ESTIMATING THE FUNCTIONAL FORM FOR THE DENSITY DEPENDENCE FROM LIFE HISTORY DATA

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Abstract. Two contrasting approaches to the analysis of population dynamics are currently popular: demographic approaches where the associations between demographic rates and statistics summarizing the population dynamics are identified; and time series approaches where the associations between population dynamics, population density, and environmental covariates are investigated. In this paper, we develop an approach to combine these methods and apply it to detailed data from Soay sheep (*Ovis aries*). We examine how density dependence and climate contribute to fluctuations in population size via age- and sex-specific demographic rates, and how fluctuations in demographic structure influence population dynamics. Density dependence contributes most, followed by climatic variation, age structure fluctuations and interactions between density and climate. We then simplify the density-dependent, stochastic, age-structured demographic model and derive a new phenomenological time series which captures the dynamics better than previously selected functions. The simple method we develop has potential to provide substantial insight into the relative contributions of population and individual-level processes to the dynamics of populations in stochastic environments.

Key words: age-structure fluctuations; nonlinear dynamics; North Atlantic Oscillation; Ovis aries; Soay sheep; time series analysis.

INTRODUCTION

Ecologists use many methods to gain insight into the processes that generate population dynamics (Tuljapurkar 1990, Royama 1992, Caswell 2001, Lande et al. 2003, Turchin 2003). These methods can be grouped broadly into two categories. First, demographic analyses where statistics describing the dynamics of a population are decomposed into contributions from age or stage-class specific demographic rates. For example, the demographic approach can be used to assess the contribution of a demographic rate like adult survival to mean population growth (Caswell 2001), or the contribution of variation in a demographic rate to population growth (Tuljapurkar et al. 2003, Engen et al. 2005, 2007, Haridas and Tuljapurkar 2005). These approaches rarely attempt to decompose population dynamics into contributions from processes like density dependence and environmental stochasticity operating via variation in demographic rates (but see Lande et al. [2006] for an exception). We define any model that explicitly incorporates parameters for birth and death

terms as a demographic model. The second category consists of time series approaches where birth, death and demographic structure is often ignored but where the dynamics are decomposed into contributions from processes like density dependence and environmental or demographic stochasticity (Royama 1992, Turchin and Taylor 1992, Ellner and Turchin 1995, Sæther et al. 2002a, b, Stenseth et al. 2004). These analyses provide insight by estimating the functional form for the density dependence and by characterizing the expected deterministic dynamics in the absence of stochasticity (May 1976). A popular current choice for the functional form is the θ-logistic model (Sæther et al. 2002b, Sibly et al. 2005, Brook and Bradshaw 2006). We define population models that do not explicitly contain birth and death terms as phenomenological time series models. Both approaches have generated substantial theoretical and empirical interest, but attempts to combine the approaches are rare (but see Reuman et al. 2006). However, in order to develop an integrated population ecology that combines the ecological and demographic processes that generate dynamics it is necessary to combine methods. In this paper we present an empirical approach that unifies the demographic and time series approaches.

Demographers have developed a range of methods that empirical ecologists have begun to use to decompose the asymptotic population growth, λ_a, the long-run stochastic growth rate, λ_s, and the variance in population growth, $\sigma^2(\lambda_a)$, into contributions from the mean and variance in age- and stage-specific survival and recruitment rates, and the covariance between them (Tuljapurkar 1990, Brault and Caswell 1993, Gaillard et al. 2000, Caswell 2001, Tuljapurkar et al. 2003, Coulson et al. 2005, Engen et al. 2005, Haridas and Tuljapurkar 2005). Related approaches include the decomposition of population growth over a time step, w_t, into contributions from each individual within the population or into contributions from the distribution of quantitative traits and genotypes (Coulson et al. 2006, Pelletier et al. 2007). These demographic decompositions have proved to be useful in devising management strategies and in characterizing fluctuating selection in stochastic environments, but they typically do not address many of the questions that population ecologists are interested in; for example, how important is density dependence compared with fluctuations in the environment in determining patterns of population dynamics?

Approaches that attempt to identify the role of density dependence in influencing population dynamics typically involve de-constructing time series of population counts into a functional form for the density dependence, or the deterministic skeleton, before characterizing variation around this skeleton (Grenfell et al. 1998, Sæther et al. 2000, 2002c, Turchin 2003). These skeletons may include only direct density dependence, or direct plus delayed density dependence. Ecologists have a tendency to select functional forms that can generate a range of exciting dynamical patterns including cycles and chaos. One reason for this is that insect populations kept in constant environments in the laboratory can exhibit complex dynamics (Costantino et al. 1997, Bjornstad et al. 1998). However, whether such deterministic dynamics are really widespread in the laboratory or the field is still unclear and the subject of debate. When analyzing time series of counts the appropriate deterministic skeleton is usually selected as a matter of personal taste, regardless of its appropriateness for the system, and unexplained variation is mopped up by environmental drivers including weather (e.g., Berryman and Lima 2006). There is also mounting evidence that the deterministic skeleton and environmental variation can interact (Coulson et al. 2004, Boyce et al. 2006), although time series approaches that attempt to identify such interactions are rare (Stenseth et al. 2004). Theoretical and empirical time series deconstructions have proved to be useful in demonstrating that density dependence and environmental variation both play major roles in generating dynamical patterns. However, the choice of functional form can be contentious (Jacobson et al. 2006, Lima and Berryman 2006, Yoccoz and Gaillard 2006) and multiple combinations of functional form and environmental variation can

generate similar patterns (Dennis et al. 2003, Ellner and Turchin 2005). Because of this the choice of functional form is to some extent arbitrary, although some general guidelines do exist. For example, if the dynamics are believed to be caused by trophic interactions then delayed density dependence should be incorporated in either a linear (Royama 1992) or nonlinear (Turchin 2003) framework. Despite these guidelines the arbitrary nature of the way that functional forms are chosen is a serious problem since different functional forms can suggest different conservation or management strategies. Needless to say, getting it right matters.

It is our opinion that there is considerable merit in both the demographic and phenomenological time series approaches. Because of this it would be helpful to decompose population dynamics into ecological processes using age-structured demographic data. A second reason to link the two approaches is that there is now a substantial literature in which ecological covariates have been fitted into models which identify causes of temporal variation in specific demographic rates (Lebreton et al. 1992, Skalski et al. 1993, Barker et al. 2002, Reed et al. 2003). For example, the growth in the use of mark–recapture methods to analyze survival means there is a multitude of published cases with convincing evidence that density dependence, environmental stochasticity, and phenotypic variation all influence survival (Skalski et al. 1993, Luiselli et al. 1996, Gaillard et al. 1997, Jorgenson et al. 1997, Loison and Langvatn 1998, Hall et al. 2001). Until such analyses can easily be incorporated into demographic models it will be challenging to identify the dynamical consequences of these processes via a specific demographic rate. In this paper we develop a way to do this and apply it to a population of Soay sheep (*Ovis aries*). First, we describe and statistically characterize the time series of the Soay sheep using up-to-date data; second we describe previously published models; third we develop new theory to estimate the functional form for the density dependence using demographic data; and finally we use our approach to decompose the population dynamics into contributions from different ecological processes. A key assumption of our approach is that because the dynamics of any population are a result of variation in birth and death rates then, whenever possible, the construction of a population model should start by analyzing these fundamental biological processes.

