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Weather and grouse population dynamics

Jan Lindström

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One paradigm in the biology of game animals is that short-term fluctuations in population densities can be explained with variations in weather. A number of empirical models have been produced supporting this view. However, validation of such models has often been lacking or insufficient. Two methods for checking the validity of such models are presented. The first method is to derive a model for one population and test it against another data set. The second method is to evaluate the forecasting power of the model. For these purposes, the relation between 36 weather variables and population parameters of capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, and hazel grouse *Bonasa bonasia* was studied using population data (1964 - 1984) from three adjacent provinces in Finland. Total population size, number of juveniles and population growth rate were used as dependent variables. Prior to the analyses, the population data were ln-transformed and detrended. Stepwise regression analysis was used with province-specific weather data as explanatory variables. These models were then used to make forecasts one year ahead for each species and province, and the prediction was tested against observed data. Transferred models from the other provinces were also used. The requirement for a good empirical model is that it should be possible to use the model on similar problems in nearby areas. Stepwise regression analyses yielded reasonable fits in most cases ($\bar{R}^2$ ranging between 0.2 - 1.0). However, a model from a given province invariably produced a poor fit when applied to another province. Forecasting the population dynamics was only occasionally successful, and was not directly related to the fit of the models. The results suggest that it may often be hazardous to use weather data for predicting population fluctuations of game species, especially for management purposes. This conclusion was further strengthened by demonstrating that using 36 province-specific white noise variables, it was possible to build models with fit and forecasting properties essentially equal to those of the weather-based models.

Key words: grouse, population dynamics, weather, forecasting

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One fundamental objective of population ecology is to understand the factors causing fluctuations in population density. It has been frequently suggested that short-term population fluctuations of many game species can be - at least partly - explained by weather factors (Siivonen 1956, 1957, Arditi 1979, Slagsvold & Grasaas 1979, Schröder et al. 1982, Eiberle & Matter 1984, 1985a,b, Eiberle 1987, Steen et al. 1988, Swenson et al. 1994). The classic hypothesis of the causal link between sunspot cycle, weather conditions and the dynamics of snowshoe hare *Lepus americanus* and Canada lynx *Lynx canadensis* (e.g. Elton 1924, Sinclair et al. 1993) is a special case of this. In general, studies of weather and population fluctuations are based on observed correlations between weather variables and population numbers or population change. My purpose is to show that this kind of approach may lead to incorrect conclusions. The reason for this is that it is temptingly easy to find biologically reasonable explanations for the effect of almost any weather-derived variable on the population. Although weather may be, for instance, a remarkable mortality factor, the causal link between a particular weather variable and population processes still remains to be proven in most cases.

Despite the difficulties in assessing causality between

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correlating factors, it is still desirable to determine how weather may influence population change. This is especially important when the study has implications for game management. In this study, I present two different approaches to assessing the explanatory power of weather-derived empirical models. First, a successful model should be portable. That is, it should perform - at least almost - as well in a nearby location as in the original location. Secondly, if the model has identified the critical processes, it should be capable of forecasting short-term population changes.

Material and methods

Grouse data

Nation-wide route censuses were used to monitor grouse populations in Finland between 1964 and 1984. Censuses were run yearly between 5 August and 4 September by voluntary observers, and the data comprise 20,000 - 30,000 route kilometres per annum. For details of the census method, see Rajala (1974), Lindén (1981) and Lindén & Rajala (1981), and for the population data, see Lindén (1989). I analyse data of capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, and hazel grouse *Bonasa bonasia* from three provinces, Oulu, Vaasa and Central Finland (Fig. 1).

