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Rarity, life history and scaling of the dynamics in time and space of British birds

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Summary

1. Many patterns in macroecology are closely related to the total abundance of a species in a region. Here we show that interspecific differences in the pattern of population fluctuations of British bird species can be predicted from knowledge of their overall abundance and some basic life-history characteristics.

2. We identify a rarity syndrome that arises through an increased stochastic influence on population fluctuations with decreasing population size, mainly resulting from an inverse density-dependent effect of demographic stochasticity. This syndrome involves an increase in the annual changes in population size with increasing rarity in the United Kingdom.

3. The relationship between the magnitude of temporal variation and local mean population size differs between species dependent on their life history, i.e. species with larger clutch size and lower survival tended to have larger annual changes in population size than low-reproducing long-lived species.

4. The probability of local disappearance from a study plot depended on the population size and was hence closely related to the overall abundance of the species in UK. For a given population size, this probability was also related to species-specific life-history characteristics, being higher in species with larger clutch sizes and smaller survival rates.

5. Rareness results in a spatial decoupling of the temporal variation in population size.

6. These patterns show that once a species has become rare, e.g. due to human activities, key population dynamical characteristics will change because of density-dependent stochastic effects, which in turn are dependent on species-specific life-history characteristics.

Key-words: extinction, macroecology, population synchrony, population variability, rarity syndrome, species abundance

Introduction

Macroecological studies covering a wide range of taxa have shown that species with large regional population sizes have bigger geographical ranges (Brown 1984, 1995; Gaston 1994, 2003; Gaston & Blackburn 2000), are found at higher proportion of available sites (Hanski & Gyllenberg 1993; Gaston *et al.* 2000; Freckleton *et al.* 2005; Freckleton, Noble & Webb 2006; Webb, Noble & Freckleton 2007) and have larger local population sizes (Hanski & Gyllenberg 1993; Gaston 1994; Gaston *et al.* 1998; Freckleton *et al.* 2005) than rare species. Such general patterns are important because they suggest that ecological processes are linked across large geographical areas. This means that factors affecting the overall abundance of a species will have an effect on the pattern of fluctuations in local population size, or conversely that local population processes are important in determining abundances at larger spatial scales. Models suggest that such scaling relationships are nonlinear (Hanski 1999; Freckleton *et al.* 2005), and are dependent on the precise nature of the interaction between local and metapopulation dynamics. However, the interactions between local and regional scale dynamics are still poorly understood (Hanski & Gyllenberg 1993; Brown 1995; Lawton 1996) .

Analyses of the dynamics of bird populations have shown that parameters affecting the expected dynamics as well as stochastic variation around the average are both important for annual changes in population size (Lande, Engen &

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Sæther 2003). Assuming no age-structure effects, the expected dynamics will be influenced by the strength of density dependence, i.e. the inverse of the return time to equilibrium (May 1981), which in turn is determined by the form of density regulation and the specific growth rate at small population size. Stochastic effects result from environmental stochasticity (random fluctuations in the environment affecting the whole or parts of the population in a similar way) as well as demographic stochasticity (random variation among individuals in fitness) (Lande, Engen & Sæther 2003). The effects of environmental stochasticity on the long-run growth rate will be independent of population size, whereas the effects of demographic stochasticity on annual variation in population growth rates increase at small population sizes (Lande, Engen & Sæther 2003). Thus, the magnitude of annual changes in population rates should increase with decreasing population size because of an inverse density-dependent influence of demographic stochasticity. An important consequence is that the time to extinction of populations is predicted to scale logarithmically with population size (Fagan & Holmes 2006).

Comparative analyses have shown that many aspects of avian population dynamics are correlated with different life-history characteristics. A tendency for higher population growth rates (Sæther & Engen 2002), increased environmental stochasticity (Sæther *et al.* 2005a), shorter times to extinction (Sæther *et al.* 2005a) and larger regional abundances (Blackburn, Lawton & Gregory 1996) are found in bird species with large clutch sizes and short generation times than in species that mature late and have long-life expectancies. Similarly, the impact of demographic stochasticity on the population fluctuations increases with the position of the species towards the fast end of such a ‘slow–fast’ continuum (Sæther & Bakke 2000) of life-history variation (Sæther *et al.* 2004). Furthermore, variation of bird abundances in space and time are also influenced by basic species-specific characteristics such as body size (Cook & Hanski 1995; Greenwood *et al.* 1996; Newton 1998; Bennett & Owens 2002; Sæther & Engen 2002) and migratory pattern (O‘Connor 1985; Paradis *et al.* 1999; Newton 2008). Thus, interspecific differences in population variability may be related to basic species-specific characteristics such as body size or life history.