The Data

The population of Soay sheep on the Island of Hirta in the St. Kilda archipelago, Scotland, has been counted annually since 1955 with counts occurring during the summer (Grenfell et al. 1998). The population is food limited and there are no vertebrate herbivores competing with the sheep (Crawley et al. 2004). Data between 1985 and the present have been collected using the same counting protocol and are good estimates of population
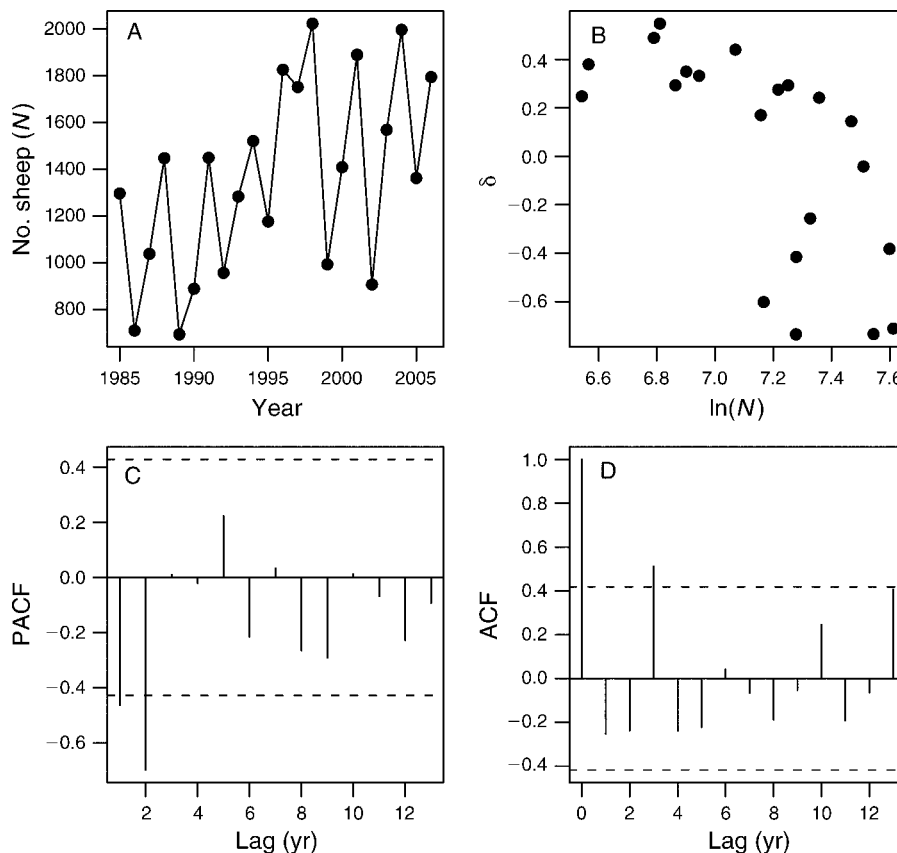
FIG. 1.   Dynamics of the Soay sheep (*Ovis aries*) population on the island of Hirta, Scotland. (A) Time series of the whole-island sheep counts (N) between 1985 and 2006. (B) Evidence of density dependence from a plot of $\delta = \ln(w) = N_{t+1}/N_t$, where w is population growth. (C) The partial autocorrelation function (PACF) of the log-transformed linearly detrended whole-island counts in panel (A). (D) The autocorrelation function (ACF) of the linearly detrended values of δ. The dashed horizontal lines in panels (C) and (D) represent statistical significance at $\alpha < 0.05$.

size (Clutton-Brock and Pemberton 2004). Between 1962 and 1984 the quality of the population estimates is unknown, and Clutton-Brock and Pemberton (2004) recommended that these data should be excluded from analyses of population dynamics. In this paper, we use the most up-to-date counts (1985–2006), but when we compare our results with earlier models, we use data from the period used in those publications. The time series we aim to understand is displayed in Fig. 1A.

Over the period 1985–2006 the population has shown 13 year-on-year increases and eight declines. The average population increase (i.e., positive values of $\delta = \ln(N_{t+1}/N_t)$), where N is population size and t is time, was 0.327, while the average population decline was −0.490. Note, we define observed population growth as the variables $w = N_{t+1}/N_t$ and $\delta = \ln(w)$. We define the parameters used to describe predictions of population growth as λ and $r = \ln(\lambda)$.

The density transition "up, up, down" over three years has been the most frequently observed temporal pattern (five cases), with "up, down" as the only other pattern observed (two cases). We have never observed two declines in a row, nor have we ever observed three

successive increases. Thus, if we have observed two successive increases in the whole island count, it is odds-on for the next transition to be a decline, whereas if we have observed one increase since the last decline, then it is five to two in favor of an increase in population size in the next year.

The population has shown a significant upward trend over this period (Fig. 1A), with an average 33 extra sheep per year at the whole-island count in August (n = 22 years, P = 0.0113; choice of start or end date for the series is not influential, and the upward trend is significant if counts with up to three of the years are trimmed from either end of the full time series). There is very clear evidence of density dependence in the time series (Fig. 1B), with detrended population differences showing significant negative partial autocorrelations at lags of 1 and 2 years (Fig. 1C). There is no significant evidence of regular cycles in the logged linearly detrended counts (Fig. 1D; Diggle 1990). The best-fit time series model to logged linearly detrended counts is of order three (autoregression estimates with standard errors = −0.166 [0.185], −0.196 [0.1832], 0.457 [0.1828]) with no evidence for a moving-average term, nor any

evidence of non-stationarity (differencing does not improve the model). This model explains 36.2% of the variance.

The relatively poor performance of these simple autoregressive models in explaining substantial amounts of variation in the time series (Coulson et al. 2000) has led to various other models being fitted in an attempt to increase the variation explained. The approaches taken have been to include environmental variables other than density and the selection of alternative functional forms for the density dependence. We now describe three previously published models of the time series. We also attempt to provide the logic that led to the identification of each functional form for the density dependence.