There is a strong decreasing trend in the Finnish grouse data (Lindén 1989, Lindström et al. 1995). As my aim is not to seek for any weather-based explanation for the decreasing trend but to study the short-term fluctuations, all the grouse data were detrended prior to the analyses by regressing species and province-specific models (ln)population density against time. This was also done for the (ln)number of juveniles, J_t. Population data were ln-transformed to remove the heteroscedasticity in the data. Since it has been suggested that the effect of weather should actually be clearer on the juvenile production and population growth rate than on the total population size (Royama 1992), I also analysed the detrended ln(number of juveniles), J_t, and population growth rate, R_t, besides total detrended ln(population size), X_t. Population growth rate, R_t, was defined as

$$R_t = X_{t+1} - X_t. \qquad (1)$$

Weather data and random variables

I used weather data from 1964 - 1984 from three weather stations, Kajaani in the province of Oulu, Vaasa in the province of Vaasa, and Jyväskylä in the province of Central Finland. The variables used were monthly minimum temperature (mi°C), monthly maximum temperature (ma°C), and monthly precipitation yielding a total of 36 variables for each province. The seasonal effect of the monthly weather data was removed by calculating

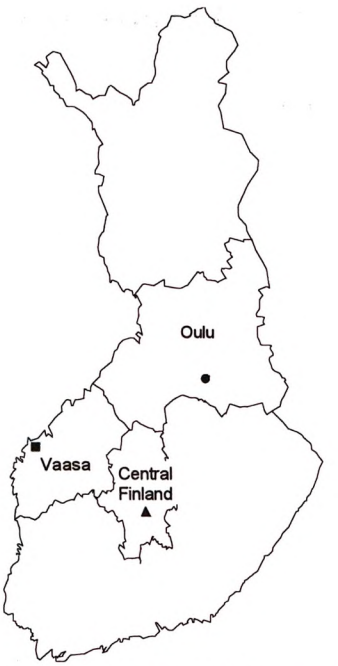


Figure 1. Location of the provinces of Oulu, Vaasa and Central Finland in Finland. The weather stations from which the weather data originate are indicated by black symbols in the corresponding provinces (circle = Kajaani, square = Vaasa, and triangle = Jyväskylä).

$$Y_t' = Y_t - \frac{1}{21}(Y_1 + ... + Y_{21}), \qquad (2)$$

where $\{Y_t\}$ denotes the observed series of the weather variable used, e.g. precipitation in January (see e.g. Chatfield 1989).

Using a large number of explanatory variables for rather short time series makes the results sensitive to the ratio of data points to explanatory variables. Therefore, I also created 36 random variables for each of the three provinces. These variables certainly do not have any causal link to the grouse fluctuations. Thus, the forecasting performance of the models based on them serves as a useful reference point in comparisons between weather-based and random variable models. All the random variables were drawn from Normal (0,0.2). The chosen variance value of this distribution does not have any effect on the results since the coefficients of the regression model take that into account.

Data analysis

Total population size, X_t, number of juveniles, J_t, and the population growth rate, R_t, were subjected to stepwise regression analyses using either province-specific weather

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data or random variables (both totalling 36) as explanatory variables. The number of variables entering the model was not restricted, as the sole purpose here was to find the best fit between model and data, and thus maximise the coefficient of determination. Adjusted coefficient of determination, $\overline{R}^2$, was used since it acknowledges the varying number of variables in the models (Pindyck & Rubinfeld 1991).

One method of model validation is the performance of a model constructed and applied in different, but nearby, locations. For this purpose I first constructed the stepwise regression model for all the species-specific population data using the weather data from the same province as explanatory variables. Then I used the models with the population data of the two adjacent provinces. That is, each model was transferred to the neighbouring provinces, applied to the weather data and validated against the observed population data. For instance, the model constructed for Central Finland was also used in Vaasa and Oulu, but with local weather and population data. From now on, I shall refer to these models as province-specific and transferred models, respectively.

When comparing the fits of province-specific and transferred models, $\overline{R}^2$ cannot be used. In such cases the values of $\overline{R}^2$ are not restricted to 0 -1, which makes their interpretation questionable (Pindyck & Rubinfeld 1991). Instead, the squared sum of errors, SSE, was used for such comparisons. Since there is one data point less in the models of R_t than in the models of X_t and J_t, SSE is not directly comparable between them. However, the amplitude of population data being much the same in all the population series between and within species (e.g. Lindén 1989), SSE is comparable between different species and provinces among the models of X_t, J_t and R_t separately.