One important feature of avian population dynamics is that geographically separated populations tend to fluctuate in synchrony (Ranta, Lundberg & Kaitala 2006). Theoretical analyses have shown that the spatial scaling of the population fluctuations increases with the covariation in space of key environmental variables (Moran 1953; Lande, Engen & Sæther 1999) and the rate of migration of individuals among populations (Lande, Engen & Sæther 1999; Ranta, Lundberg & Kaitala 2006), and decreases with the strength of density regulation (Greenman & Benton 2001; Engen & Sæther 2005; Liebhold, Johnson & Bjørnstad 2006) and increasing demographic stochasticity (Sæther *et al.* 2007). Thus, small populations should show non-synchronized population fluctuations because demographic stochasticity will desynchronize populations even when located close to each other in space.

The general patterns that arise from analyses of simple stochastic population models indicate that rarity should affect the patterns in population dynamics, mainly caused by an inverse density-dependent effect of demographic stochasticity. We suggest that this provides a novel mechanism for a link between micro- and macroecological processes. Here we will examine the empirical evidence for such a relationship between local population dynamics and overall abundance by analysing time series of population fluctuations from the Common Bird Censuses. This scheme was run by the British Trust for Ornithology (BTO) during a period of 40 years and is based on censuses of territorial birds in study plots distributed all over Britain (Marchant *et al.* 1990). By fitting simple stochastic models to each time series we show that many basic features of the population dynamics change when the local abundance decreases. Because there is a relationship between mean local population size and overall abundance of the species in United Kingdom (Gaston 1994; Blackburn *et al.* 1998; Gaston & Blackburn 2000), this results in some general relationships between patterns in the population dynamics and rarity. Many of these relations should be general because they are predicted from stochastic population models, independent of the actual processes causing the rarity of a species. This is supported by the fact that interspecific variation in these patterns can be explained by interspecific differences in basic life-history characteristics, assumed to affect the stochastic components of the population dynamics.

Population model

We model the population dynamics of each species in the different study plots by assuming density independence, no age-structure effects and no autocorrelations in the noise. Writing N_t for the population size at time t, the mean and the variance of the change in population size from year t to $t+1$ $\Delta X_t = X_{t+1} - X_t = \ln N_{t+1} - \ln N_t$ is then to the first order

$$\mathrm{E}(\Delta X_t | X_t) = r - \frac{1}{2}\sigma_p^2 \qquad \text{eqn 1a}$$

and

$$\mathrm{var}(\Delta X_t | X_t) = \sigma_p^2. \qquad \text{eqn 1b}$$

Here r is the specific population growth rate and $\sigma_p^2 = \sigma_d^2 e^{-X_t} + \sigma_e^2$ is the process variance, where σ_d^2 is the demographic variance and σ_e^2 the environmental variance (Lande, Engen & Sæther 2003). The long run growth rate of the population then becomes $s = r - \frac{1}{2}\sigma_p^2$.

Materials and methods

We analysed data from the Common Birds Census (CBC) of British birds between 1962 and 2001. These data are based on annual censuses by the mapping method of breeding bird populations in plots scattered all over Britain that provides an estimate of the number of stationary pairs of birds in the plot (Enemar 1959). Because estimates of many population dynamical parameters are sensitive to the length of the time series (Marchant *et al.* 1990), we only included the first continuous period of 10 years without any missing census in each plot.

Estimates of the total abundance in United Kingdom were obtained from the Royal Society for Protection of Birds (\http://www.rspb.org.uk/wildlife/birdguide/name/a/index.asp) and are listed in Table S1, Supporting Information.

Data on body mass and life-history characteristics were usually extracted from comparative studies involving several species, e.g. Dobson (1990) and Peach, Hammer & Oatley (2001) The migratory pattern was classified into three groups according to Appendix 6 in Wernham *et al.* (2002) as (i) Sedentary; (ii) Short-distance migrant; (iii) Long-distance migrant. For estimates and sources, see Table S1, Supporting Information.

As the population estimates were affected by observation error we estimated the parameters by adopting a Bayesian approach in combination with Markov Chain Monte Carlo techniques (Gilks, Richardson & Spiegelhalter 1996; Millar & Meyer 2000; Clark & Bjørnstad 2004; Clark 2007). Using this approach we define the pair of equations

$$X_t = f(X_{t-1}) + \varepsilon_t$$

$$Y_t = X_t + \omega_t$$

The first equation is the process equation that models the population dynamics and the second equation is the observation equation relating on a logarithmic scale the observations, Y, to the underlying actual population size, X. The deterministic component $f(X_{t\text{-}1})$ of the process equation is obtained by using the density-independent dynamics in eqn. 1a

$$f(X_{t-1}) = X_{t-1} + s$$

where $s = r - \frac{1}{2}\sigma_p^2$. Assuming that the process error and the observation error is normal on a logarithmic scale, $\varepsilon_t \sim \mathrm{N}(0, \sigma_p^2)$ and $\omega_t \sim \mathrm{N}(0, \sigma_y^2)$, where σ_Y^2 denotes the variance of the observation error.

After defining the full probability distributions of all unobservable $(X_1, \ldots., X_T)$ and observed $(Y_1, \ldots., Y_T)$ quantities at the log scale, we chose independent and uninformative prior probability distributions (priors) for parameters that were not directly conditioned on other parameters or data, in this case s, σ_p^2 and σ_Y^2 (see Sæther *et al.* 2009 for further information).