TIME SERIES MODELS FIT TO THE SOAY SHEEP DATA

The first stochastic model of the Soay sheep population was developed by Grenfell et al. (1998). They examined a plot of $\ln(N_{t+1})$ against $\ln(N_t)$ and noted considerable heteroscedasticity in the relationship. They consequently felt that a single function to describe the form of the density dependence was not appropriate and fitted a self-exciting threshold autoregressive regime (SETAR) model of the form

$$\begin{aligned} x_{t+1} &= a_1 + b_1 x_t + \varepsilon_1 & x_t \leq C \\ x_{t+1} &= a_2 + \varepsilon_2 & x_t > C \end{aligned} \quad (1)$$

where x_t is the natural log of population size, N, in year t and $\varepsilon_2 > \varepsilon_1$. They were able to explain some of the high-density residual variation, ε_2, with the number of days of winter storms.

Following the observation by Coulson et al. (2001) that significant interactions between density dependence and climate influence demographic rates such that bad weather at low population densities has little impact on over-winter mortality, but bad weather at high population densities can lead to severe crashes, Stenseth et al. (2004) adapted the approach of Grenfell et al. (1998) to include an interaction between density and climate. Specifically, they agreed with Grenfell et al. (1998) that there is no evidence for density dependence on population growth at low density, but that at high density, climate and density interact to influence population growth. They constructed a continuous threshold model with separate linear regimes above and below a threshold, except that the slope of the linear regime above the threshold was determined by the North Atlantic Oscillation (NAO). The r^2 values between observed and predicted population size from the models of Grenfell et al. (1998) and Stenseth et al. (2004) were both approximately 0.2.

Berryman and Lima (2006) felt that there was little theoretical justification for the inclusion of a threshold in the functional forms of Grenfell et al. (1998) and Stenseth et al. (2004). Instead, they modeled the dynamics with a modified logistic (often referred to as the θ-logistic) of the following form:

$$N_{t+1} = N_t \exp\left[R_m \left(1 - \frac{N_t}{K} \right)^Q \right] \quad (2)$$

where R_m is the maximum growth rate of the population, K is the carrying capacity, and Q determines the curvature of the functional form (Fig. 2). Berryman and Lima (2006) proposed two models: one where the carrying capacity varied linearly and another invoking a step change in carrying capacity in 1994. This step model fitted the data best and gave an r^2 between predicted and observed population size of 0.85. Berryman and Lima (2006) concluded that the shape of the functional form for the density dependence is not altered by climatic effects, but that environmental variation, specifically the NAO, can influence K, invoking Royama's (1992) "lateral" perturbation.

The functional forms of Grenfell et al. (1998), Stenseth et al. (2004), and Berryman and Lima (2006) were fit to different data sets. Grenfell et al. (1998) used the whole-island time series between 1955 and 1998 including the poor quality data for 1962–1984, while Stenseth et al. (2004) used the time series between 1955 and 2002. Berryman and Lima (2006) followed Clutton-Brock and Pemberton's (2004) recommendation and used data of known quality collected between 1985 and 2004. Because the different studies used different time series it is not clear how to easily make quantitative comparisons between the various functional forms. Although it would be straightforward to refit each model to data collected since 1985, we choose not to do this because the original choice of these phenomenological time series models was guided by those data available at the time of analysis; fitting these models to currently available data may not provide a fair comparison. We also do not consider the recent model published by Hone and Clutton-Brock (2007) because one of the climatic drivers identified, March rainfall, cannot strongly influence dynamics because in many years mortality of most age classes has occurred before March (Hallett et al. 2004).

As well as counts of the whole-island population, the Soay sheep living in the Village Bay catchment of the island have been the focus of an individual-based study since 1985 (Clutton-Brock and Pemberton 2004). The Village Bay represents approximately one-third of the whole of the island. Since 1985, >90% of individuals living within the study area have been caught within days of birth and uniquely marked with ear tags. They are then followed throughout life with demographic data collected during lambing (March–April), an annual summer catch (August), the rut (October–November), ~30 censuses per year, and regular mortality searches. The age and sex structure of the population in each year is known. Full details of methodological data collection are given in Clutton-Brock and Pemberton (2004).

The individual-based data have been the focus of a range of analyses to identify individual and population
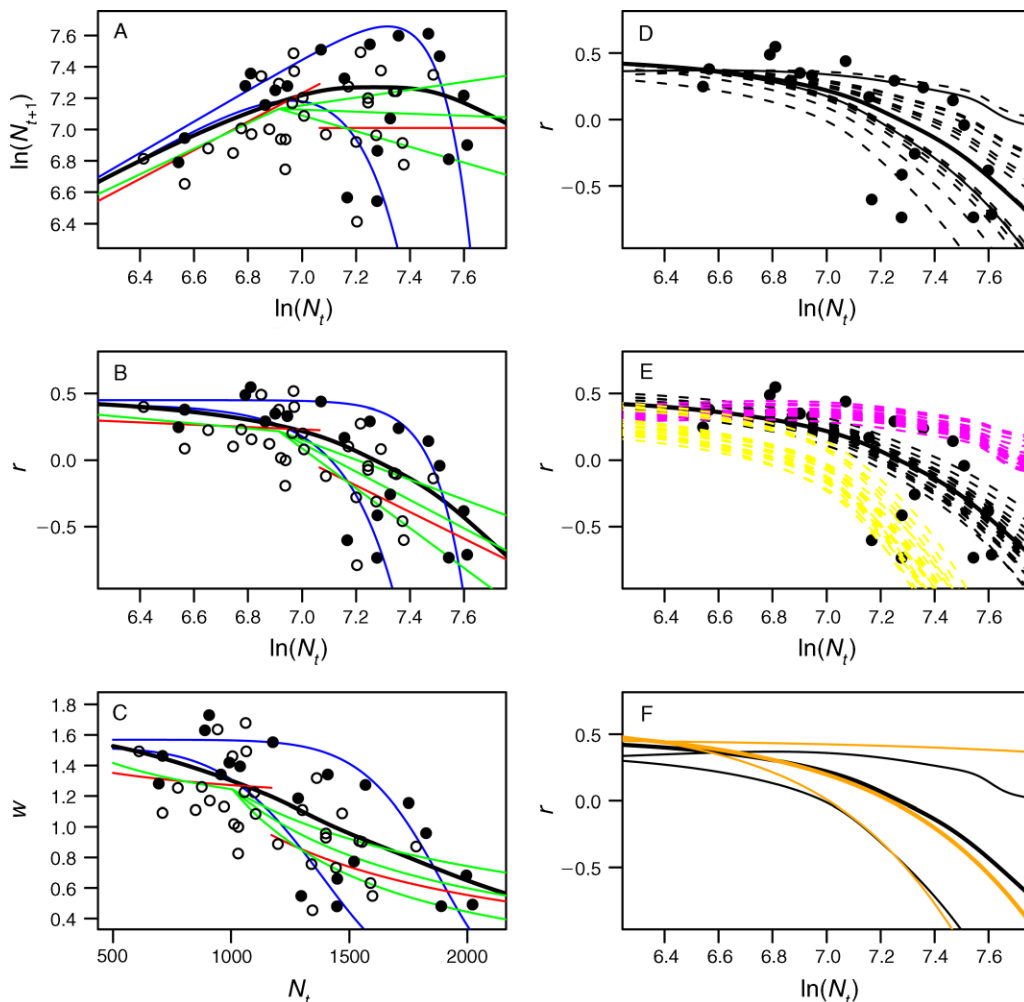
Fig. 2. Functional forms for density dependence used in different models. Heavy black lines represent the functional form estimated from demographic data holding NAO and age structure at their mean values. Red lines represent the model of Grenfell et al. (1998), green lines the model of Stenseth et al. (2004), and blue lines the model of Berryman and Lima (2006). The functional form for density dependence is plotted in three ways: (A) the Ricker curve describing the association between logged population size in consecutive years; (B) $r = \ln(w)$, where w is population growth, vs. log-transformed population size; and (C) $w = \ln(N_{t+1})/N_t$ vs. (untransformed) population size. Filled symbols represent years when detailed demographic data were collected. Note that in panels (D) and (E) only these years are shown in plots. (D) The effects of varying the NAO on the functional form of the density dependence. Each thin dashed line represents the functional form of density dependence for each observed value of the NAO during the course of the study. Thin solid lines show the functional form of density dependence for the values Stenseth et al. (2004) chose to illustrate the nonadditive effects of climate. (E) Effects of age structure on the functional form of density dependence assuming average weather (black lines), good weather (pink lines), and poor weather (yellow lines). (F) A comparison of our full demographic model (black lines) with the simplified time series model (orange lines) for low, average, and high NAO years. Solid symbols represent years when the detailed demographic data were collected.