To avoid misinterpreting the validity of the model due to different population densities in adjacent provinces, the effect of the regression model constant was removed from the calculation of SSE by setting the mean of the fit equal to the mean of the data. This is to say, that in cases where the adjacent provinces have different grouse densities, the resulting difference in the value of the constant parameter of the regression model would easily yield a higher SSE when applying the model elsewhere - even in cases where the actual relation between weather factors and population processes were exact matches.

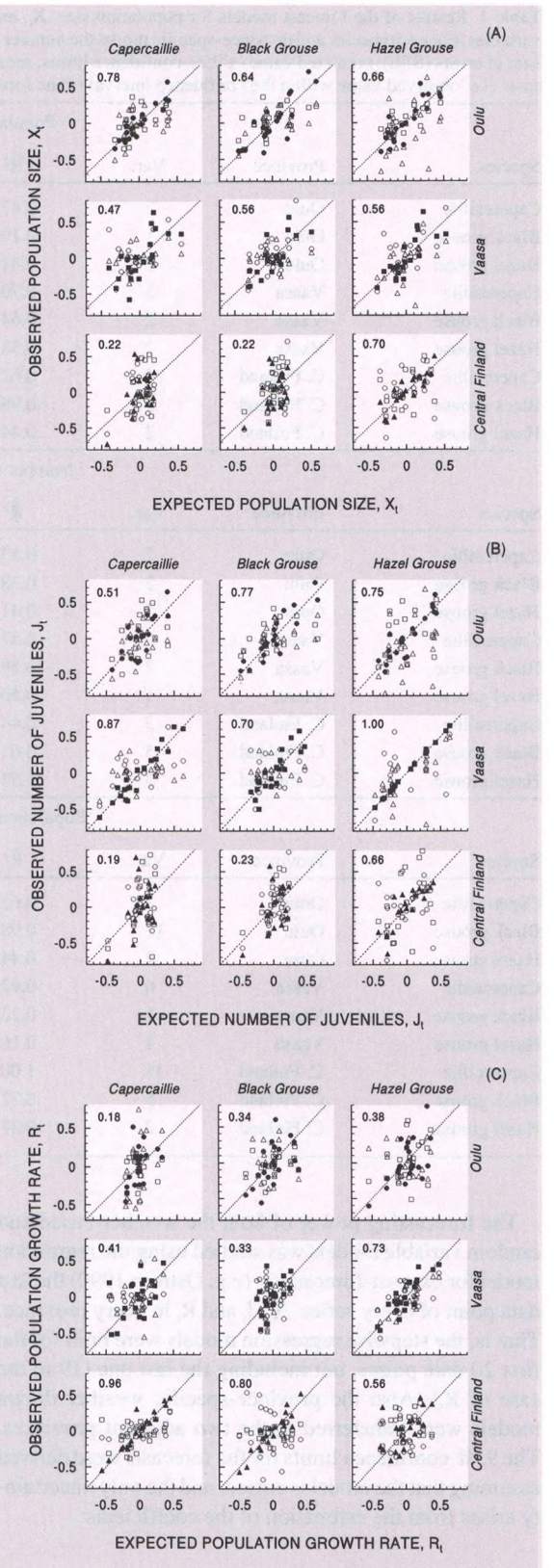


Figure 2. Expected and observed population sizes, X_t (A), number of juveniles, J_t (B), and population growth rate, R_t (C). Filled symbols represent the result of the province-specific models, and open symbols show the results of the transferred models. Circles denote Oulu, and squares and triangles represent Vaasa and Central Finland, respectively. Identical expected and observed values are indicated by a dotted line.The adjusted coefficient of determination, $\overline{R}^2$, for the model of focal province is shown in the upper left corner in each panel. For brevity, the models are not specified here.

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Table 1. Results of the forecast models for population size, X_t, number of juveniles, J_t, and population growth rate, R_t, based on random variables. For each species and province-specific model the number of variables used (var.), adjusted coefficient of determination, $\bar{R}^2$, squared sum of errors (SSE), predicted value (± 95% confidence limits, see equation 3 in the text), and the observed value are given. Successful forecasts (i.e. observed value within the confidence interval of the forecast) are given in italics.