If conditioned on the data, the joint posterior distribution of the unknown quantities, $\pi(s, \sigma_p^2, \sigma_Y^2, X_1, \ldots..X_T \big| Y_1, \ldots.. Y_T)$, for the density-independent model is according to Bayes' theorem proportional to

$$\pi_1(s)\pi_2(\sigma_p^2)\pi_3(\sigma_Y^2)\mathrm{N}(X_1 \big| Y_1, \eta^2)\prod_{t=2}^{T}\mathrm{N}(X_t|f(X_{t-1}), \sigma_p^2)) \\ \times \prod_{t=1}^{T-1}\mathrm{N}(X_{t+1}|f(X_t), \sigma_p^2))\prod_{t=1}^{T}\mathrm{N}(Y_t \big| X_t, \sigma_Y^2).$$

This distribution is analytically intractable, but was estimated by successive simulations from the posterior distributions using the program WinBUGS (Spiegelhalter *et al.* 2003). WinBUGS requires a prior for the first unobservable population size X_1, which was set to $\mathrm{N}(Y_1, \eta^2 = 10^6)$. The results were not sensitive to the choice of this prior.

We computed the probability of extinction of a population over a period of 10 years after year T, the last year of census of the population, using the concept of Population Prediction Interval (PPI) (Engen, Sæther & Møller 2001). A PPI is defined as the stochastic interval that includes a given population size with probability (*1-α*), so that α is the probability that the variable we want to predict is not contained in the stochastic interval. The width of the PPI is affected by changes in expected population size e.g. due to density regulation, fluctuations in population size because of demographic and environmental stochasticity and uncertainties in parameter estimates and biases in estimates of population size (Sæther *et al.* 2009). This provides a way to compare the risk of extinction across populations or species.

We found the log population sizes forward in time by successively simulating $X_{T+1} = \mathrm{N}\Big(f(X_T), \sigma_p^2\Big)$, $X_{T+2} = \mathrm{N}\Big(f(X_{T+1}), \sigma_p^2\Big)$, ... a given number of time steps using a set of parameters obtained from the simulation of the posterior distribution. To estimate the PPI, we simulated 20 time series from each of 5000 posterior distribution sets of the estimated parameters obtained by selecting every 100th iteration of the Markov Chain after burn-in, giving a total of 100 000 simulated time series per observed series.

We defined local disappearance as a failure to record a species in a study plot one or more years, including only time series of at least 10 years of census after the final year used in estimating the population parameters. In addition, the probability of extinction of a species in a plot was estimated from the quantile of the PPI at which the extinction barrier of $N = 0$ was reached after 10 years.

We used an information theoretic approach (Burnham & Anderson 2002) to evaluate how different variables affected the process variance and the probability of local disappearance.

As we were conducting interspecific comparisons there is a possibility that the statistical relationships we observed could be affected by phylogenetic non-independence (Harvey & Pagel 1991). We therefore tested the residuals of the regressions between estimated parameters and log national population size using the lambda statistic of Pagel (Pagel 1999; Freckleton, Pagel & Harvey 2002) using the phylogeny of British Birds of Thomas (2008). We found that the estimated values of lambda were either not statistically significantly different from zero (relationship between mean local population size in a plot and total population size in UK) or equal to zero (relationship between process variance σ_p^2 and total population size, and between probability of extinction and total population size), indicating that there is no phylogenetic signal.

Results

Firstly we show that demographic stochasticity drives the variability in population growth rate in a density-dependent manner. In 31 of 36 species (see Table S1, Supporting Information for the species included), the logarithm of process variance in the population fluctuations decreased linearly with the logarithm of the mean population size in the plot (Fig. 1, the regression coefficient significantly ($P < 0{\cdot}05$) less than 0 in 14 species; the plot for each species is shown in Fig. S1, Supporting Information). A model selection analysis (Burnham & Anderson 2002) revealed that this relationship was best explained by a model with a common slope for all species of the relationship between process variance and mean population size on a logarithmic scale, but with different intercepts for each species (Table 1). This model gave much smaller AIC-values than a model that included species-specific slopes ($\Delta\mathrm{AIC} = 32{\cdot}38$, see Table 1 for further details). This indicates a general density-dependent increase in process variance with decreasing population size (Fig. 1).