level covariates that influence age- and sex-specific survival and recruitment (Clutton-Brock et al. 1991, 1992, 1997, Catchpole et al. 2000, Tavecchia et al. 2005, King et al. 2006). Such functions were combined by Coulson et al. (2001) into a stochastic matrix model. This model, which was parameterized using data collected between 1985 and 1996, accurately described the dynamics over 12 years (r^2 between observed and predicted population size of 0.92) and has provided good predictions of subsequent population behavior (see, for example, Coulson et al. [2001] for predictions to

2000). In this model, different climate variables influenced survival in different age classes. Stenseth et al. (2004) re-parameterized the model using all data to 2001 but used only one explanatory climatic variable, the NAO, to model the effects of weather. The simplification of the climatic drivers reduced model performance compared to Coulson et al. (2001) but it did reduce the number of state variables. Full details of parameter estimation are given in Catchpole et al. (2000), Coulson et al. (2001), and Stenseth et al. (2004) and are not repeated here. We use the demographic model described

TABLE 1. Parameter estimates for the effects of density, the North Atlantic Oscillation (NAO), and their interaction from statistical models of survival, fecundity, and lamb neonatal survival rates for individual Soay sheep (*Ovis aries*) in different demographic classes.

Class and parameter	Intercept	Density	NAO	Interaction
Survival				
Female lambs	0.5403	−0.3078	−1.6086	−0.6602
Female yearlings	2.2797	−0.1924	−2.4922	−0.5816
Female 2–6 years	2.7725	−0.1702	−1.975	−0.5041
Female >6 years	1.6199	−0.2409	−1.2312	−1.316
Male lambs	−0.2068	−0.3053	−3.5837	−0.4202
Male 1–6 years	3.4038	−0.5066	−14.7928	1.6893
Male >6 years	−0.4812	0	0	0
Fecundity				
Female lambs	−0.915	−0.376	−2.069	0
Female yearlings	0.815	−0.1017	−2.085	0
Female 2–6 years	1.3869	−0.0797	0	0
Female 7–9 years	1.106	−1.09	−2.052	−0.812
Female >9 years	−1.099	0	0	0
Neonatal survival				
Female lambs	−0.654	−0.3436	−2.313	0
Female yearlings	1.293	−0.2318	−3.55	0
Female 2–9 years	2.084	−0.0614	−1.433	−0.562
Female >9 years	0.887	0	0	0

Notes: All models were linear on the logit scale (Eq. 3). Population density was transformed prior to model fitting such that population density = (actual population density − 1202.86)/100. The NAO was transformed such that NAO = (actual NAO − 1.73)/10. The average litter sizes of breeding females aged 1 to 10 years were, respectively 1, 1.06, 1.11, 1.17, 1.23, 1.26, 1.27, 1.25, 1.2 and 1.14 lambs. No individuals >10 years old produced twins.

in Stenseth et al. (2004) to demonstrate our new methods.

The model incorporates functions to describe age-specific survival from August to August, when the whole-island censuses are conducted, and recruitment. Each function is linear on the logit scale and takes the form

$$\frac{1}{1 - 1/\exp(a + bz_1 + cz_2 + \cdots + kz_n)} \quad (3)$$

where z's are the covariates that significantly influence the age- or sex-class-specific demographic rate being modeled. Mark–recapture analysis of individual capture histories (Lebreton et al. 1992) identified seven separate demographic groups: female lambs (first year of life), female yearlings (second year of life), two- to six-year-old females, females older than six, male lambs, one- to six-year-old males, and males older than six (Catchpole et al. 2000). Survival was explained with two covariates: population size as described by the whole-island counts at the beginning of the period, and winter weather, as described by the winter NAO. In some age classes, there was a significant interaction between population density and the NAO (Table 1; Stenseth et al. [2004]).

Recruitment was modeled as a product of age-specific fecundity, lamb survival from birth to the summer census as a function of mother's age, and mean litter size of reproducing females (Tavecchia et al. 2005). Five female age classes were defined for fecundity (lambs, yearlings, two to six years old, seven to nine years old, and greater than nine years old) and four age classes for

neonatal survival (lambs, yearlings, two to nine years old, and greater than nine years old) (Stenseth et al. 2004). Fecundity and neonatal survival were modeled as a function of the whole-island population size at the beginning of the period, the winter NAO and their interaction; twinning rate was set as an age-specific constant. Recruitment was calculated as the product of fecundity, the average litter size of breeding females, and neonatal survival (Stenseth et al. 2004). Female lambs can conceive in their first rut and never produce more than one offspring. In contrast, approximately 15% of older females produce twins. Parameter values for the most parsimonious models (significance level $\alpha = 0.05$) are provided in Table 1, and these are used to demonstrate our approach.

The different models described above each have constraints on the shape of the functional form they can predict. For example, Eq. 2 constrains the shape such that the rate of change in the population growth rate increases with density. Regardless of the values used for R_m, K, and Q in Eq. 2, the model cannot produce the flat, horizontal function identified by Grenfell et al. (1998). Because of these constraints, the choice of model structure should be based on an understanding of the biology of the system, and the parameter values that determine the actual shape of the functional form should be identified through statistical analysis of existing data. One downside of phenomenological time series models is they do not have to be informed by biological understanding.

