hunting, which makes it a model and reference system for ecological studies in temperate Europe (Falińska 1973, 1991, Faliński 1986, Jędrzejewska and Jędrzejewski 1998). The long-term and highly standardized monitoring of the small mammal community has been conducted for several decades in this forest (Aulak 1970, 1973, Pucek *et al*. 1993, Jędrzejewski and Jędrzejewska 1996).

The average age of tree stands in the strict reserve of BNP is 130 years (the maximum over 400 years) and 81% of the forested area is covered with tree stands over 80 years old, that is mature, reproducing stands. Among those, the stands dominated by oak *Quercus robur* are most widely distributed (19.4% of the area), followed by hornbeam *Carpinus betulus* (17.2%), spruce *Picea abies* (13.7%), and

Fig. 1. Map of Białowieża Primeval Forest with the location of study plot for long-term monitoring of small mammals; inserted map in the lower right corner shows the location within Europe on the border between Poland and Belarus.

pine *Pinus silvestris* (10.9%). Detailed information on the vegetation of BNP is provided by Faliński (1986).

The ecological system – a synoptic account of the rodents and their environmental interactions

The yellow-necked mouse is predominantly a seed eater (Drożdż 1966). The bank vole is a polyphagous animal that eats seeds, fruits of trees and bushes and green plants (see Gębczyńska 1983 for review). Both species occasionally eat invertebrates in order to substitute for plant proteins: *C. glareolus* – 7–23% and *A. flavicollis* – 15–37% of the stomach contents, depending on the season (cf Hansson 1971, 1985, Zemanek 1972, and reviews by Obrtel 1974, Pucek 1984).

A clear pattern in the seasonal density changes is observed: the numbers are lowest in spring and grow till autumn (sometimes till summer only) due to reproduction (cf Petrusewicz 1983b, Pucek *et al.* 1993). Although extensive multiannual density variation is observed in Białowieża Forest, no clear cyclic density fluctuations are recorded (Petrusewicz 1983b, Pucek *et al.* 1993, Jędrzejewski and Jędrzejewska 1996, Hansson *et al.* 2000, see also Stenseth 1999).

In *C. glareolus* the breeding season extends from April to the end of September. Females produce 3–4 litters, 3–5 (range 2–8) young each (Pucek 1984). In *A. flavicollis* the breeding season lasts from March to October. Females produce 2–3 litters, 2–8 young each. With the exception of winters following heavy mast years, winter reproduction does not occur (Adamczewska 1961, Pucek 1984, Pucek *et al.* 1993). Outbreaks in number of mice are response to heavy crop of seeds, outbreaks of voles are shaped partly by other factors, unless seed crop is overabundant (Adamczewska 1961, Pucek *et al.* 1993). Usually, outbreaks are followed by one year of very low densities of rodents ('crash' years).

Based on numerous data obtained by parallel trapping on grids, Jędrzejewska and Jędrzejewski (1998) calculated that the typical densities of forest rodents in Białowieża National Park (bank voles and yellow-necked mice combined) were 6–15 ind/ha in spring (12–121 ind/ha in springs following heavy seed crops) and increased to 11–155 ind/ha in autumn (186–315 ind/ha in autumn seasons of outbreak years).

Conceptually then, based on the above summarized biology of the two species, we may write the following model (where N_t is the abundance of rodents in the autumn of year *t*): $N_t = N_{t-1}R$, where R is the specific net annual growth rate; this latter quantity may further be written as $R = R_{winter}R_{summer}$ (for a general discussion see eg Stenseth and Saitoh 1998b), where R_{winter} and R_{summer} are the specific net growth rates during the winter and the summer, respectively. From the above we know that R_{summer} is the result of both reproduction and survival, whereas R_{winter} generally is the result of only survival except for after mast-years, when R_{winter} also has a reproductive component.

The overall purpose of this paper may now be specified as finding the density--dependent and density-independent structure of the overall R-function (ie the annual model) as well as finding the density-dependent and density-independent structures of the seasonal components, R_{winter} and R_{summer}. On the basis of the obtained statistical results (relating to the annual and seasonal density-dependent and density-independent structures), we will then discuss the above-summarized basic biology.

Throughout we treat the yellow-necked mouse and the bank vole as independent of each other. Although there might be some direct and indirect competitive interactions between the two species (Andrzejewski and Olszewski 1963, Wójcik and Wołk 1985), no quantitative effects of the possible competition on population dynamics of either species have been observed (Pucek *et al.* 1993). Thus, we believe that we are justified in considering the two species as independent of each other.

Material and sampling methods

The rodent data

The material used in this paper derives from long-term trappings of terrestrial small mammals being conducted by the Mammal Research Institute, Polish Academy of Sciences, Białowieża under special care of one of us (ZP). During the study period of 1965–2001, two dominating rodent species have been recorded – bank voles and yellow-necked mice (see Fig. 2A and B). Rodents were sampled in the oak-lime-hornbeam forest in the section 371 of the Białowieża National Park (52°43'N, 23°54'E). We used the total number of individuals of each of the two rodent species from 50 metal pitfalls (cylinders or cones) placed in a 5   10 m trapping grid as well as from trapping lines consisting of 50 snap-traps plus a line of 50 wooden box live traps, placed at 10 m intervals (as a parallel extension of the grid). During the period 1965–1970, the trapping area was operated twice a year: in spring (April/May) and in autumn (September/October). Since 1971, three trapping sessions were conducted each year: spring (from 15 April), summer (from 1 July), and autumn (from 15 September). Since our objective in this paper is focused on the winter-summer dichotomy in the density-dependent and density-independent structure, we are only using the spring and autumn rodent data. Although trapping continued for more than 21 days, the numbers of rodents caught during the first 21 days of each seasonal series of removal trappings were used as a standardized measure of the rodent abundance. Sampling methods were described in details in Pucek *et al*. (1993).

Fairly long series of removal trapping conducted 3 times a year may bias the results towards capturing more transient and dispersing individuals, especially in summer and autumn. This possible bias is, however, likely to be small in our case. Furthermore, population dynamics and other para- meters (reproduction rates, proportion of breeding adults in the population) estimated from the removal trapping series were in concordance with the data obtained from other short-term studies on bank voles and yellow-necked mice, conducted in parallel by Capture-Mark-Recapture method (for sources and references to those CMR studies in Białowieża National Park, see Jędrzejewski *et al*. 1995, 1996). In the following, we denote the number of voles and mice caught during the spring and autumn session at a given site in year t be given by $z_{s,t}$ and $z_{f,t}$, respectively.