Population size, X_t						
Species	Province	Var.	$\bar{R}^2$	SSE	Pred. ± 95% cl.	Obs.
Capercaillie	Oulu	2	0.47	0.62	*-0.21* ± 0.15	-0.08
Black grouse	Oulu	1	0.19	1.68	0.34 ± 0.26	-0.24
Hazel grouse	Oulu	2	0.41	1.07	*-0.23* ± 0.19	-0.31
Capercaillie	Vaasa	3	0.70	0.61	-0.55 ± 0.20	0.06
Black grouse	Vaasa	2	0.64	0.51	*-0.23* ± 0.15	-0.11
Hazel grouse	Vaasa	2	0.58	0.71	*-0.27* ± 0.17	-0.14
Capercaillie	C. Finland	4	0.62	0.61	-0.53 ± 0.22	-0.05
Black grouse	C. Finland	9	0.98	0.02	-0.29 ± 0.07	-0.38
Hazel grouse	C. Finland	2	0.44	0.71	*0.02* ± 0.22	-0.06
Number of juveniles, Jt						
Species	Province	Var.	$\bar{R}^2$	SSE	Pred. ± 95% cl.	Obs.
Capercaillie	Oulu	2	0.53	0.76	-0.29 ± 0.16	-0.00
Black grouse	Oulu	2	0.38	1.37	*-0.27* ± 0.22	-0.22
Hazel grouse	Oulu	2	0.41	1.14	*-0.28* ± 0.20	-0.28
Capercaillie	Vaasa	2	0.57	1.11	-0.57 ± 0.26	0.11
Black grouse	Vaasa	2	0.59	0.68	*-0.24* ± 0.17	-0.16
Hazel grouse	Vaasa	1	0.50	1.12	*-0.36* ± 0.20	-0.16
Capercaillie	C. Finland	3	0.44	1.29	*-0.44* ± 0.29	-0.19
Black grouse	C. Finland	3	0.61	0.74	*-0.29* ± 0.28	-0.38
Hazel grouse	C. Finland	3	0.53	0.74	*-0.10* ± 0.25	0.03
Population growth rate, R_t						
Species	Province	Var.	$\bar{R}^2$	SSE	Pred. ± 95% cl.	Obs.
Capercaillie	Oulu	3	0.62	0.49	-0.32 ± 0.16	0.10
Black grouse	Oulu	11	0.98	0.03	*-0.18* ± 0.10	-0.09
Hazel grouse	Oulu	2	0.44	1.09	*0.11* ± 0.21	-0.05
Capercaillie	Vaasa	6	0.92	0.12	*0.20* ± 0.09	0.20
Black grouse	Vaasa	1	0.23	0.86	-0.09 ± 0.12	0.07
Hazel grouse	Vaasa	1	0.16	1.12	*0.15* ± 0.17	0.05
Capercaillie	C. Finland	15	1.00	0.00	-0.07 ± 0.05	0.31
Black grouse	C. Finland	5	0.72	0.40	0.13 ± 0.15	-0.23
Hazel grouse	C. Finland	2	0.37	0.75	-0.12 ± 0.11	0.34

The forecasting power of both the weather-based and random variable models was studied using the regression model for ex-post-forecasting (e.g. Ostrom 1990) the last data point of every series, X_t, J_t and R_t in every province. That is, the stepwise regression models were built for the first 20 data points, not including the last one (19 in the case of R_t). Also the province-specific weather drawn models were transferred to the two adjacent provinces. The 95% confidence limits for the forecasts were derived assuming that the model is correct and the only uncertainty arises from the estimation of the coefficients:

$$f = \sum_i \hat{c}_i x_i \pm 1.96\hat{\sigma}_c, \quad (3)$$

where f = forecast, $\hat{c}_i$ = coefficient, x_i = explanatory variable, and

$$\hat{\sigma}_c^2 = \sum_i \hat{c}_{c_i}^2 x_i^2. \quad (4)$$

Here $\hat{\sigma}_{c_i}^2$ is the estimated variance of the estimate for c_i. This kind of confidence limits yield conservative estimates when the statistical dependence of the coefficients is ignored (e.g. Pindyck & Rubinfeld 1991).