Theory Linking Demographic and Time Series Methods

If we define the number of recruits to the population at time t as r_t and the number of deaths between t and $t+1$ as m_t, then

$$N_{t+1} = N_t - m_t + r_t. \tag{4}$$

The number of survivors, s_t, is simply $N_t - m_t$, which means that population growth over a time step, $w_t = N_{t+1}/N_t$, can be written as follows:

$$N_{t+1} = s_t + r_t$$
$$w_t = \frac{s_t + r_t}{N_t} \tag{5}$$
$$= \bar{s}_t + \bar{r}_t.$$

If $\bar{s}_t$ and $\bar{r}_t$ are influenced by a range of environmental or individual covariates ($x_{1,t}$ to $x_{k,t}$), and functions describing these associations, $f(\bar{s}_t | x_{1,t}, x_{2,t}, \ldots, x_{k,t})$ and $f(\bar{r}_t | x_{1,t}, x_{2,t}, \ldots, x_{k,t})$, can be characterized, then $\lambda = f(w_t | x_{1,t}, x_{2,t}, \ldots, x_{k,t})$ can be written as the sum of these functions:

$$\lambda = f(\bar{s}_t | x_{1,t}, x_{2,t}, \ldots, x_{k,t}) + f(\bar{r}_t | x_{1,t}, x_{2,t}, \ldots, x_{k,t}) \tag{6}$$

which describes how covariates influence the population dynamics via recruitment and survival. Note that survival and recruitment do not need to be of the same form or influenced by the same covariates.

It is straightforward to extend Eq. 6 to include demographic structure. If p_i is the average proportion of the population in age class i over time, then

$$\lambda = \sum_{i=1}^{X} p_i [f(\bar{s}_{i,t} | x_{1,t}, x_{2,t}, \ldots, x_{k,t}) + f(\bar{r}_{i,t} | z_{1,t}, z_{2,t}, \ldots, z_{k,t})]. \tag{7}$$

$f(\bar{s}_{t,i} | x_{1,t}, x_{2,t}, \ldots, x_{k,t})$ and $f(\bar{r}_{t,i} | z_{1,t}, z_{2,t}, \ldots, z_{k,t})$ for each of the X age classes can be estimated using individual-based survival and recruitment data using, for example, generalized linear models (Crawley 2002) and mark–recapture methods (Lebreton et al. 1992).

In Eq. 7, we have set the age structure to the average proportions in each age class observed over the course of the study. If p_i is permitted to vary with time, $p_{i,t}$, then a function describing the dynamics can be obtained having corrected for fluctuations in the demographic structure:

$$\lambda = \sum_{i=1}^{X} p_{i,t} [f(\bar{s}_{i,t} | z_{1,t}, z_{2,t}, \ldots, z_{k,t}) + f(\bar{r}_{i,t} | z_{1,t}, x_{2,t}, \ldots, z_{k,t})]. \tag{8}$$

If one of the covariates, $z_{t,k}$, is density then the functional form of the density dependence can be obtained by holding all other covariates constant while varying the effects of density in the age-specific survival and recruitment functions. It is also possible to hold density constant in one age-class-specific demographic function (or one age class) while letting it vary in the others. Different resulting functional forms can then be compared.

Eq. 7 describes how fluctuations in population size are influenced by covariates, but it does not describe the contribution of each of the covariates to overall population dynamics. This contribution can be estimated by calculating how the inclusion of the covariate influences the fit between observed and predicted dynamics (as measured, for example, by r^2 [Kvalseth 1985]). Suppose that two variables, z_1 and z_2, interact to influence both survival and recruitment in a non-age-structured population (Eq. 6). Then, to assess the contribution of z_2 via both its additive contribution and its interaction with z_1, we wish to compare the r^2 values between observed population growth, w_t, and model predictions for population growth for the two models:

$$\lambda = f(\bar{s}_t | z_{1,t} + z_{2,t} + z_{1,t} \times z_{2,t}) + f(\bar{r}_t | z_{1,t} + z_{2,t} + z_{1,t} \times z_{2,t}) \tag{9}$$

and

$$\lambda = f(\bar{s}_t | z_{1,t}) + f(\bar{r}_t | z_{1,t}). \tag{10}$$

We use this logic to estimate the overall contribution of density dependence, the NAO, and age-structure fluctuations to the population dynamics of Soay sheep. It is also possible to estimate the contribution of density dependence or climate to population growth via a specific demographic rate by holding rate-specific parameters at their mean values, but space precludes us from reporting these results here.

Of course, the r^2 value of an association is only one measure of goodness of fit: as with all measures of goodness of fit it has its strengths and limitations (Kvalseth 1985). Although we use r^2 values in this paper, it would be straightforward to compare information criteria like the AIC (Akaike's information criteria) and BIC (Bayesian information criteria) or even cross-validation statistics between models. We choose r^2 values as they provide a straightforward way to estimate the relative contributions of different processes to the population dynamics.

Methods

The shape of the functional form for the density dependence was identified using the parameter values in Table 1 and Eq. 7 and setting and holding the NAO at its mean value while varying density. The effect of varying the NAO on the functional form for the density dependence was explored by setting the NAO to a value different from its mean and recalculating predictions using Eq. 7. We calculated the functional form for the density dependence for each value of the NAO observed during the course of the detailed demographic study.

TABLE 2.   The proportion of variation explained by demographic models incorporating density, NAO, their interaction, and fluctuations in the age structure.

Model	Density	NAO	Age structure	Density × NAO	r	r^2
1	+				0.680	0.462
2		+			0.471	0.222
3			+		0.460	0.212
4	+	+			0.835	0.697
5	+		+		0.709	0.503
6		+	+		0.612	0.374
7	+	+	+		0.851	0.725
8	+	+		+	0.844	0.712
9	+	+	+	+	0.872	0.761

Notes: Correlation coefficients (r) and the proportion of variance explained by each model are also given (r^2). A "+" indicates that the parameter is included in the model. Model 9 is the full demographic model parameterized with values in Table 1. To obtain the other models, some parameters in Table 1 are set to 0. For example, model 1 is a model with all parameters set to 0 except for those in the third column in Table 1 (density) and age structure set to the population mean, p.

The effect of changing the age structure on the shape of the functional form was examined in a similar manner. Initially we set the age structure to the mean observed proportions, p_i. Next we examined how altering these proportions influenced the functional form. We used observed demographic structures in each year for values of $p_{i,t}$. We repeated the examination of age-structure effects for three values of the NAO: the mean value, the highest observed value and the lowest observed value.

Using the demographic model summarized in Table 1, we examined how density dependence, the NAO, their interaction and age-structure fluctuations contributed to the observed population dynamics by comparing the r^2 values between observed population growth in each year and predicted population growth from models incorporating different processes. The terms that were incorporated into each model are shown in Tables 2 and 3.