Seed crop data

As in an earlier paper (Pucek *et al*. 1993), we used two sources of information relating to seed crop (prepared for this study by WJ). The data on hornbeam (1972–1990, collected by the Białowieża Geobotanical Station of Warsaw University and kindly granted to us by Prof J. B. Faliński) were obtained from the BNP on three permanent plots located in the rich deciduous (oak-lime-maple- -hornbeam) forest (see Fig. 2C). Each sample plot was divided into 25 squares, 2   2 m each. Seed crop was estimated on the basis of photographs of forest floor taken in late October and early November, at which time seeds fell to the ground most intensely and are easily visible on the ground. The forest floor was photographed (75 photos, each picturing 0.50 m^2 of the forest floor) at 5-day intervals from 1972 to 1989, and at 10-day intervals in 1990. Detailed description of the sampling plots and sampling technique is provided by Faliński (1977).

Data on oak seed crop in 1975–2000 were provided by the Białowieża Forest Administration. The indices of crops (in kilograms) were the annual purchases (for re-plantation purposes) of acorn from the local people, who gathered them in the exploited part of Białowieża Primeval Forest. We maintain that the amount of acorn purchased relates closely to the seed crop; it cannot, however, be excluded that this assessment is somewhat influenced by current prices, making the oak index less reliable than the others.

In the analyses we used the log$_e$-transformation (after adding a constant of one to account for zeros) of the oak records (Fig. 2C). The Pearson correlation between oak records (ln-transformed) and hornbeam records are 0.61 (for the 15 years they have in common). In 1984, there was a missing value of oak seed crops. In order to obtain as long and continuous series as possible, the missing oak value was interpolated from the hornbeam data (based on a linear regression of oak data on hornbeam data). In the Bayesian analyses (see below), the uncertainty of this value was taken into account by specifying
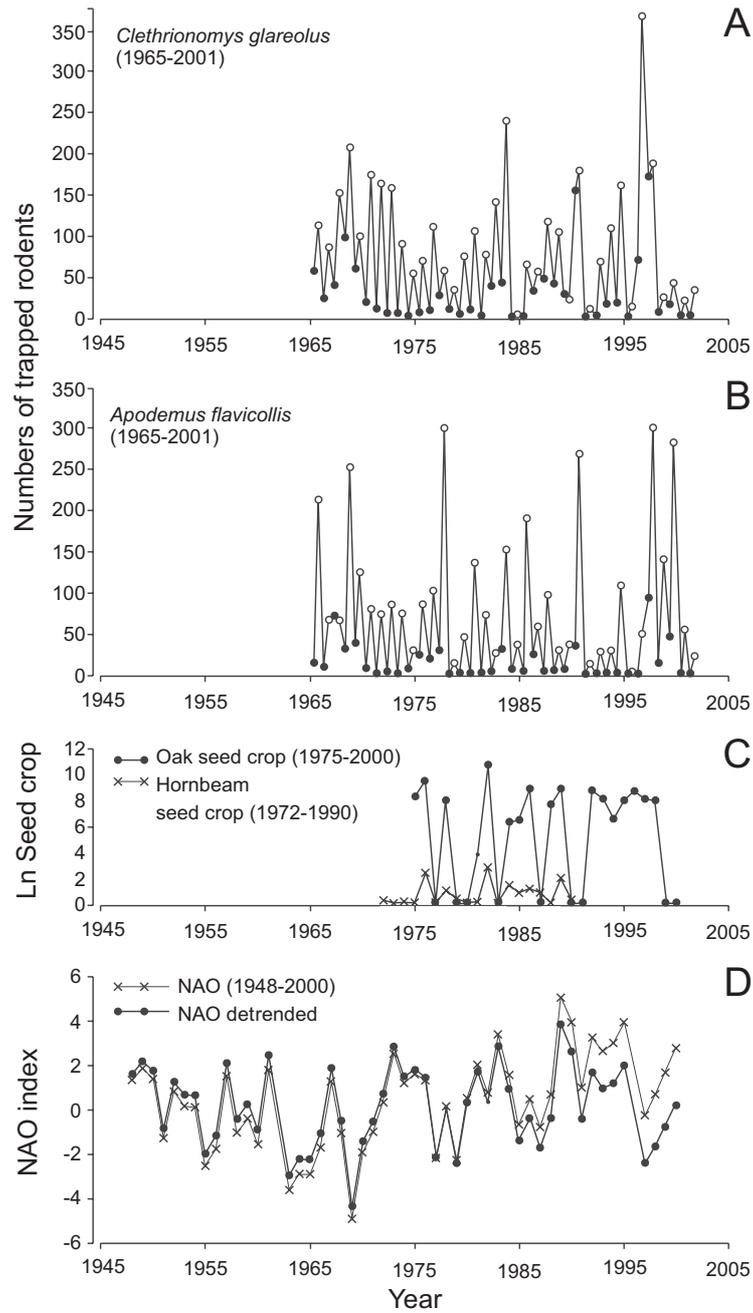
Fig. 2. Indices of bank voles *Clethrionomys glareolus* (A) and yellow-necked mice *Apodemus flavicollis* (B) abundance (filled circles – spring, open circles – autumn) and seed production (log-transformed values of oak *Quercus robur* and hornbeam *Carpinus betulus* crops) in Białowieża Primeval Forest (C), as well as the index of North Atlantic Oscillation (NAO) (D). See 'Material and sampling methods' for further explanations.

a prior distribution such that normally distributed noise (with a variance of 10) was added to the interpolated value.

Weather and climatological data

Data on local climatic variables (temperature, precipitation and snow depth) on a daily basis are available from January 1948 to December 2000, and originate from the Białowieża Meteorological Station, placed in the central part of Białowieża Glade. It is included in the system of meteorological stations of the Institute of Meteorology and Water Management. We also used data on climatic variability referring to a more global/regional scale – essentially representing a 'package of weather' (Stenseth *et al*. 2002b). For this purpose we used the North Atlantic Oscillations (NAO, Hurrell 1995; see Fig. 2D), an index known to relate to several ecological processes (Mysterud *et al*. 2001, Ottersen *et al*. 2001, Stenseth *et al*. 2002b). The NAO is a large-scale alternation in atmospheric pressures across the North Atlantic Ocean (Van Loon and Rogers 1978, Lamb and Peppler 1987), and its fluctuations and decadal phases are strongly linked to interannual variation as well as long-term changes in temperatures and precipitation in the Northern Hemisphere (Hurrell and Van Loon 1997). For NAO, we used the winter index of Hurrell (1995), which is the average standardized pressure difference between Stykkisholmur (Iceland) and Lisbon (Portugal) for the months December through March (data available at http://www.cgd.ucar.edu/~jhurrell/nao.html#winter).

In order to avoid spurious effects, a detrended NAO index was used in the time state-space modelling; however, the raw data are used when analysing the relationship between the NAO and local climatic factors. It should be realised though, that there is a high correlation between the original and the detrended data ($r = 0.967$ for years 1864–1998). We always used the maximal possible length of the NAO time series – which varies from one analysis to another since the data against which the NAO time series was compared to, varied in length.

