

Climatic modelling of Black Grouse population dynamics: a game or a tool?

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Statistics is like a game: to find the best relationship between variables, the researcher tests different ways to improve a model. Here, we present new statistical results for a modelling approach to the climatic influence on the Black Grouse population dynamics in Belgium. The method, initially successfully developed for the Belgian population and then applied to several European Black Grouse populations, has been modified to refine more precisely the real time of the birds' breeding period during which climatic conditions are crucial. Statistical and biological values of the results with periods defined for 7 days rather than for 3 or 4 weeks are interpreted and discussed for three sub-populations of the Hautes-Fagnes plateau in Belgium.

Keywords: modelling, population dynamics, climate, Black Grouse *Tetrao tetrix*, statistical method, Belgium

INTRODUCTION

Modelling is at the centre of both experimental and theoretical ecology: it is usually understood to involve prediction of future events. It is a job for statisticians: they use statistics and modelling to reproduce observed events, and they apply probabilistic methods to understand observations or events. Most biologists do not claim to be statisticians. Of course, biologists use statistics to test their hypotheses, but many often use the same simple statistical estimates and methods: parametric tests, normal distribution, R², Pearson 2, Student *t*, Principal Component Analysis, ANOVA, MANOVA, linear regression, and so on (Schwarz 1963, Dagnelie 1975). Biostatisticians try to apply elaborate statistics to biological events and introduce

new methods in biology (Crawley 1993, Burnham & Anderson 1998, Leirs et al. 1997, Lindsey 1999b). Unfortunately, even with sophisticated model building, outmoded statistical procedures with poor properties are still often used, such as assuming that $\log(N_{t+1})$ has a conditional normal distribution, where N_t are fairly small counts over time (e.g., Lima et al. 2002). Such models are extremely difficult to interpret biologically. In our autoregressive models, we shall not transform the data but rather use the more appropriate assumption that such counts have a conditional Poisson distribution, with a log link, and use checks for overdispersion (Lindsey 1999b, Chapter 8). Our goal here is not to introduce novel methods of analysis, but rather to show the value of applying

models that are recent and already widely used to a new biological field.

Our work on Black Grouse population dynamics is a case study for such a new approach by bio-statisticians. We use modelling as an exploratory method to test the expected influence of local climate on Black Grouse population dynamics. The climate is effectively a major factor in ecology (Stenseth et al. 2002). It acts directly on the condition and behaviour of the birds at all stages of life. It also influences food production and growth, vegetation, as well as small arthropods in the case of the Black Grouse. The availability of food acts again indirectly on the behaviour of the birds and on the chicks' growth (overview in Loneux & Ruwet 1997). Results of that modelling have shown the importance of climate to explain the dynamics observed in Belgian Hautes-Fagnes (details in Loneux et al. 1997, 2000). The results of modelling various European populations with their own meteorological data have confirmed the role of climate and the relevance of the method (Loneux 2001). They have pointed out the relation between Black Grouse and weather during the wintertime for the non-mountainous populations: winter should be cold rather than mild. They stressed the impact of weather during brooding and hatching times: it should be warm and dry rather than cold and wet. Dynamics were well reproduced by modelling, using judicious explanatory variables translating these relations, including when updating the model till 2003 in Belgium (Loneux et al. 2003, this volume). But certain explanatory variables were not independent and could overlap. An improved modelling should consider variables without time overlap.

We previously presented this approach at several international conferen-

ces, such as: 'Arbeitstagung Birkhuhnschutz Heute' Fladungen, Germany April 1998 (Loneux et al. 2000); 8th International Grouse Symposium Rovaniemi, Finland 1999 (Loneux et al. 1999); Birkhuhn Tagung Zinnwald, Germany April 2000; 1st International Black Grouse Conference Liège, Belgium 2000 (Loneux 2001); 23rd International Ornithological Congress Beijing, China 2002 (Loneux 2002a); 9th International Grouse Symposium Beijing, China 2002 (Loneux 2002b). But the nature of questions asked have lead us to focus this paper on the method itself, and on the limits of a comparison with what most of biologists used to consider. We illustrate this focus with results obtained by the first method for three subpopulations in the Belgian Hautes-Fagnes and with an improved analysis for the whole Hautes-Fagnes population.