We simplified the full demographic model specified in Eq. 7 by first ignoring age-structure fluctuations and simplifying the recruitment term (Appendix). We fitted the resulting time series model to the time series data collected since 1985. We fitted this model using nonlinear least squares regression using the nls function in R 2.4.1 (R Development Core Team 2006).

RESULTS

Comparing functional forms

The functional form estimated using Eq. 7 for the mean value of the NAO is displayed in Fig. 2A–C where it can be compared with those identified from time series models. The models of Grenfell et al. (1998) and Stenseth et al. (2004) qualitatively capture the functional form estimated from the demographic data, while the model of Berryman and Lima (2006) does not. The key difference between the functional form of Berryman and Lima (2006) and the others is the rate at which the

population growth rate declines with population size. The functional form of Berryman and Lima (2006) predicts that a small increase in density at high numbers produces a large decline in population size. Such huge density-dependent declines are not predicted by the other functional forms.

The shape of the functional form for the density dependence estimated from the demographic data varies with both the NAO (Fig. 2D) and changing age structure (Fig. 2E), and when both these processes are included the fully specified model covers nearly the entire range of observation (Fig. 2E). The only exceptions are two points at low density when the population grew faster than predicted. As winter weather gets progressively worse (higher values of the NAO), the functional form for the density dependence becomes steeper. With increases in the proportion of the population consisting of those age classes that are least strongly influenced by density, the functional form becomes shallower.

Contribution analysis

The correlation between observed population growth and population growth predicted by the full demographic model (Table 1) is 0.872 ($r^2 = 0.761$). We estimated the dynamics of population growth by fitting a model where the NAO was held constant at its mean value and the age-structure was held at p_i but observed density was fit as a covariate. The r^2 between predicted values from this model and observed population growth was 46.2%, which we interpret as the additive contribution of density dependence to the population dynamics. When we held density and the NAO at their mean values but fitted $p_{i,t}$ as observed covariates, the resulting model explained 21% of observed fluctuations, which suggests that the additive effects of age-structure fluctuations contribute about one-fifth to the observed dynamics, approximately the same contribution as the NAO (Tables 2 and 3). When combined, the additive contribution of density, NAO and age-structure fluctuations was 72.5%, with age-structure fluctuations contributing least. When interactions between density and NAO were included in the model, a further 3.6% of the variation was explained (Tables 2 and 3). All model fits are summarized in Table 2. When assessing the contribution of different terms to the full model by deletion, we found that density contributed most to the population dynamics, followed by climate, age-structure

TABLE 3.   An estimate of the contribution of density, the NAO, their interaction, and the difference in r^2 values between models (Δr^2) in Table 2.

Contribution	Model comparison	Δr^2 (%)
Density	model 9 − model 6	38.7
NAO	model 9 − model 5	25.8
Age structure	model 9 − model 8	4.9
Density × NAO	model 9 − model 7	3.6

TABLE 4. Parameter estimates of time series models based on Eq. 13, parameterized to include the additive and interactive effects of population density and the NAO.

Model and term	1955–2006		1986–2001	
	Estimate	SE	Estimate	SE
Model 3				
Intercept	0.1996	0.1158	0.1565	0.1302
Density	**−0.1528**	**0.0283**	**−0.1369**	**0.0351**
NAO	**−1.7773**	**0.5345**	**−1.5844**	**0.5899**
Model 4				
Intercept	0.1884	0.1187	0.1478	0.1306
Density	**−0.1622**	**0.0310**	**−0.1423**	**0.0357**
NAO	**−1.6194**	**0.5594**	**−1.4236**	**0.5967**
Density × NAO	−0.1687	0.1938	−0.2298	0.2114

Notes: The table shows parameter estimates for a model that does not include the interaction between the NAO and population density (model 3) and a model that does include the interaction (model 4). These can be compared with parameter values in Table 1, but a formal comparison is not provided here. Boldface type represents significance at $\alpha < 0.5$.

fluctuations, and the interaction between density and the NAO (Table 3).

The fit of the full demographic model summarized in Table 2 shows that, when density and weather are fitted simultaneously, there is no apparent need to invoke the two distinct time periods used by Berryman and Lima (2006) to explain substantial amounts of variation. However, examination of Fig. 1 does show that a post hoc division can be made. Between 1985 and 1995, the maximum population size achieved was always less than 1500 sheep, while subsequently, population sizes prior to a population decline have all been above 1800 individuals.

Model simplification

Structured demographic models often have many parameters. Can we simplify them, and if we do, how does the simplified model perform? If we ignore age structure and assume all individuals are identical, we can start with Eq. 6. As long as the form of the survival and recruitment functions are the same, and the shape of these forms is similar then it is algebraically inevitable that

$$f(\bar{s}_t | z_{1,t}, z_{t,2}, \ldots, z_{k,t}) + f(\bar{r}_t | z_{1,t}, z_{t,2}, \ldots, z_{k,t}) \quad (11)$$

can be approximated as

$$f(w_t | z_{1,t}, z_{t,2}, \ldots, z_{k,t}). \quad (12)$$

The functions in Eqs. 11 and 12 will have the same form but parameters associated with the covariates $x_{k,t}$ will (generally) differ. Because Eq. 12 does not explicitly have terms describing birth and death, we consider this to be a phenomenological time series model and not a demographic model. In the specific case of the Soay sheep we derive the following (see Appendix):

$$\lambda = \frac{1 + \xi L}{1 + \exp^{-(a + bN + c\text{NAO} + dN \times \text{NAO})}} \quad (13)$$

where L is a constant describing the average litter size of breeding individuals, and ξ is a constant. The equation can then simplified by deleting any nonsignificant terms using standard model simplification methods (Crawley 2002).

The time series model parameterized with population density, the NAO, and their interaction provided a good description of observed fluctuations in the time series between 1985 and 2006 and for the shorter time series between 1985 and 2001. This latter parameterization permits comparison with the demographic model (Table 4). The estimates for density and the NAO were larger in the analysis of the longer time series (Table 4) suggesting more pronounced (but not significantly so) effects of population density and climate in later years. The r^2 value between observed and predicted values for a model including density, the NAO and their interaction for the time series between 1985 and 2001 was 0.694 (Table 5), which is reasonably close to that obtained for the demographic model described in Table 1 (0.761). The functional form for the density dependence was similar between the full demographic model and this parameterization of the time series model (Fig. 2F). However, a comparison between Tables 3 and 5 shows that the time series model identifies a larger additive contribution of the NAO (55.5%) to the population dynamics compared with the full demographic model (22.2%). A plot of the association between observed and predicted population growth (Fig. 3) shows why: a model with density, NAO and their interaction is well behaved, but model simplification leads to increasingly nonlinear associations between observed and predicted dynamics.