The population dynamics model

The annual model

Let N_t be the abundance of rodents in the autumn of year t. On the basis of earlier studies on rodent dynamics (Stenseth 1999, Stenseth *et al*. 2002a), a possible general order-two population model being influenced by environmental factors (E_i being various current and delayed environmental factors such as climatic conditions and/or seed production) is

$$N_t = N_{t-1}\exp(\alpha_0 + \alpha_1 y_{t-1} + \alpha_2 y_{t-2} + \Sigma c_i E_i + \varepsilon_t) \qquad (1)$$

where $y_t = \log(N_t)$ and α_i and c_i are parameters to be determined on the basis of data. The quantity ε_t is a process noise accumulated over the year [$\varepsilon_t \sim N(0, \sigma^2)$]. Taking the logs on both sides of Eq. (1), we obtain

$$R_t = y_t - y_{t-1} = \alpha_0 + \alpha_1 y_{t-1} + \alpha_2 y_{t-2} + \quad c_i E_i + \varepsilon_t. \qquad (2)$$

In order for this system to correspond to a stationary process, the two autoregressive parameters $(1+\alpha_1)$ and α_2 must – assuming no density-independent influence – fall within the triangle defined by (–2,–1), (0,1) and (2,–1) (Royama 1992, see also Stenseth 1999). What might (in an order-one process) be referred to as the carrying capacity of the population, would then correspond to $N_e = \exp(\mu_e) = \exp[(c_i E_{e,i} + \alpha_0)/\alpha_1]$, where $E_{e,i}$ is the long-term equilibrium level of the environmental covariates. The model given by Eq. (2) will represent our basic ecological model – to which we need to link the trapping data (which, as a result, will be represented to a log-scale).

The bivariate seasonal model

The above annual dynamics may be decomposed into its seasonal components. For this purpose, let x_t correspond to the log-transformed population abundance in the spring of year t and (as above) let y_{t-1} correspond to the log-transformed abundance in the preceding autumn. The seasonal net winter growth rate, R_{wt} ($= x_t - y_{t-1}$), and the net summer growth rate, R_{st} ($= y_t - x_t$), will be (see Hansen *et al*. 1999):
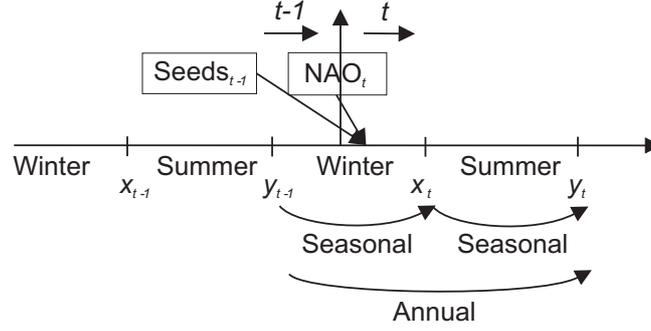
Fig. 3. Diagrammatic representation of the effect of NAO and seeds. See text for details and further discussion.

$$R_{wt} = x_t - y_{t-1} = a_0 + a_1 y_{t-1} + a_2 x_{t-1} + a_3 y_{t-2} + a_4 x_{t-2} + \Sigma c_{w,i} E_{w,i} + \varepsilon_{wt} \qquad (3)$$

and

$$R_{st} = y_t - x_t = b_0 + b_1 x_t + b_2 y_{t-1} + b_3 x_{t-1} + b_4 y_{t-2} + \Sigma c_{s,i} E_{s,i} + \varepsilon_{st} \qquad (4)$$

where ε_{wt} is a process noise during the winter [$\varepsilon_{wt} \sim N(0, \sigma_w^2)$] and ε_{st} is a process noise during the summer [$\varepsilon_{st} \sim N(0, \sigma_s^2)$]. The parameters $a_.$, $b_.$, $c_{w.}$ and $c_{s.}$ define the seasonal density-dependent and density-independent structure during winter and summer, respectively. Similar to the annual model, we will use the models given by Eqs (3) and (4) as our basic ecological model to which we need to link the seasonal trapping data.

Figure 3 illustrates how environmental covariates such as seed-crop and the NAO enter the model.

The seasonal equilibrium (spring and autumn, respectively) will be given by $N_{e,autumn} = \exp(\mu_{e,autumn})$ $= \exp[(\ c_{w,i}E_{e,w,i} + a_0)/a_1]$ and $N_{e,spring} = \exp(\mu_{e,spring}) = \exp[(\ c_{s,i}E_{e,s,i} + b_0)/b_1]$. The link to the annual model is $(\ c_i E_{e,i} + \alpha_0) = [(\ c_{w,i}E_{e,w,i} + a_0)/a_1] + (\ c_{s,i}E_{e,s,i} + b_0)$. Assuming that we can properly identify the intercepts in the models given by Eqs (2)–(4), we can link the annual and seasonal equilibria to each other. Unfortunately, since we do not know the overall trappability of the rodents under study, we cannot do so (see below).

Taken together, Eqs (3) and (4) define the annual net growth rate (Hansen *et al*. 1999, Stenseth *et al*. 2002a). This will be an order four model, but with the higher order terms typically being relatively weak (Hansen *et al*. 1999) making the resulting model approximately similar to an order two autoregressive structure as found to be a good description of annual population dynamics (Turchin 1993, Stenseth *et al*. 1996a, b, Stenseth 1999); that is, the model given by Eq. (2).

Statistical modelling

Meteorological data were analysed using basic correlation analysis as well as General Additive Modelling (GAM; see Hastie and Tibshirani 1990). The time-series analysis, the core of the paper, is described in the following section.

State-space modelling

The number of voles and mice caught during a trapping session is related to their abundance at the site and on the trapping effort. As a first approximation, the ecological process model described above is assumed to be linked to the observed number of voles and mice caught through a Poisson model. For the autumn samples this will then be given as:

$$P(z_{f,t} = z | y_t) = \exp(-\lambda_{f,t})\lambda_{f,t}^z z!, \qquad (5)$$

where the Poisson mean (assumed to be proportional to the trapping effort and the population abundance) is defined as

$$\lambda_{f,t} = q_f \exp(\mu_f + y_t). \tag{6}$$

The trapping effort (being constant among years) and the "trappability" (ie the average probability for any present individual to be trapped) in the given environment is represented by $q_.$. Due to the nature of the data, the average level of the true population ($\mu_.$) is confounded by $q_.$. We can, however, estimate the product of the average level ($\mu_.$) and $q_.$, defined as $\exp(\gamma_.) = q_. \exp(\mu_.)$. This yields the following parameterisation (for the autumn; and equivalently for the spring):