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Results

The interpretation of the results is clear-cut. It is relatively easy to find a good fit for the regression model for all the series of population size, X_t, number of juveniles, J_t, and population growth rate, R_t, in the province-specific weather-based models (Fig. 2A-C). The number of the explanatory weather variables ranged within 1 - 14 (the mode being 1), $\overline{R}^2$ averaged 0.56, and ranged within 0.2 - 1.0 (capercaillie R_t in Oulu, and hazel grouse J_t in Vaasa, respectively) in the province-specific stepwise regression models. In these models SSE ranged within 0.2 - 1.1 for X_t ($\overline{SSE}$ = 0.62), 0.02 - 1.7 for J_t ($\overline{SSE}$ = 0.59), and 0.03 - 1.0 for R_t ($\overline{SSE}$ = 0.58; filled markers in Fig. 2A-C).

The corresponding figures for the transferred weather-based models are 1.3 - 2.8 for X_t ($\overline{SSE}$ = 1.51), 1.4 - 3.3 for J_t ($\overline{SSE}$ = 2.15), and 0.8 - 4.0 for R_t ($\overline{SSE}$ = 1.63; empty markers in Fig. 2A-C). Thus, the results show that the fit of the province-specific empirical models is reasonable - and occasionally excellent - for any given province and population data. However, when the models were transferred to a different province the results were much less successful.

Also the random variable models yielded reasonable fits for population size, X_t, number of juveniles, J_t, and population growth rate, R_t in every province and species (Table 1). The number of explanatory variables selected by the stepwise regression analysis was mostly low but occasionally high, as for the R_t of capercaillie in Central Finland (15) and black grouse R_t in Oulu (11). The average $\overline{R}^2$ was 0.56 as in the weather-based models, and it ranged within 0.16 - 1.0 (hazel grouse R_t in Vaasa, and capercaillie R_t in Central Finland, respectively). The SSEs also ranged much like the ones for the weather-based models: 0.02 - 1.07 for X_t ($\overline{SSE}$ = 0.73), 0.68 - 1.37 for J_t ($\overline{SSE}$ = 0.99), and 0.00 - 1.12 for R_t ($\overline{SSE}$ = 0.54; Table 1).

Validating the estimated regression model with its forecasting properties is an effective way of establishing the explanatory capacity of the model (e.g. Ostrom 1990). This is an important feature in empirical modelling since the models with the highest fits are not self-evidently the best ones for forecasting (Pindyck & Rubinfeld 1991). This procedure revealed that although the fit of the weather-based models is very high in some cases, the forecasting properties of the models are weak in general, to say the least (Fig. 3). Figure 4 gives an example of such a situation. The population growth rate, R_t, of capercaillie in Central Finland seems easy to describe with a regression model (see Fig. 2C; $\overline{R}^2$ = 0.96, SSE = 0.03). However, the observed value for the 1983 point is not within the 95% confidence limits of the forecast (Fig. 4A). Also the models of the adjacent provinces, Oulu and Vaasa, fail to forecast the last data point of R_t in Central Finland. Note