METHODS

The required conditions are to have available a long time series of quantitative demographic observations (spring census of Black Grouse cocks, performed by the same way each year and being as complete as possible, Ruwet et al. 1997) and appropriate continuously recorded explanatory variables for the same time points (daily meteorological records at a local weather station close to the study area in our case). The climatic variables used must be well chosen for their known or supposed effects, based on a large overview of the literature, on the condition and survival of the birds at different stages of their life cycle. We used rainfall and mean minimum temperature related to crucial time periods of the life cycle of the species. The defined periods are the winter (1 November to 31 March), the beginning of spring (April), the brood-

ing, hatching and rearing times (estimated from field observations and the literature), and the beginning of autumn. The analysis is Poisson multiple regression in the "R" software (a free S-Plus clone, Ihaka & Gentleman 1996), with formula:

$$\log(\mu_t) = \beta_0 + \beta_1 x_{1t} + \beta_2 x_{2t} + \dots + \beta_t x_{rt}$$

for explanatory variables ' x_{it} ' with μ_t the mean number of cocks for year t

Models will be ranked using an information-theoretic approach (Burnham &

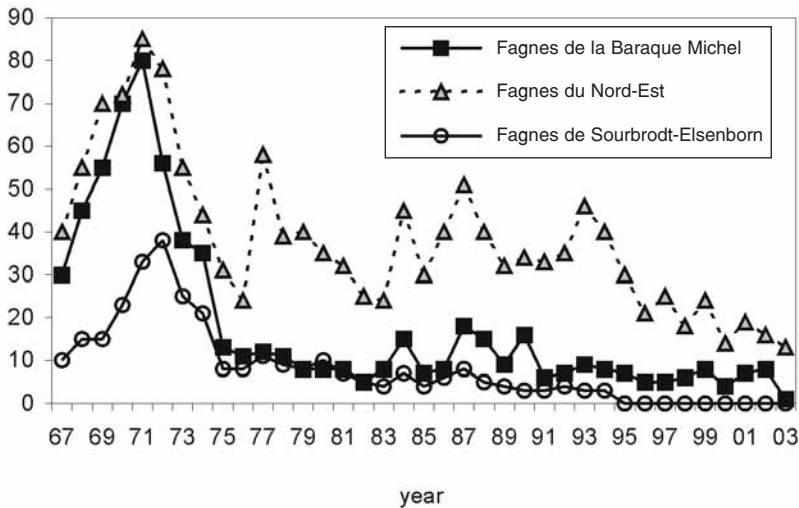
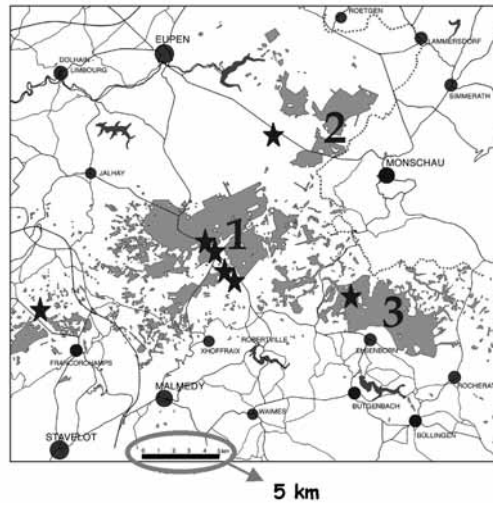


Fig. 1. Location of the weather stations (stars) and of the three Black Grouse sub-populations in Belgian Hautes-Fagnes: (1) Fagnes de la Baraque Michel (FBM), (2) Fagnes du Nord-Est (FNE), (3) Fagnes de Sourbrodt-Elsenborn (FSE).

Anderson 1998) to determine the most parsimonious model. The criterion used will be the AIC with smaller values indicating more preferable models.

Automatic step-wise procedures were not used. Order for entering variables into the model was determined by our previous knowledge of the biological system under study (Loneux et al. 1997).

The following explanatory variables were retained in at least one of the final models:

spring cocks number previous year (**no1**), spring cocks number two years before (**no2**), sum of rainfall during September previous year (**ppSept**), sum of rainfall during November previous year (**ppNov**), minimum temperature mean over 3 weeks beginning the day 'dd' of month 'm' (**t3wdd.m**), minimum temperature mean over 1 week beginning the day 'dd' of month 'm' (**t1wdd.m**), sum of rainfall during 3 weeks beginning the day 'dd' of month 'm' (**pp3wdd.m**), sum of rainfall during 4 weeks beginning the day 'dd' of month 'm' (**pp4wdd.m**), sum of rainfall during 1 week beginning the

day of month (**pp1wdd.m**), minimum temperature mean during previous winter period defined from 1 November previous year to 31 March year 't' (**twinter**), minimum temperature mean during previous last winter period (**twinter1**), spring cocks number previous year for 'Fagnes de la baraque Michel' (**noFBM1**), spring cocks number two years before for 'Fagnes de la baraque Michel' (**noFBM2**), spring cocks number previous year, for 'Fagnes du Nord Est' (**noFNE1**), spring cocks number two years before, for 'Fagnes du Nord Est' (**noFNE2**), spring cocks number previous year, for 'Fagnes de Sourbrodt-Elsenborn' (**noFSE1**), spring cocks number two years before, for 'Fagnes de Sourbrodt-Elsenborn' (**noFSE2**).