DISCUSSION

In this paper, we do three novel things. First, we demonstrate how it is possible to identify the association between population density and the population growth rate—the functional form for the density dependence—using detailed individual-based life history data. We apply the approach to data from a population of Soay sheep and compare results obtained with detailed demographic data with those obtained from phenomenological time series analyses. Second, we decompose the population dynamic process into contributions from a range of ecological processes including density dependence, fluctuations in the age and sex structure,

TABLE 5. Performance of time series models based on Eq. 13.

Model	Density	NAO	Density × NAO	r
1	+			0.450
2		+		0.555
3	+	+		0.665
4	+	+	+	0.694

Note: The table shows the r^2 between observed and predicted population growth using four different models; a "+" indicates that the term is included in the model.
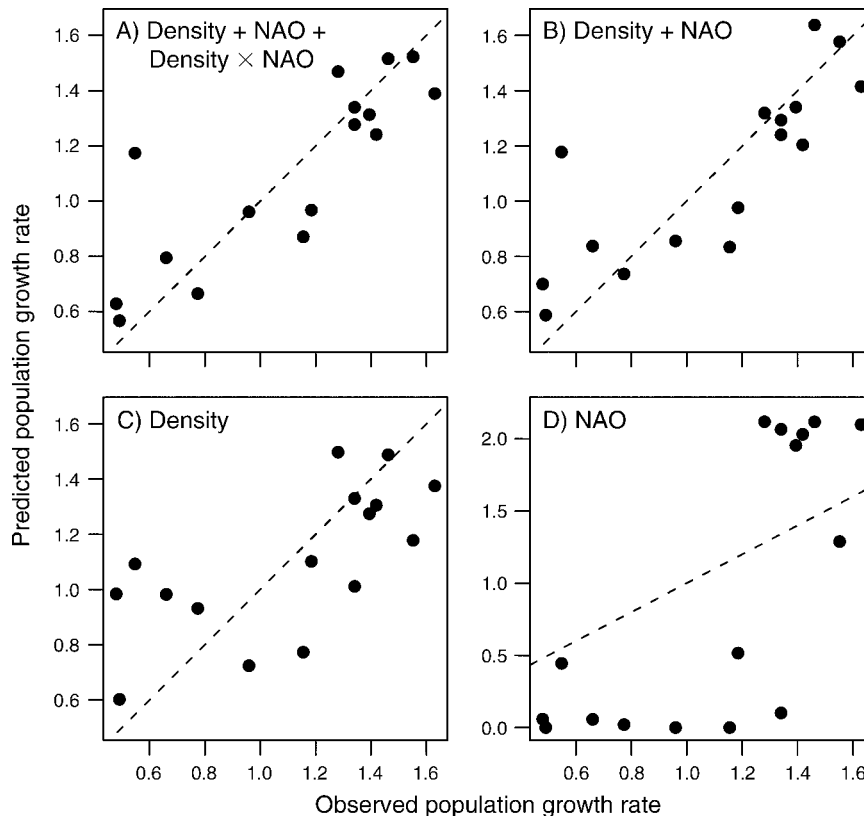
FIG. 3. Model checking plots comparing observed and predicted values for the four time series models (Eq. 13) summarized in Table 5. (A) The behavior of the full model with main effects of weather and density and their interaction; (B) main effects for density and weather; (C) the main effect of density alone; (D) the behavior of the model containing a main effect of weather alone. Dashed lines represent $y = x$. Note that the y-axis scale differs in (D), the model for the NAO.

and environmental variation. In the population analyzed, the additive effects of density dependence are approximately twice as important in determining dynamics as are the additive effects of age-structure variation or climate. However, in order to gain a good understanding of the dynamics, density dependence, environmental stochasticity and differences between individuals have to be considered. Third, we simplify our fully specified demographic model to generate a phenomenological time series model. This model performs well in capturing the key processes identified by the full demographic approach.

There are substantial differences between the time series models that have been fitted to the Soay sheep data in the past. Berryman and Lima (2006) argued that only the carrying capacity was a function of environmental drivers, but that other parameters were not. This means that the functional form for the density dependence maintains its shape, but moves horizontally along the x-axis in Fig. 2 as a function of environmental variation. Royama (1992) referred to this as a "lateral perturbation" effect. The SETAR model of Grenfell et al. (1998) also suggests that the functional form for the density dependence maintains its shape above the threshold they identify, and that climate does not move

it along the x-axis in Fig. 2, but rather shifts it vertically in what Royama (1992) calls a "vertical perturbation." The nonadditive model of Stenseth et al. (2004) proposes that climate alters the functional form for the density dependence by effectively rotating it above the threshold. The demographic analyses broadly support the conclusion that weather only matters at high density (Fig. 2; see also Coulson et al. 2001), but the decomposition we report here suggests that the nonadditivity makes a relatively small contribution to the population dynamics (Tables 2 and 3). This highlights the interesting point that nonadditivity in one model can be captured with additive effects in another. Overall, however, the model of Stenseth et al. (2004) provides estimates of the functional form that agree most closely with those identified from the demographic data, although the model of Grenfell et al. (1998) also performs well. The model proposed by Berryman and Lima (2006) provides a picture of the dynamics that is at odds with the demographic analyses. However, this model does fit the data well when goodness of fit is assessed with r^2. This demonstrates that if some measures of statistical fit are used independently of biological understanding (in this case the processes influencing birth and death) they do not necessarily help

in providing insight (Kuparinen et al. 2007). We suspect that analyses of individual survival and recruitment records are, in general, more likely to provide insight that is closer to reality than phenomenological models of population counts that do not incorporate such detail.

The phenomenological time series model we derive provides a description of the dynamics which is consistent with that identified from the demographic analyses. This should not be surprising given the equation is approximated directly from the demographic equations. The time series model incorporating density, NAO, and their interaction (Tables 4 and 5) captures the functional form for the density dependence identified with the demographic model more accurately than any of the other time series approaches. The model we derive can easily be extended to incorporate lagged effects of density or other environmental drivers simply by incorporating more terms in the exponential part of the function as is standard in linear autoregressive models (Royama 1992). If the initial demographic functions to be simplified are nonlinear, simplification may be more challenging than in the linearized example we used. However, linearized analyses of demographic data are frequently used (e.g., Lebreton et al. 1992, Jorgenson et al. 1997, Hall et al. 2001, King et al. 2006), although nonlinear analyses of demographic rates within the mark–recapture framework have recently been developed (Gimenez et al. 2006). One assumption of our method as we apply it here is that the association between environmental drivers and survival and recruitment are well described by linearizable functions that can be estimated from mark–recapture approaches or general linearized modeling with a binomial error structure. This assumption is not general, it is specific to the application we report here.