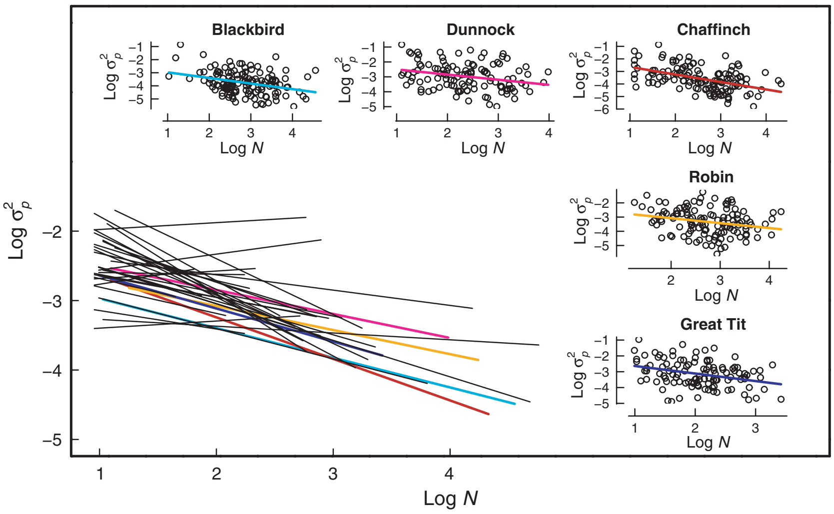

Fig. 1. The relationship at a logarithmic scale between the process variance σ_p^2 and the mean population size during the first 10 years of study in a study plot for 36 species in the United Kingdom. The panels show the scatterplot of some selected species.

Table 1. The results of the model selection analyses of the relationship between the (log–) process variance $\log(\sigma_p^2)$ and the (log–) mean population size in the plot $\log \bar{N}$ for the different species. AIC is the Akaike's information criterion. *Δ*AIC is the change in AIC and the AIC weights gives the weight of evidence in favour of the model. x indicates that the variable was included in the model. Model 5 includes a common intercept for all species as the only parameter

Model	$\log \bar{N}$	Species	$\log \bar{N}$*Species	AIC	ΔAIC	AIC weights
1	x	x		4922·34	0	1
2	x	x	x	4954·72	32·38	9·32E-08
3		x		5062·02	139·68	4·65E-31
4	x			5069·05	146·71	1·39E-32
5				5320·94	398·60	2·78E-87

Secondly we show that the degree of temporal variability in local population fluctuations is related to total regional population size. As would be predicted from previous work (Gaston 1994; Gaston & Blackburn 2000; Freckleton *et al.* 2005), the mean local population size of a species is strongly correlated at a logarithmic scale with the total abundance of the species in Britain (Fig. 2a, $r = 0{\cdot}78$, $n = 36$, $P < 0{\cdot}001$; for estimates of the total abundance, see Table S1, Supporting Information). This positive relationship between local and regional abundance is one of the most general relationships in macroecology (Hanski & Gyllenberg 1993; Brown 1995; Gaston & Blackburn 2000). This decrease in mean abundance at both the regional and local level was associated with an increase of the average process variance in local population dynamics with rarity of the species in Britain (Fig. 2b, $r = -0{\cdot}54$, $n = 36$, $P = 0{\cdot}0006$). Thus, the stochastic influences on the annual changes in local population size were on average larger in rare than in abundant species in Britain.

In our third set of analyses we examined whether variation in life-history traits or ecological characteristics could explain interspecific differences in the relationship between process variance and population size (Fig. 1, Table 1). A model selection analysis revealed that the explained effects on the process variance by the interaction terms between migratory pattern and mean population size were small ($\Delta\mathrm{AIC} = 0{\cdot}86$) and thus were excluded in the following analyses. When the life history and the ecological characteristics were included in the analyses, the model with all variables included gave the second-most smallest value of AIC (Table 2). However, the differences in AIC between the different models were small. In all models within $\Delta\mathrm{AIC} < 2$ from the best models body mass and adult survival rate were included. Accordingly, a model with only those two variables in addition to mean population size had almost the same effects on the explained variation as in the most complex model ($\Delta\mathrm{AIC} = 1{\cdot}11$). Thus, relatively high process variance at a given local population size was found in short lived species as well as in larger species.

In our fourth set of analyses we examined whether the probability of local disappearance, i.e. that the species was not recorded in the plot for at least one year, could be explained by some species-specific characteristics. One general pattern that emerges from analyses of stochastic population models is that the probability of extinction increases curvilinearly with decreasing population size (Fagan & Holmes 2006). In species with a positive specific growth rate, this is mainly due to increased influence of demographic stochasticity at smaller population sizes (Sæther & Engen 2003). We found as expected from theory that in all species the probability of local disappearance decreased with increasing population size (Fig. 3). Very few populations went extinct when the last recorded population size was larger than 10 individuals (Fig. S2, Supporting Information). The relationship between the probability of local disappearance and the population size after 10 years of study N_{10} was best explained