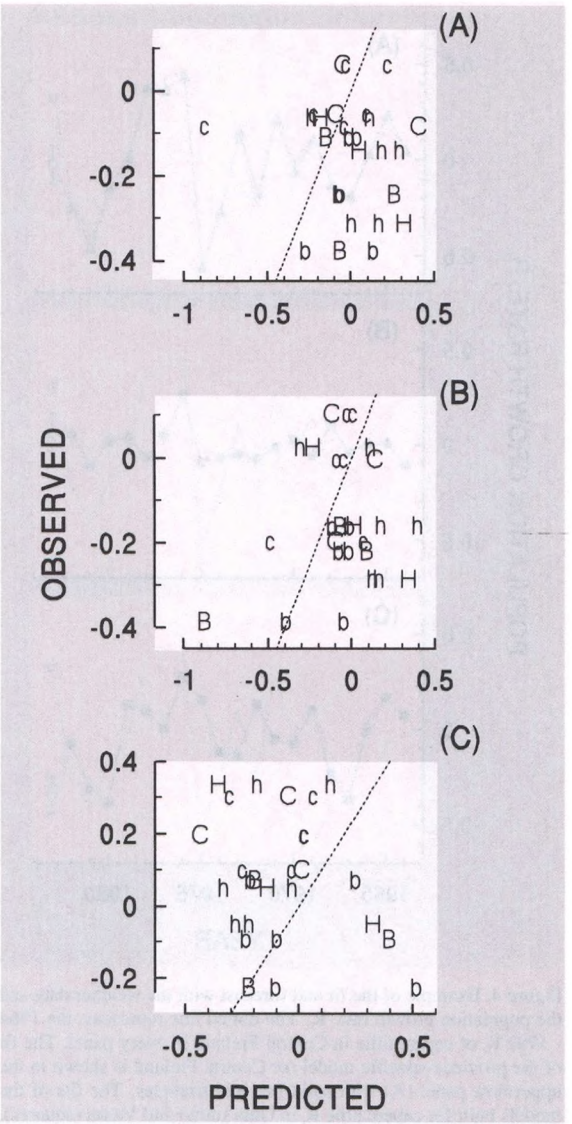


Figure 3. Observed and predicted values for population size, X_t (A), number of juveniles, J_t (B) and population growth rate, R_t (C). All the provinces are pooled. C refers to capercaillie, B to black grouse, and H to hazel grouse. Upper case letters denote the forecasts based on the province-specific models, and lower case letters show the forecasts based on the transferred models. Matching forecasts and observations are indicated by the dotted line.

that in this particular case, the model constructed in Oulu actually yields a better forecast than the model of Central Finland despite its poorer fit.

Moreover, the forecasting power of the weather-based models is not consistent in terms of $\overline{R}^2$ or SSE, which explains why the forecasts of province-specific models are not better than those of the transferred models (see Fig. 3): there were only eight (out of 27) successful forecasts for X_t, and only three of them were based on the prov-

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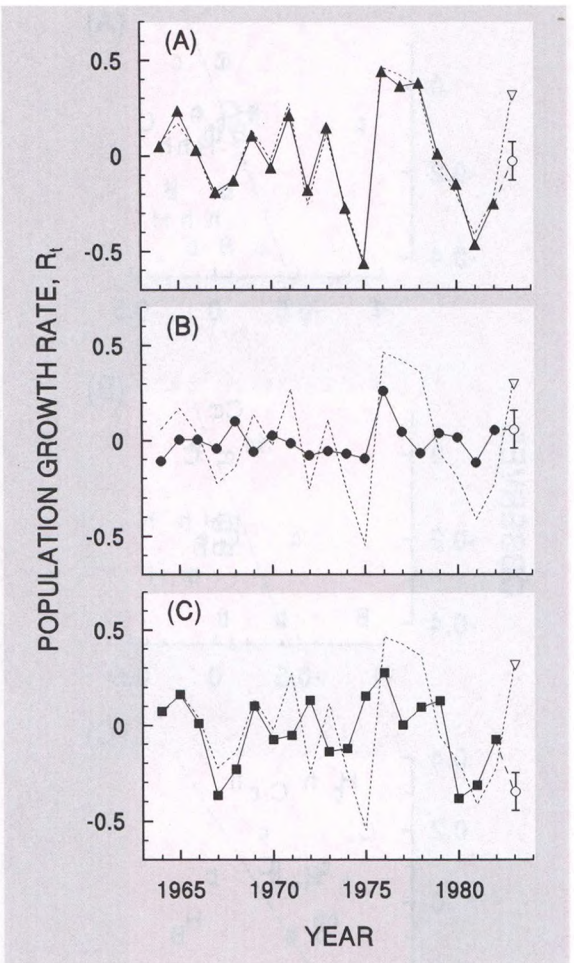