$$\lambda_{f,t} = \exp(\gamma_f + y_t). \tag{7}$$

By using the software package BUGS (Bayesian inference using Gibbs sampling; Spiegelhalter *et al.* 2000), a Bayesian approach was adopted to estimate parameters in the model. For further details, see Stenseth *et al.* (2002a). A complete Bayesian model consists of the joint prior distribution for all unobservables, here (for the annual model) α_i's, c's, σ, $\lambda_{f,t}$, γ_f and the unknown states $y_1, y_2, \ldots, y_N$, and the joint distribution of the observables, here the abundance data ($z_{f,1}, z_{f,2}, \ldots, z_{f,N}$). Bayesian inference is then based on the posterior distribution of the unobservables given the data. By conditioning on the observed data, the posterior distribution (ie the conditional probability of the unobservable quantities of interest, given the observed data) is calculated (by successive application of Bayes theorem; see Gelman *et al.* 1995). The posterior distribution usually can not be obtained analytically but can be computed using Markov Chain Monte Carlo methods, like for instance, Gibbs sampling (Gilks *et al.* 1996). To fully specify our model, a prior distribution has to be defined for all unobservable parameters which are not directly conditioned on other parameters or observed data (for the annual model these are: α_0, α_1, α_2, c_i, σ and γ_f). Only vague (ie essentially flat) prior distributions were used [$\alpha_0 \sim N(0,1000)$, $\alpha_1 \sim N(0,100)$, $\alpha_2 \sim N(0,100)$, $c_i \sim N(0,1000)$, $\gamma_f \sim N(0,1000)$ and $1/\sigma^2 \sim$ Gamma(0.001, 0.001), meaning that the prior tells us extremely little about the parameters relative to what is learned from the sample.

For both the annual and the joint seasonal model we performed 100 000 iterations of the Gibbs sampler, using WinBUGS (the BUGS version for Windows; http://www.mrc-bsu.cam.ac.uk/bugs/) version 1.3, after a "burn-in" of 10 000 iterations. Convergence was assessed through the runs of multiple chains and Gelman-Rubin convergence statistics (see Spiegelhalter *et al.* 2000).

Assuming that density-dependent population has a negative parameter, the probability of density dependence is at least 95%, if the upper limit of the 95% credible interval (a Bayesian alternative to confidence interval) of the posterior distribution is smaller than zero. Strong evidence for density dependence is found, if the upper limit of the 95% credible interval is negative. A possible positive or negative effect of any covariate may be assessed in a similar way. We use the term 'significant effect' whenever the 95% credible interval does not include zero.

Results

GAM-modelling of weather and climatic data –
some environmental background results

A positive correlation between the NAO and temperature during winter is observed (Table 1). There is no correlation between the NAO and precipitation, while there is negative correlation between the NAO and snow depth. Hence, since precipitation is not correlated with the NAO, the increasing temperature with increasing NAO is likely to reflect that precipitation falls to a lesser degree as snow when the NAO is high.

There is no clear non-linearity in the relation between the NAO and temperature, rainfall and snow depth (but see Fig. 4). The relationship between the NAO and temperature during December–March (GAM, $df_{splines}$ 1 vs 2, $F = 1.4707$, $p = 0.23$) and precipitation is linear (GAM, $df_{splines}$ 1 vs 2, $F = 0.28304$, $p = 0.60$). The

Table 1. Correlation between the NAO (Hurrell's winter NAO) and mean temperature, precipitation and snow depth for the months December (previous year), January, February and March and as an average for the period December through March in Białowieża Primeval Forest (eastern Poland). Data are from the period 1948–2000 (53 years).

Months	Temperature		Precipitation		Snow depth	
	r	p	r	p	r	p
December	0.217	0.126	−0.114	0.416	−0.217	0.126
January	0.549	< 0.001	0.109	0.439	−0.481	< 0.001
February	0.575	< 0.001	−0.125	0.371	−0.522	< 0.001
March	0.623	< 0.001	0.224	0.107	−0.635	< 0.001
Dec–Mar	0.743	< 0.001	−0.167	0.237	−0.425	0.002
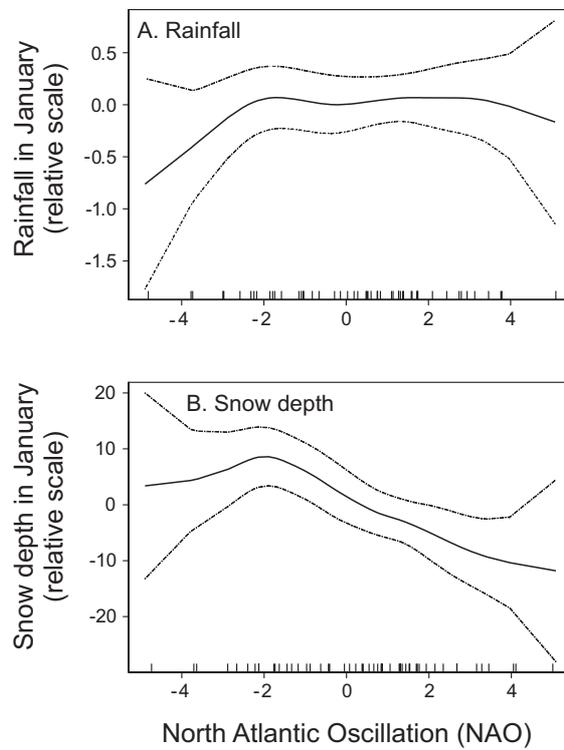
Fig. 4. The relationship between the local climatic variables [(A) rainfall (GAM, df_{spline} = 4, not significant nonlinearity) and (B) snow depth (GAM, df_{spline} = 5, not significant nonlinearity)] in Białowieża, Poland, and the North Atlantic Oscillation, an index of large-scale winter climatic variability for the period 1948–2000. The dashed lines are 95% point-wise confidence intervals. The tick marks show the locations of the observations on that variable.

relationship between the NAO and snow depth during December–March is weakly non-linear (curve was weakly concave; GAM, $df_{splines}$ 1 vs 2, $F = 7.0180$, $p = 0.011$). Neither is there any clear non-linearity when relating monthly weather patterns to the NAO. For snow depth in January, there is a slight peak around NAO = –2. Also, precipitation in January shows no relation with the NAO. However, for values below around NAO = –2, there seems to be decreasing amount of precipitation the lower the NAO.

It is, in this connection, relevant to observe that Mysterud *et al*. (2001) – on a much larger data set – found a clear non-linear relationship between the NAO and local climatic variables at the west coast of Norway. It is intriguing to observe that a NAO value of about –2 was a turning point – just like that observed for Norway. Although the relationship between the NAO and local climatic variables in Białowieża does not seem to exhibit any significant non-linearity, it would – in light of the results reported by Mysterud *et al*. (2001) – be premature to conclude that there in fact is no non-linearity between the NAO and local climatic factors in Białowieża. Indeed, our results suggest some non-linear pattern. These results do suggest that it might be advisable to introduce some non-linearity effect of NAO into the population model. It is, however, beyond the scope of this paper to investigate to what extent such non-linear effects ought to be included.