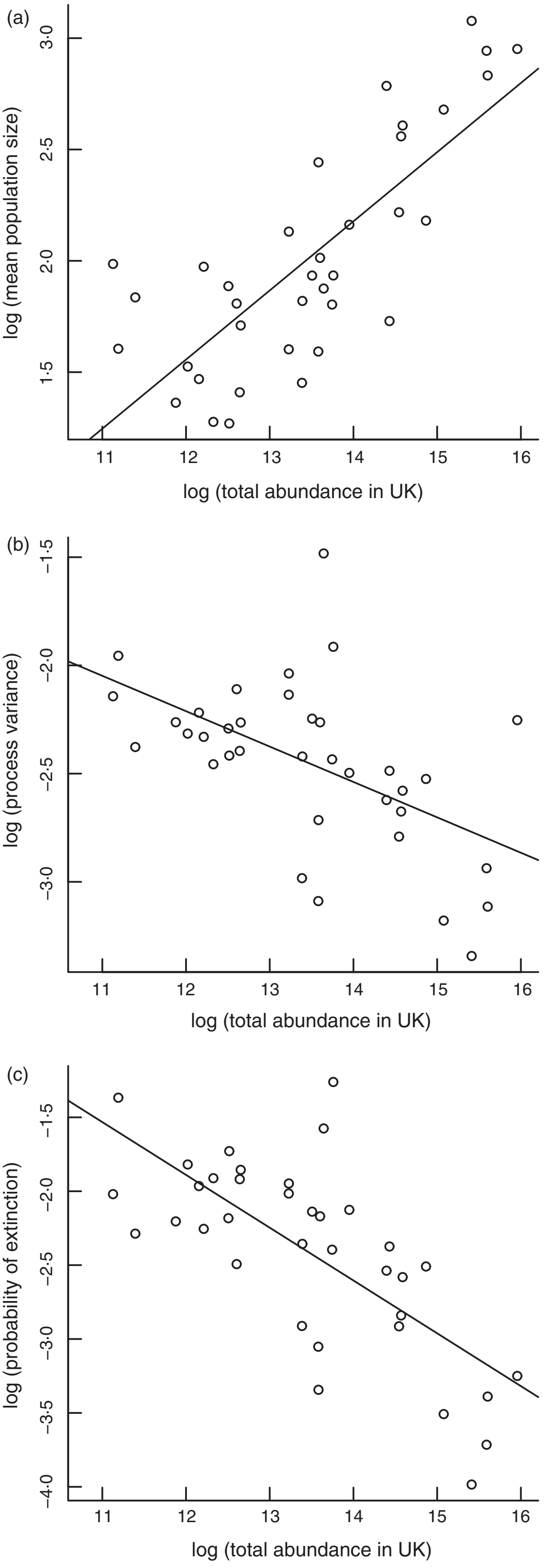

Fig. 2. The effects of interspecific variation in total abundance on average population dynamical characteristics of British bird species. (a) The mean population size (pairs) during the first 10 years of censuses at plots in which the species was recorded is plotted against the overall abundance (breeding pairs) of the species in UK. In (b) the mean of the estimates of local process variance σ_p^2 and in (c) the mean probability of extinction in a local plot after 10 years is related to the total overall abundance in UK at a logarithmic scale.

by a model that included a common slope and intercept for all species, whereas the second best model with different intercepts for each species gave a far poorer explanation (ΔAIC = 10·53, see Table 3 for further details). Other parameters influencing the risk of local disappearance, i.e. the stochastic population growth rate and the process variance σ_p^2, were not included in the best model. This shows that the probability of disappearance from a local area generally increased with decreasing population size. When species-specific characteristics were included, the best model contained the last population size in addition to body size, clutch size and adult survival rate (Table 4). The population size after 10 years was included in all models in which ΔAIC < 2, whereas adult survival rate was included in 9 of 12 models. According to the principle of parsimony, a model including only N_{10} and clutch size should be favoured. Thus, the probability of local disappearance increased with decreasing population size, but with a tendency for species with small clutch size or high survival to persist longer at a given population size.

We then evaluated whether the probability of local extinction of British birds was related to the overall abundance of the species in Britain using a Population Prediction Interval (PPI) based on population parameters estimated from the first ten years of data. We used the estimates of population parameters from the first 10 year time series to predict the probability of extinction of the population by examining in which quantile of the PPI the prediction for the extinction barrier, defined as $N = 0$, was located after 10 years. The logarithm of the mean probability of extinction of a local population increased with decreasing (log−) overall abundance of the species in Britain (Fig. 2c, $r = -0{\cdot}70$, $n = 36$, $P < 0{\cdot}001$). This means that the probability of local extinction increased with the overall national rareness of the species. There was no significant relationship of the mean probability of extinction either to body mass ($r = 0{\cdot}20$, $n = 33$, $P = 0{\cdot}91$), to any of the two life-history traits ($r = 0{\cdot}24$, $n = 33$, $P = 0{\cdot}12$ and $r = -0{\cdot}23$, $n = 30$, $P = 0{\cdot}23$ for clutch size and adult survival rate, respectively) or to migratory pattern ($F = 1{\cdot}53$, d.f = 1,28, $P = 0{\cdot}23$).