Figure 4. Example of the fit and forecast with the weather data and the population growth rate, R_t. The dotted line represents the 1964 - 1982 R_t of capercaillie in Central Finland in every panel. The fit of the province-specific model for Central Finland is shown in the uppermost panel (A) with solid line and triangles. The fits of the models built for capercaillie R_t in Oulu (dots) and Vaasa (squares), when transferred to Central Finland, are shown in panels (B) and (C), respectively. Open inversed triangle shows the last observed data point of R_t in Central Finland in each panel. Open circle in the end of each time series denotes the forecast (± 95% confidence limits) of each model one time step forward. The regression models are: for Central Finland (A): $-0.01 - 0.05 \cdot ma°C_{10} - 0.03 \cdot ma°C_{11} - 0.03 \cdot ma°C_{12} - 0.05 \cdot mi°C_9 + 0.04 \cdot mi°C_{10} - 0.02 \cdot mi°C_{12} - 0.004 \cdot p_6$, for Oulu (B): $-0.01 - 0.04 \cdot ma°C_{10}$, and for Vaasa (C): $-0.03 - 0.04 \cdot mi°C_4 - 0.005 \cdot p_{10}$. Here ma°C and mi°C represent the monthly maximum and minimum temperatures, and p is the monthly precipitation. The corresponding months are indicated as subscripts. The SSEs of the models fitted to the R_t of Central Finland are 0.03, 1.16 and 1.24 for Central Finland, Oulu and Vaasa, respectively.

ince-specific models. Here, the forecasts are considered successful if the observed value fits the 95% confidence limits of the forecast. Similarly, there were eight successful forecasts for the J_t (three of them based on province-specific models) and seven for R_t (of which two were forecasts of province-specific models).

In case of the random variable models, the observed values were within the 95% confidence interval of the forecast rather often (16 cases of 29 when calculated as a sum of each species and province for X_t, J_t and R_t; see Table 1). However, the wide confidence intervals of those forecasts hamper their usefulness - should anybody ever find it reasonable to use these random variable based models in practice.

Discussion

The idea of explaining population fluctuations with weather variables originates from the climatic control theory (Bodenheimer 1938, Andrewartha & Birch 1954). This theory states that the fluctuations of many animal populations are strongly influenced by weather, and that they are thus regulated by these factors. However, population regulation by weather is fragile (Royama 1977, 1992) as long as the weather affects the population processes independently of the population density. This is due to the fact that a population cannot be regulated without any feedback to its own density, as was already noted by Nicholson (1933) and Lack (1954). Although it is not generally explicitly stated in studies attempting to explain game population fluctuations with weather, they are implicitly related to the idea of the climatic control theory. When a good fit for the model has been found, it is relatively easy to find - seemingly - biologically relevant explanations.

However, it has been shown in this study that despite the good fit of linear regression models explaining population fluctuations with weather variables, the models are not valid when transferred to similar situations in nearby regions, nor are they able to yield successful short-term forecasts. Furthermore, the apparently good fit achieved using random variables should be considered a strong warning against using explanatory variables extrinsic to the population without careful model validation. The almost equal success of the weather-based and random variable models reveals that these models are not better than, for instance, any *n*th order polynomial fitted to the population data; although the fits are mathematically correct, they cannot uncover the dynamics of the underlying processes. This certainly cautions against deriving ecological interpretations for the model variables.

Thus, the results of this study very strongly suggest that a good fit of the linear regression model alone does not reveal the causal structures behind the observed processes. Although stepwise regression analysis may serve well in pointing out possible explanatory factors among many for further exploration, it cannot be used for deducting the causality. This is based on the assumption that the model is correctly specified in *t*- and *F*- tests, which

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makes it risky to reject null hypothesis at a given level of significance: with many variables and good fit we obtain significant *t*-values too often (Pindyck & Rubinfeld 1991).

Causality is in a key position here. In order to be reliable, weather derived models aiming to explain population fluctuations should be firmly based on observed causal links between weather variables and population response. At least, the model should be validated by studying its forecasting power, which will reveal the most serious flaws. Prior to model validation, any attempt to give a biological interpretation for the observed fit is extremely hazardous and misleading.

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