The Soay sheep study is unusual in that we have such a detailed biological understanding of the system (Clutton-Brock and Pemberton 2004). The population is food limited (Crawley et al. 2004). During the summer months vegetation biomass increases as plant productivity is always greater than losses to herbivory. At the end of the main growing season, in the autumn, the biomass of available vegetation depends on the number of sheep, possibly the composition of the population, and weather during the growing season (April to September). At the onset of winter, sheep are in peak condition (Clutton-Brock and Coulson 2002) although summer weights do vary from year to year (Clutton-Brock and Pemberton 2004). During winter, sheep deplete the standing biomass produced over the summer. Depending on sheep numbers and the size of the standing crop, the biomass may run out before the start of the next growing season. Overwinter grass growth can occur when the temperature is above 5°C. Thus, two sets of weather variables may have indirect effects on sheep dynamics: those determining the size of the forage crop at the end of the growing season; and those affecting the rate of primary production during the winter when green

biomass is low. Finally, climate also influences sheep directly by imposing energetic demands, and this in turn influences the food requirements of individuals (Grenfell et al. 1998). In previous work, we have shown that the timing of spells of harsh weather within a winter influences the mortality schedule within the population and that this can generate an interaction between climate and density (Hallett et al. 2004). For example, if many sheep die relatively early, this reduces competition among survivors for the remaining biomass, and survival rates through the rest of the winter are relatively high. In contrast, if few sheep die early in the winter, competition for food remains high, leading to high mortality later in the winter as a relatively small proportion of sheep succeed in fulfilling their energetic demands (Hallett et al. 2004). Our understanding of the biology points to a complex interaction between climate and population dynamics mediated through food availability. This conclusion is also supported through analysis of individual demographic rates (Catchpole et al. 2000, Coulson et al. 2001). Biologically, it seems highly unlikely that climate operates only via the carrying capacity and, more likely, that both of Royama's (1992) lateral and vertical perturbations need to be invoked to accurately capture the modus operandi of density and climate within this population. We are keen for population ecologists to use the Soay sheep time series to test the performance of a range of models and approaches, and we hope that our biological understanding of the system described above is helpful when constructing models.

Clearly, it is not desirable to incorporate every potentially important process in a general model of population dynamics. Detailed understanding of individual systems is most useful if it can advise on the appropriate form for simple models that provide useful insight into the dynamics of systems where detailed data are not available. We now consider the classical theoretical approaches that ecologists have used, before advocating the more statistically rigorous frameworks that have recently been championed. The standard approach to identifying the functional form for the density dependence is to examine the association between logged population size or the population growth rate and logged population size in previous time steps, while ignoring other drivers. When density in many previous steps is required to describe population growth the functional form is usually assumed to be linear (Royama 1992). If only direct density dependence is considered then the association is often assumed to be nonlinear (May 1976). Direct nonlinear density dependence, or linear direct and delayed density dependence, can generate dynamical patterns that qualitatively resemble patterns observed in nature, and this may be one reason why these forms are so often selected. Density is typically fitted independently as a first step in analyses because if only one process needs to be invoked to capture an observed dynamical pattern, then dynam-

ics are comparatively simple and analytical solutions are often tractable. However, there is mounting evidence that the dynamics of free-living populations can be influenced by a range of factors (Stenseth et al. 2002, Bonsall and Benmayor 2005, Benton et al. 2006, Hanski and Saccheri 2006), and that focusing on one factor, or failing to fit model terms simultaneously can influence results. In a linear and purely additive framework where density and climatic drivers are not correlated and do not interact to influence population growth, the order of adding terms will make no difference to results. However, in non-additive and nonlinear frameworks the order in which terms are fitted into models can influence results. Given how easy it is to fit terms simultaneously into statistical models of population growth, we argue that population ecologists should no longer focus on attempting to join the dots with nonlinear univariate functions prior to explaining away residuals with linear associations with covariates, but should embrace a more sophisticated statistical framework. Fortunately, many such approaches are currently being developed that do this (Sæther et al. 2002b, 2005, Lande et al. 2003, Stenseth et al. 2004, Clark 2007). The approach we develop here has substantial potential to investigate the relative importance of different population and individual-level processes for the population dynamics. As long as a variable is statistically associated with survival or recruitment its contribution to the dynamics can be assessed. The biggest assumption is the choice of function describing the association between variables and demographic rates, although this choice is typically straightforward.

Before invoking nonlinear effects it seems sensible to examine the performance of linear, or linearized, direct density dependence when combined with climatic variation. There is a growing number of papers where this is done (Sæther et al. 2002b, 2005). It is becoming apparent that linear, or linearized, interactions between density dependence and environmental drivers can generate a range of dynamical patterns seen in nature (Royama 1992, Coulson et al. 2004, Boyce et al. 2006) and that strong nonlinear density dependence does not necessarily need to be invoked to generate complex dynamics. The time series model we derive in Eq. 13 is linearized and links directly to the fundamental biological processes of birth and death. It also has the added advantage that it does not include parameters like carrying capacity that are difficult, or impossible, to measure directly in the field: something that makes model validation difficult. We suspect that considerable insights into the dynamics of populations can be obtained by simultaneously considering the effects of density and environmental variation in a linear framework.

We also present a decomposition of the population dynamic process into relative contributions from density dependence, environmental stochasticity, and age-structure fluctuations. A comparison of a model that incorporated age-structure fluctuations with one that

did not suggested that age-structure fluctuations explain ~5% of the observed dynamics. In contrast, when fitted alone, age-structure effects explained about as much variation as climate (~20%). The relative contribution of age-structure fluctuations to population dynamics depends on how much the structure of the population fluctuates (Tuljapurkar 1990, Caswell 2001), the correlation between the structure of the population and other drivers like population density and climate (Coulson et al. 2001), and the similarity of the effects of these drivers on age-specific survival and recruitment. In the model we use here, each age and sex class is influenced by the NAO: a useful, but crude, approximation of local climate (Hallett et al. 2004, Stenseth and Mysterud 2005). However, previous research on this population has shown that survival and recruitment in different age and sex classes are actually influenced by different climatic drivers (Catchpole et al. 2000, Coulson et al. 2001). We suspect that a model that includes different drivers within each demographic class would lead to greater variation being apportioned to age-structure fluctuations, but we do not develop that argument here.

In this paper, we have demonstrated that it is straightforward to estimate the functional form for the density dependence from demographic data, and to decompose observed population dynamics into contributions from different ecological processes. We have also derived a simple time series model from demographic analyses. This model is very flexible and can be extended to incorporate a range of ecological factors of interest to population biologists. We hope that application of this approach to other detailed demographic data sets will help provide insight into interactions between density, climate variation, and population growth, and that these will lead to the development of improved simple models that can be used where detailed long-term data are not available.

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APPENDIX

Derivation of time series model (*Ecological Archives* E089-100-A1).