In the final analyses we show that the density dependence of stochastic influences on the population dynamics affects an important temporal macroecological pattern: the spatial synchrony in population fluctuations. If demographic stochasticity affects the spatial synchrony in population dynamics, we expect that the temporal correlations in

Table 2. The results of the model selection analyses of the influence of interspecific differences in life-history characteristics, total abundance, migratory pattern (Migr) and body mass on the relationship between the (log–) process variance $\log(\sigma_p^2)$ and the (log–) mean population size in the plot $\log \bar{N}$. AIC is the Akaike's information criterion, *Δ*AIC is the change in AIC and the AIC weights gives the weight of evidence in favour of the model. The migratory pattern is classified according to Wernham *et al.* (2002) as (i) Sedentary; (ii)Short-distance migrant and (iii) Long-distance migrant. x indicates that the variable was included in the model. Only models in which *Δ*AIC < 2 are shown. AIC = 4278·92 (*Δ*AIC = 96·83) for the model with only $\log \bar{N}$ included

Model	$\log \bar{N}$	Body mass	Adult survival	Clutch size	Total population size	Migr	AIC	*Δ*AIC	AIC weights
1	x	x	x	x			4182·09	0	0·17
2	x	x	x	x	x	x	4182·45	0·37	0·14
3	x	x	x	x		x	4182·59	0·50	0·13
4	x	x	x				4183·19	1·11	0·10
5	x	x	x		x		4183·38	1·29	0·09
6	x		x	x	x	x	4184·08	1·99	0·06

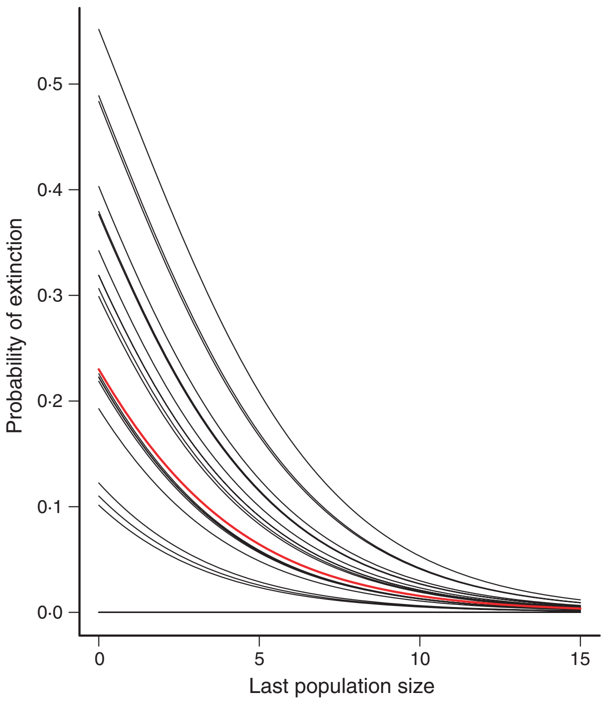

Fig. 3. Interspecific variation among British passerine bird species in the relationship between local disappearance of a species for 1 or more year in a plot in relation to the last recorded population size after the first 10 years of census. The red line show the best model based on model selection.

Table 3. The results of the model selection analyses of the relationship between the probability of extinction and the population size in the plot after the first 10 years of study N_{10} for the different species using a generalised linear model with a logit link function. AIC is the Akaike's information criterion. *Δ*AIC is the change in AIC and the AIC.weights gives the weight of evidence in favour of the model. x indicates that the variable was included in the model. Model 5 includes a common intercept for all species as the only parameter

Model	N_{10}	Species	N_{10}*Species	AIC	ΔAIC	AIC.weights
2	x			337·75	0	0·995
3	x	x		348·28	10·53	5·15E-03
4	x	x	x	378·80	41·05	1·21E-09
1		x		385·76	48·00	3·75E-11
5				398·21	60·45	7·42E-14

annual changes in the size of two populations separated in space should decrease with decreasing size of the smaller of the two populations. To account for other factors that affect population synchrony (Lande, Engen & Sæther 1999; Greenman & Benton 2001; Liebhold, Koenig & Bjørnstad 2004; Engen & Sæther 2005; Ranta, Lundberg & Kaitala 2006), we calculated the residuals after fitting a density-independent model to each population and examined the covariation in space in these residuals and chose, according to previous approaches (Engen *et al.* 2005), an exponential model for the spatial autocorrelation function. An important characteristic of this model is the correlation at zero distance ρ_0, which allows us to compare the degree of synchrony of two populations located close to each other in space. In 9 of 11 species in which the number of pairwise comparisons was larger than 400, ρ_0 increased with the threshold for the smaller size of the pair of populations included (Fig. 4, significant ($P < 0{\cdot}05$) for the Blackbird *Turdus merula*, Blue Tit *Cyanistes caeruleus*, Chaffinch *Fringilla coelebs*, Dunnock *Prunella modularis*, Great Tit *Parus major*, Skylark *Alauda arvensis*, Song Thrush *Turdus philomelos* and Yellowhammer *Emberiza citrinella*. Thus, the spatial synchrony in the fluctuations of populations located close to each other in space decreases with decreasing population size. For the Wren an opposite relationship was found with a significant ($P < 0{\cdot}001$) decrease in synchrony at zero distance ρ_0 with increasing size of the minimum population (Fig. 4).