The order of the process in the absence of environmental forcing – the annual density-dependent structure

Figure 5 (see also Table 2) shows that, when fitting an order-two model to the data, both species show a non-significant second-order term (as typically is found for northern rodents; Stenseth 1999); that is, for both species there is a clear and direct density dependence ($\alpha_1 < 0$), whereas there is no indication of any delayed density dependence (α_2 0). This finding is consistent with no multiannual periodic cyclicity in the studied populations (see Stenseth 1999). On this basis, we conclude that both species exhibit an order-one process; the corresponding order-one models for both species are shown in Fig. 5. As can be seen from Table 2 and Fig. 5, the estimated direct density dependence is around one, being compatible with observations on several other small mammals (Stenseth 1999).

The seasonal density-dependent and density-independent structure

The seasonal density-dependent structure

For the two species, both the winter-component (a_1) and the summer-component (b_1) of the direct density dependence are clearly different from zero. Below we will expand on this by incorporating environmental effects (climate and seed-production) into the models. It should further be noticed that most of the among-year variation in density is due to variations between the winters (ie, σ_w is higher than σ_s; see Tables 3 and 5, and Figs 6 and 8).

A. *Clethrionomys glareolus*

B. *Apodemus flavicollis*
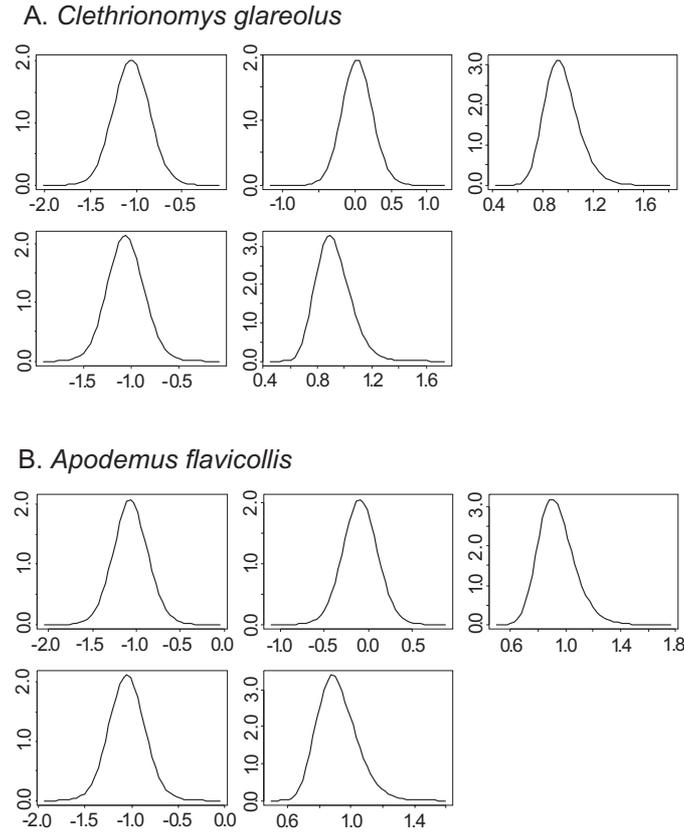
Fig. 5. Order-two (upper) and order-one (lower) models for *Clethrionomys glareolus* (A) and *Apodemus flavicollis* (B) depicted as kernel density estimates of the resulting posterior distribution. Further and additional information of the posterior distribution is given in Table 2.

Table 2. The annual density-dependent structure [see Eq. (2) in the text] of *Clethrionomys glareolus* and *Apodemus flavicollis* in Białowieża Forest. Parameter estimates (ie summary statistics of the posterior distribution) for both an order-two and an order-one model is shown. See text for further explanations.

	Clethrionomys glareolus					*Apodemus flavicollis*				
	Mean	2.50%	Median	95.00%	97.50%	Mean	2.50%	Median	95.00%	97.50%
Annual second order										
α_1	−1.05	−1.43	−1.06	−0.74	−0.67	−1.07	−1.44	−1.07	−0.75	−0.68
α_2	0.04	−0.35	0.03	0.36	0.43	−0.09	−0.46	−0.09	0.22	0.29
σ	0.95	0.73	0.94	1.19	1.24	0.94	0.73	0.92	1.16	1.22
Annual first order										
α_1	−1.06	−1.42	−1.06	−0.76	−0.69	−1.05	−1.41	−1.05	−0.75	−0.68
σ	0.92	0.71	0.91	1.14	1.19	0.92	0.71	0.90	1.13	1.19

There seems to be a weak effect of the overall climate on the annual dynamics (Fig. 6; see also Table 3: annual models). It should be noticed that the effect of both NAO_t and NAO_{t-1} has the same direction of the effect (not reported); both being negative implying a possible positive effect of an increased snow cover and/or of cooler summers (remembering that the higher the NAO-value is, the less snow there is, and the warmer is the summer).

For the seasonal decomposition of the annual dynamics in *Clethrionomys* we observe a slightly negative climatic effect during the winter-period but not during the summer (Table 3: seasonal model). A negative effect of the NAO during the winter is consistent with a negative correlation between the NAO and snow depth (Table 1), suggesting that there may be some positive effect of snow depth. For *Apodemus* we cannot detect any clear effect of the NAO in the seasonal dynamics (Table 3: annual model); however, there is some indication of a negative effect during the summer.

It is interesting that we can demonstrate both density-dependent and density-independent effects; this is yet another example demonstrating that both density-dependent and density-independent effects are important in shaping the dynamics of populations (Turchin 1995). Our result is, we feel, important since we have investigated both effects within the same model setting.
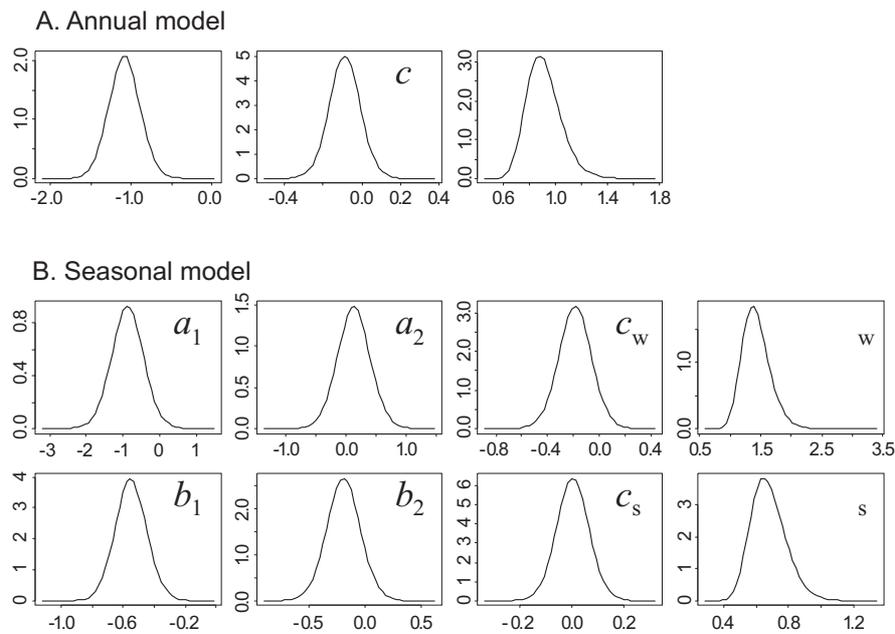
Fig. 6. The annual and seasonal models for *Clethrionomys glareolus* involving the NAO. Parameters are depicted as kernel density estimates of posterior distribution. See Table 3 for further details and additional results.