Discussion

These results show that general predictions from stochastic population models can provide a link between macroecological relationships and the dynamics of local populations. This interrelationship is generated by changes in the population dynamics which occur when local populations decrease in size (Figs 1 and 3). The mean local population size and overall abundance of birds in United Kingdom are closely correlated (Fig. 2a), most likely because abundant birds have

Table 4. The results of the model selection analyses of the probability of extinction in relation to the population size after ten years of census N_{10}, the specific stochastic population growth rate s and the process variance σ_p^2, and interspecific differences in life-history characteristics, total abundance, migratory pattern (Migr) and body mass. AIC is the Akaike's information criterion, ΔAIC is the change in AIC and the AIC weights gives the weight of evidence in favour of the model. The migratory pattern is classified according to Wernham *et al.* (2002) as (i) Sedentary; (ii) Short-distance migrant and (iii) Long-distance migrant. Only models in which $\Delta\text{AIC} < 2$ are shown. The interactions $N_{10} * s$, $N_{10} * \sigma_e^2$, $s * \sigma_e^2$ and $N_{10} * s * \sigma_e^2$ were not included in any of the 12 best models and are therefore not presented in the table

Model	N_{10}	s	σ_p^2	Body mass	Clutch size	Adult survival	Migr	Total population size	AIC	ΔAIC	AIC weights
1	x			x	x	x			256·35	0	0·030
2	x			x		x			256·48	0·12	0·028
3	x				x				257·35	1·00	0·018
4	x	x		x	x	x			257·69	1·34	0·015
5	x			x	x	x		x	257·85	1·49	0·014
6	x								257·99	1·64	0·013
7	x	x		x		x			257·97	1·62	0·013
8	x			x	x	x	x		258·00	1·66	0·013
9	x					x			258·31	1·96	0·011
10	x				x	x			258·29	1·94	0·011
11	x	x			x				258·30	1·95	0·011
12	x			x		x	x		258·34	1·99	0·011

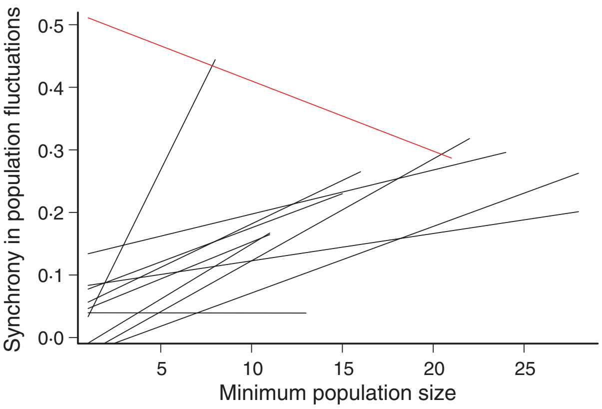

Fig. 4. Interspecific variation in the relationship between the synchrony in the population fluctuations of two populations located at zero distance ρ_0 in relation to the lower limit for the size of the smaller population involved in the pairwise comparison. The red line shows the relationship for the wren *Troglodytes troglodytes*.

higher availability of resources (Gregory & Gaston 2000). This relationship is likely to be independent of whether a species has become rare because of negative long-term population growth rate over a long period of time or whether it is rare because the availability of some critical resources are limited (Caughley 1994). However, the relationship between the variance and local mean population size are also influenced by the species-specific life-history characteristics (Table 2 and 4) because species with large clutch size and high mortality tend to have, for a given population size, larger values of σ_p^2.

Our analyses are based on a density-independent model without any age-structure. One reason for the choice of such a simplified model is that the population sizes in the plots in general were quite small (Figs 1 and 2a). Previously, Sæther *et al.* (2009) showed that such simple models were able to predict the dynamics of these populations quite well and including density dependence often produced biased variance estimates. Furthermore, most species included in the present study had high adult mortality rates (Table S1, Supporting Information) and an age of maturity of 1 year, which makes fluctuations in population size due to changes in age-structure of less importance than in long-lived species (Lande, Engen & Sæther 2003).

Whatever the mechanism causing the rarity, our results indicate that many important dynamical characteristics of populations are closely related to the overall rareness of species. This provides support for a rarity syndrome, which involves changes in the dynamical characteristics of populations both in time and space once they have become rare. An important characteristic of this syndrome is small local population size (Fig. 2a) but large annual variation in log population size (Fig. 1a). If this relationship is caused only by demographic stochasticity we would expect the slopes of these relationships at a logarithmic scale to be equal to −1 (Lande, Engen & Sæther 2003; Desharnais *et al.* 2006). In all species the slopes between the (log−) process variance and (log−) mean population size were significantly larger than −1, indicating a contribution also of σ_e^2 to the variance in population growth rates of these species. However, because $\sigma_d^2 > > \sigma_e^2$ (Sæther *et al.* 2005b) for species with life-history characteristics as those included in the present study (Fig. 1, Table 1), the larger contribution to the density-dependent increases in σ_p^2 will be demographic stochasticity. Such an inverse density-dependent decrease have also previously been noted in several North American prairie duck species (Sæther *et al.* 2008). These dynamical characteristics are also correlated with other macroecological patterns in spatial distributions, e.g. rare species have smaller geographical ranges (Gaston 1994; Brown 1995) and occupy a smaller proportion of suitable sites than common species (Gaston *et al.* 2000; Freckleton, Noble & Webb 2006; Webb, Noble & Freckleton 2007). This effect of rarity was life-history dependent because the process variance and the probability of local disappearance were at a given local population size larger in species with large clutch sizes and high mortality (Table 2 and 4), which are related to higher demographic variance in species with short generation times (Sæther *et al.* 2004). Accordingly, Sæther *et al.* (2005a) found in a set of smaller bird species that the population size necessary for obtaining a certain expected lifetime increased with clutch size because of larger influence of environmental stochasticity on the dynamics in high-fecundity species.

One general pattern in population ecology is that there is a relationship between abundance and population variability (Taylor 1961, 1986; Taylor & Taylor 1977). Accordingly, in many British (Taylor & Woiwood 1982; Hanski & Tiainen 1989) and North American (Curnutt, Pimm & Maurer 1996) bird species there is a relationship between the temporal variation and the mean population size. Theoretical analyses have shown these relationships are strongly affected by the stochastic components of the population dynamics as well as their spatial scaling (Anderson *et al.* 1982; Engen, Lande & Sæther 2008). Here we show that an important contributor to the mean-variance relationships in population size will be the decrease in variance in the annual changes in log population size with increasing population size (Fig. 1).

Analyses of stochastic population models have revealed that the risk of extinction increases with decreasing population size (Lande, Engen & Sæther 2003). In accordance with this theoretical prediction the probability of local disappearance was a small number effect, independent of species-specific characteristics (Fig. 3). A similar pattern has previously been recorded for eight species of British woodland species, in which the probability of local extinction was inversely related to population size (Bellamy, Hinsley & Newton 1996). A major contribution to this small-number effect is the large effect of demographic stochasticity at smaller population size (see eqn 1a).

A general feature of the population dynamics of many species is that the fluctuations in population size at different localities are correlated (Liebhold, Koenig & Bjørnstad 2004; Ranta, Lundberg & Kaitala 2006). However, there is large interspecific variation even among closely related species in how the spatial synchrony in the population fluctuations decreases with distance (Koenig 1998, 2001; Paradis *et al.* 2000; Ranta, Lundberg & Kaitala 2006). Our results (Fig. 4) suggest that the degree of synchrony should depend on the size of the local populations because the inverse density-dependent effects of demographic stochasticity tend to reduce synchrony in the population fluctuations as population size decreases (Sæther *et al.* 2007). This occurs because demographic stochasticity will increase the process variance and cause population at different locations to fluctuate more independent of each other and reduce the effects of a common environmental noise. This implies that a given spatial covariation in the environment e.g. caused by similar climate variation recorded over large areas (Koenig 2002) will result in larger population synchrony in abundant than in rare species. Accordingly, Paradis *et al.* (2000) showed that abundant British bird species had more synchronous population fluctuations than rare species. In this study, the only exception was the Wren showing synchronized covariation of annual changes in population size over large areas even among small populations (Fig. 4). The population dynamics of this species is strongly influenced by large-scale variation in weather (Robinson, Baillie & Crick 2007), probably able to induce spatial covariation in the fluctuations of even small populations.

The presence of a dynamical rarity syndrome has many implications for our understanding and interpretation of ecological patterns. Rarity can arise in several ways (Rabinowitz 1981). For instance, rare species can be locally abundant, but may occur only in a few localities. However, rare British bird species tend to have more non-uniform distribution and occur at fewer suitable sites over a similar geographical range than common species (Gaston *et al.* 2000; Freckleton, Noble & Webb 2006; Webb, Noble & Freckleton 2007), indicating that they disappear locally by chance due to the density-dependent stochastic effects. Accordingly, simulating habitat-specific differences in population dynamics Baillie *et al.* (2000) found that declines in one particular type of habitats also will influence changes in other habitat types, dependent on specific assumptions about the dispersal. Thus, this shows that stochastic processes contribute in a fundamental way to link macroecological distribution patterns and fluctuations in the sizes of local populations (Bjørnstad & Grenfell 2001). Because these relationships are driven by the effects of small numbers, we predict that these patterns can be useful in deriving general principles for management strategies for rare species.

The patterns here may also have important implications for the management and conservation of small populations of rare and endangered species. Recently, considerably advances in extinction as a process have been obtained by characterizing the species included in the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (see review in Purvis 2008). The patterns derived in the present study suggests that there may be no clear distinction between rare and common species but rather that there is a rare-common continuum of species. This implies that a reduction of the abundance of a relative common species may result in changes in population dynamical characteristics over large areas because of an increased influence of demographic stochasticity. As a consequence, common species which face dramatic declines should also receive huge attention by conservation biologists (Gaston & Fuller 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Species-specific characteristics used in the analyses.

Fig. S1. The relationship between the (log−) process variance $\log(\sigma_p^2)$ and the (log−) mean population size in the plot $\log \bar{N}$ for the different species.

Fig. S2. The relationship between the probability of extinction and the population size in the plot after the first ten years of study $\log \bar{N}$ for the species in which a local 'extinction' in a plot was recorded.