Table 3. Annual [Eq. (2)] and seasonal [Eqs (3)–(4)] models with the North Atlantic Oscillation (the NAO at time t) as an external forcing variable. Parameter estimates are described by summary statistics of the posterior distribution.

	Clethrionomys glareolus				*Apodemus flavicollis*			
	Mean	2.50%	Median	97.50%	Mean	2.50%	Median	97.50%
Annual model								
α_1	-1.12	-1.48	-1.12	-0.75	-1.11	-1.45	-1.11	-0.76
c	-0.09	-0.24	-0.09	0.07	-0.10	-0.25	-0.10	0.05
σ	0.91	0.71	0.90	1.20	0.90	0.69	0.89	1.17
Seasonal model								
a_1	-0.82	-1.71	-0.87	-0.04	-0.81	-1.96	-1.18	-0.46
a_2	0.08	-0.43	0.09	0.60	0.50	-0.04	0.50	1.03
b_1	-0.55	-0.75	-0.55	-0.35	-0.55	-0.74	-0.53	-0.32
b_2	-0.21	-0.50	-0.21	0.08	-0.23	-0.52	-0.23	0.05
c_w	-0.19	-0.44	-0.19	0.06	-0.02	-0.24	-0.02	0.20
c_s	0.00	-0.12	0.00	0.12	-0.07	-0.19	-0.07	0.05
σ_w	1.43	1.07	1.40	1.81	1.23	0.93	1.21	1.65
σ_s	0.68	0.50	0.67	0.86	0.67	0.50	0.66	0.90

Using seed crops as an environmental proxy

Figure 7 (see also Table 4) summarizes the effect of seed crop (hornbeam and oak) on the annual dynamic structure of both rodent species. There is a clear positive effect of seeds on their annual dynamics (the c's being clearly positive), an effect that earlier has been demonstrated using other methods of analysis (cf Pucek *et al*. 1993). It seems that, by incorporating climatic effects, the density-dependent components are strengthened, but without changing the structure of the density dependence (except for *Apodemus,* for which there is some evidence of delayed density dependence when hornbeam seeds are incorporated in the annual model; results not shown) – presumably making the intrinsic model being more appropriate.

Figure 8 (see also Table 5) shows how the annual structure decomposes into their seasonal components. This decomposition shows that the effects of seeds are particularly strong during the winter ($c_w > 0$) and essentially absent during the summer ($c_s \approx 0$). However, for *Apodemus*, there seems to be a weak positive effect of the hornbeam seeds also in the summer dynamics.

When seed crops are incorporated in the models, there is no longer any detectable effects of the NAO. This suggests that the NAO may primarily operate through the seed production.

A. *Clethrionomys glareolus*

B. *Apodemus flavicollis*
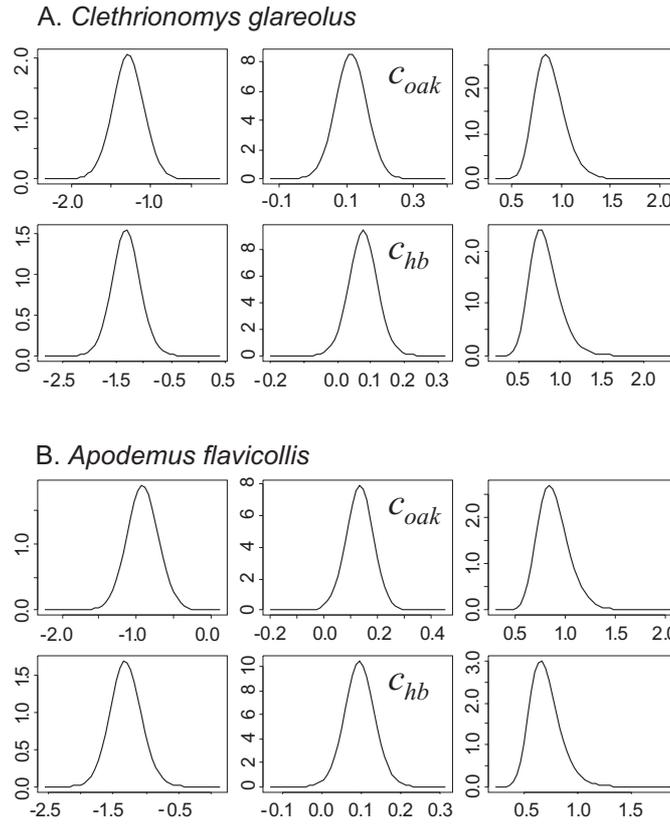
Fig. 7. The annual models with seeds as an external forcing variable. Parameters are depicted as kernel density estimates of posterior distribution. See Table 4 for details and additional results.

Table 4. Annual models with the seed production as an external forcing variable. Parameter estimates are described by summary statistics of the posterior distribution. For the common period of both hornbeam and oak data (16 years, covering 1975–1990), we found by using AIC_c, that for the annual model the oak and hornbeam performs about equally good. For the seasonal model (see Table 5), oak seems to do better than hornbeam, especially so for *Apodemus* during the winter.

	Clethrionomys glareolus				*Apodemus flavicollis*			
	Mean	2.50%	Median	97.50%	Mean	2.50%	Median	97.50%
Oak (1975–2001)								
α_1	-1.29	-1.67	-1.29	-0.91	-0.91	-1.32	-0.91	-0.50
c	0.12	0.03	0.12	0.21	0.14	0.04	0.14	0.23
σ	0.89	0.65	0.87	1.23	0.89	0.65	0.88	1.24
Hornbeam (1972–1990)								
α_1	-1.33	-1.82	-1.33	-0.81	-1.32	-1.78	-1.32	-0.83
c	0.08	-0.01	0.08	0.16	0.09	0.02	0.09	0.17
σ	0.82	0.55	0.79	1.23	0.70	0.48	0.68	1.03
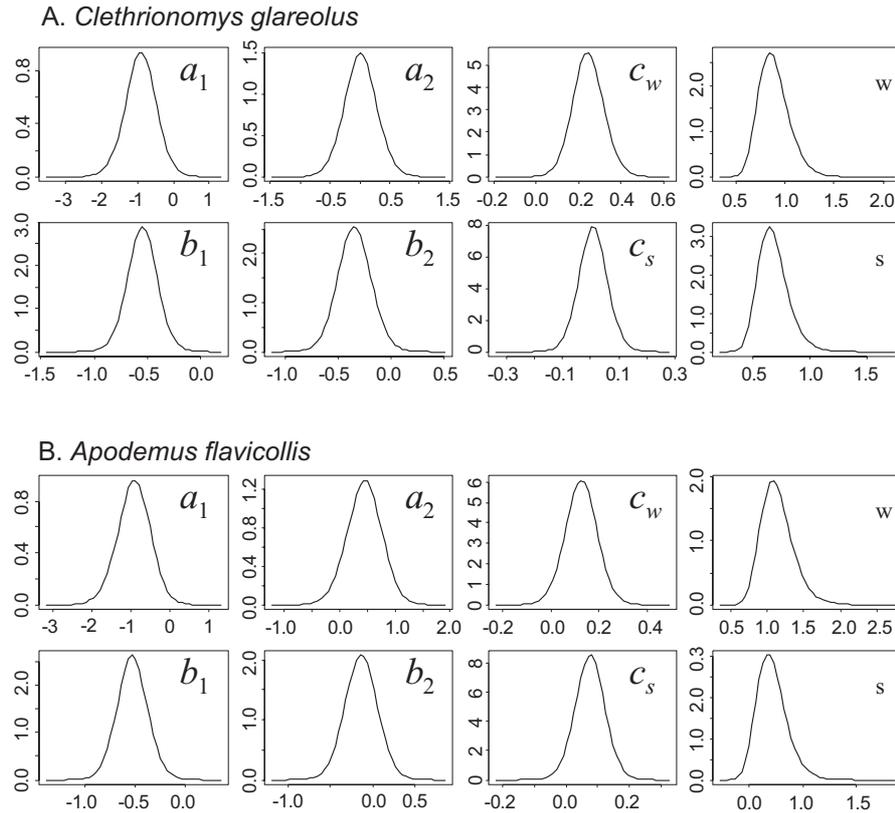
Fig. 8. Best seasonal models with seeds as an external environmental forcing variable. In both cases, oak seeds tend to enter the best models. Parameters are depicted as kernel density estimates of posterior distribution. See Table 5 for further details.

Discussion

In this paper we have adopted the approach of Hansen *et al*. (1999) to the modelling of seasonality, an approach that is different from that of Turchin and Ostfeld (1997) (as well as that of Hanski *et al*. 1991, 1993, 2001, Hanski and Korpimäki 1995, Turchin and Hanski 1997, 2001, Turchin and Ellner 2000). The approach taken by Turchin and Ostfeld (1997) assumes *a priori* that there is no difference in the degree of density dependence between the seasons, whereas our approach *a priori* assumes that there may be differences in the density-dependent component of seasonality. Through our approach, we have demonstrated that the restrictive assumptions of Turchin and Ostfeld (1997) are not warranted. If adopting their approach we would wrongly have concluded that the difference between the seasons is to be found only in the density-independent component.

Table 5. Seasonal model decompositions corresponding to the models shown in Table 4. Parameter estimates are described by summary statistics of the posterior distribution.

	Mean	2.50%	5.00%	Median	95.00%	97.50%
Clethrionomys glareolus						
Oak seeds (1975–2001)						
a_1	−0.92	−1.77	−1.62	−0.91	−0.22	−0.08
a_2	0.01	−0.51	−0.42	0.01	0.45	0.53
b_1	−0.55	−0.82	−0.77	−0.55	−0.33	−0.28
b_2	−0.34	−0.64	−0.59	−0.34	−0.09	−0.04
c_w	0.24	0.11	0.13	0.24	0.36	0.39
c_s	0.01	−0.09	−0.07	0.01	0.09	0.11
σ_w	1.31	0.91	0.96	1.28	1.74	1.87
σ_s	0.68	0.48	0.50	0.67	0.91	0.97
Hornbeam (1972–1990)						
a_1	−1.20	−2.31	−2.10	−1.19	−0.31	−0.10
a_2	0.03	−0.61	−0.49	0.04	0.55	0.66
b_1	−0.72	−1.04	−0.98	−0.73	−0.65	−0.39
b_2	−0.33	−0.79	−0.71	−0.33	0.05	0.14
c_w	0.12	−0.02	0.00	0.12	0.25	0.28
c_s	0.04	−0.04	−0.03	0.04	0.11	0.13
σ_w	1.43	0.94	1.00	1.38	2.03	2.18
σ_s	0.74	0.49	0.52	0.72	1.05	1.14
Apodemus flavicollis						
Oak seeds (1975–2001)						
a_1	−0.92	−1.76	−1.61	−0.92	−0.26	−0.13
a_2	0.44	−0.17	−0.06	0.45	0.93	1.03
b_1	−0.53	−0.83	−0.77	−0.53	−0.28	−0.23
b_2	−0.14	−0.51	−0.45	−0.14	0.17	0.23
c_w	0.12	0.00	0.02	0.12	0.23	0.25
c_s	0.08	−0.02	0.00	0.08	0.15	0.16
σ_w	1.14	0.80	0.84	1.11	1.53	1.63
σ_s	0.72	0.50	0.53	0.70	0.95	1.02
Hornbeam (1972–1990)						
a_1	−1.28	−2.10	−1.95	−1.27	−0.63	−0.49
a_2	0.15	−0.47	−0.36	0.15	0.66	0.77
b_1	−0.68	−1.14	−1.06	−0.68	−0.28	−0.20
b_2	−0.30	−0.75	−0.67	−0.30	0.09	0.17
c_w	0.10	0.00	0.02	0.10	0.19	0.20
c_s	0.06	−0.03	−0.02	0.06	0.13	0.15
σ_w	0.88	0.56	0.59	0.85	1.26	1.37
σ_s	0.66	0.44	0.47	0.64	0.92	0.99

Altogether we have – when taking account of the sampling variance – demonstrated that both species only exhibit direct density dependence; no delayed density dependence can be seen. When decomposing the annual density dependences into their seasonal components, we find that density dependence during the winter is consistently stronger than during the summer. Seed crops also have a stronger effect during the winter than during the summer – as is also the case with the climate.

Studying the same system using shorter series of data and other methods, Pucek *et al.* (1993) concluded that in years of moderately high densities, summer and autumn numbers of rodents correlated with food-related factors (seed crop, temperature affecting vegetation biomass). Spring numbers were, on the other hand, determined by the density-dependent winter mortality. In our new analysis, we found that autumn densities of mice were shaped by tree seed crop of the previous year. Pucek *et al.* (1993) furthermore found that summer densities of voles were strongly influenced by the summer temperature (in June–July), which they assumed acted through an increased production of herbaceous vegetation biomass. No ambient factor could explain the observed variations in autumn densities of voles. For both species, the intensity of reproduction in autumn was inversely related to autumn densities. For bank voles, Pucek *et al.* (1993) found that high temperature during July–September typically led to prolonged breeding. In our analysis, winter mortality of rodents was concluded to be density-dependent for both species and mast-crop was found to increase over-winter survival of both species.

Expressed in the terminology of this paper, the earlier conclusions by Pucek *et al.* (1993) suggest that the population growth rate during the winter (R_{wt}) is dependent on both previous autumn's density (that is density dependence) as well as on climatic factors and/or seed production of the preceding summer. Furthermore, they suggest that the population growth rate during the summer (R_{st}) is influenced by both density-dependent and density-independent factors. In this study, we have provided results directly relating to these earlier expectations. For both species there is a clear density dependence both during the summer and during the winter (the latter being the stronger), and the seed crops clearly enter during the winter model. For bank vole, we have demonstrated an effect of the overall winter climate (as measured by the NAO). This is consistent with earlier studies on predation rates on forest rodents in Białowieża Primeval Forest: Jędrzejewski *et al.* (1993, 1994) documented that snow cover decreased the efficiency with which tawny owls *Strix aluco* and pine martens *Martes martes* hunted for bank voles but not for mice.

The observed effect of seed-production is also consistent with the results of Crespin *et al.* (2002) working on the bank vole in Belgium, who found that the seed crop seemed to explain a major part of the among-year variations. Food supply studies using small rodents typically report that the length of breeding season is extended (Boutin 1990, Löfgren *et al.* 1996, Verhagen *et al.* 2000), and that winter

reproduction may occur when the food availability is increased (for an example in the bank vole; see Andrzejewski 1975). A clear positive effect of heavy mast crop years on survival has been found in a number of studies (Jensen 1982, Pucek *et al*. 1993, Wolff 1996a, b, Crespin *et al*. 2002). These studies as well as ours are therefore inconsistent with that of Andrzejewski (1975) who reported that food supply had no effect on survival – for which there may be many reasons, not least the power of the analysis used and the sample size available.

The fact that the overall structure of the population dynamics of both *C. glareolus* and *A. flavicollis* correspond to an order-one process – that is, only direct density dependence – suggest that there seems to be no strong closed feedback interaction with either specialist predators (supposed to have delayed numerical response; Oksanen *et al*. 2000) or food supply (Yoccoz *et al*. 2001). Interestingly, in Białowieża Forest, no time lag has been found in the numerical response of weasels *Mustela nivalis* to fluctuations of forest rodents (Jędrzejewski *et al*. 1995). Realizing that regular multiannual density cycles like those observed in more northern regions (Stenseth 1999) are not observed in Białowieża, the lack of delayed annual density dependence is indeed reasonable.

We have furthermore demonstrated an external forcing corresponding to the climate of the year – an effect, which is found to further be accounted for by a positive effect of the summer/autumn's seed production on the winter component of the annual dynamics (see Fig. 3). This agrees with the observed winter reproduction following years of good seed-production for both species at our study site (Adamczewska 1961, Pucek *et al*. 1993).

Altogether, we have found a combined density-independent (seed crop and climate) and density-dependent structure. The seed production (and climate) generated the among-year variability in rodent abundance. The density-dependent factors regulated their populations (*sensu* Sinclair 1989, Sinclair and Pech 1996) and stabilised the dynamics. Predation, intrinsic social factors (such as territoriality), and competition for food have been most frequently discussed as factors acting in a density-dependent way and capable of stabilising rodent numbers. Predation impact on bank voles and yellow-necked mice in Białowieża Forest was studied for several years (including moderately high densities as well as an outbreak and crash triggered by heavy crop of seeds) and although predators appeared the most important proximate cause of rodent mortality, predation rate was inversely density-dependent (Jędrzejewski *et al*. 1995, 1996, Zalewski *et al*. 1995, Jędrzejewski and Jędrzejewska 1996, Jędrzejewska and Jędrzejewski 1998). This result suggests that predators are capable of limiting numbers of rodents in Białowieża Forest at some lower level, although they cannot regulate and stabilise their dynamics.

Density dependence may be generated by intrinsic factors, such as territoriality or other social interactions. Adult bank-vole females have, for instance, been shown to be strongly territorial (Viitala and Hofmeyer 1985, Bujalska 1990, Bujalska and

Saitoh 2000) – the consequences of which lead to direct density dependence (Stenseth and Łomnicki 1980, Stenseth 1981, 1985a, b, 1986, Stenseth and Fagerström 1986). Data on social interactions of yellow-necked mice are lacking, but studies on the wood mouse *Apodemus sylvaticus* evidenced that male aggression influenced juvenile survival and might be involved in the regulation of numbers (Flowerdew 1974, Gurnell 1978). However, there is no territoriality within the two species during the winter, when these rodents live in social groups and often huddle in nests and shelters (eg Jędrzejewski *et al*. 1992). Therefore, social behaviour alone is unlikely to produce the observed strong density dependence in winter.

Density dependence in population processes (ie increased rates of mortality and/or lower rates of reproduction/recruitment with growing density of population) was suggested to reflect food competition (eg Messier 1991, 1994). In the temperate deciduous forests such as Białowieża, standing crop of biomass of herbaceous vegetation is fairly large in summer but very small during the cold season (see review in Jędrzejewski and Jędrzejewska 1996), Under such conditions, Jędrzejewski and Jędrzejewska (1996) proposed that forest rodents regularly face shortage of food in winter and early spring. Thus, density dependence in the winter mortality rates may indeed reflect competition for food, namely green biomass of soft-tissue plants on forest floor (Hansson 1987, 1988, 2002). This interpretation is supported by the fact that both species of rodents always responded by increase in densities to the natural food addition "experiments" represented by heavy crops of oak and hornbeam seeds. However, much more needs to be done before we understand how the annual density-dependent structure is decomposed into its seasonal components [cf Yoccoz *et al*. (2001) reporting a seasonal density-dependent structure being opposite of what we have found].

Throughout this study we have taken a phenomenological pattern-oriented approach and tried to deduce the possible underlying processes generating the observed pattern. The seed production (particularly oak seeds) accounted for the among-year variation in vole and mouse abundance – although within a profound density-dependent structure. Although our study represents only one location, we have a particularly long record of the rodent populations and good environmental data from this site. In-depth insight into the structuring of the dynamics of populations, as provided here, are an important platform for predicting what changes might appear if environmental conditions (eg climate and seed production) should change, as well as to understand what happens in different parts of a species range of distribution. Therefore, we provided a building block for better understanding gradients in small rodent dynamics in northern Europe (Hansson and Henttonen 1985a, b, Bjørnstad *et al*. 1995), central Europe (Tkadlec and Stenseth 2001), various biomes of the Palaearctic zone (Jędrzejewski and Jędrzejewska 1996), as well as the dynamics of these species in other parts of their range (Yoccoz and Mesnager 1998, Ivanter and Osipova 2000, Moshkin *et al*. 2000, Yoccoz *et al*. 2001).

Altogether we have – through this study – incorporated the insights obtained by Polish pioneers in the field of rodent population biology into the overall picture of differential dynamics depending upon the geographic location of the population.

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