Rainfall or minimum T° formerly calculated for three or four weeks with overlap during the breeding period (brooding, hatching and chicks' first weeks of life) have been this time calculated for 1 week, without overlap with the next one. The first week begins on 10 May, the last one begins on 25 July. All

Table 1. Explanatory variables in the best model with 1-week periods, with P-values referring to partial effects of each variable. The formulation used in R for the final model is: $\text{glm}(\text{formula} = \text{no} \sim \text{no1} + \text{no2} + \text{twinter} + \text{t1w17.5} + \text{t1w21.6} + \text{pp1w31.5} + \text{pp1w07.6} + \text{pp1w28.6} + \text{pp1w05.7} + \text{ppSept} + \text{ppNov}, \text{family} = \text{poisson})$. For explanation of variable names see Methods. Null deviance: 935.420 on 35 df, residual deviance: 42.096 on 24 df, AIC: 274.19.

coefficients:	estimate	std. error	z-value	P-value
(intercept)	3.3119654	0.1962206	16.879	
no1	0.0120754	0.0009814	12.305	<0.001
no2	-0.0022583	0.0009402	-2.402	<0.05
twinter	-0.0794338	0.0242595	-3.274	<0.01
t1w17.5	-0.0278092	0.0112979	-2.461	<0.05
t1w21.6	0.0935770	0.0109331	8.559	<0.001
pp1w31.5	-0.0016653	0.0011565	-1.440	<0.20
pp1w07.6	-0.0046126	0.0014327	-3.220	<0.01
pp1w28.6	-0.0049216	0.0009273	-5.307	<0.001
pp1w05.7	0.0019563	0.0009431	2.074	<0.05
ppSept	-0.0015556	0.0003948	-3.940	<0.001
ppNov	-0.0025447	0.0005102	-4.988	<0.001

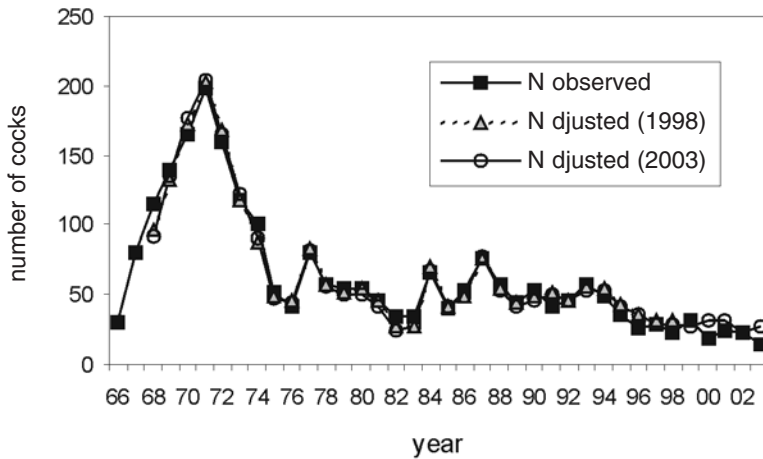


Fig. 2. Models for spring numbers of Black Grouse cocks in the Belgian Hautes-Fagnes. Plot of the numbers on the arenas (*N* observed) and their estimated values from the model (*N* fitted) for 1966 to 1998 and updated to 2003. This model, using minimum mean temperature and rainfall covering 1-week periods in May, June, or July without overlap, is better than the model using 3–4-week periods variables (cf. Loneux et al. this volume).

other variables and time periods are the same ones previously used in the first modelling (Loneux et al. 1997, 2000, Loneux 2001).

The three sub-populations (Baraque Michel, Nord-Est, Sourbrodt-Elsenborn) occupy the different parts of the Hautes-Fagnes nature reserve, are distant from each other from 5 to 10 km (Fig. 1) and form together a ‘metapopulation’ isolated from the other breeding populations in Europe. The climatic data come from weather stations close to the sub-population 1, which is also the main one (Ruwet et al. 1997).

RESULTS

The results of the improved modelling (Table 1, Fig. 2) confirm the role of weather to explain the fluctuations. The spring number of birds increases when the previous brooding and hatching periods are warm and dry rather than rainy, when the previous autumn is dry rather than rainy and when the previous and current winters are cold rather than

mild. We have investigated the climate trends and shown that cold winter means snowy rather than rainy, and that global warming affects locally the explanatory variables taken in the model, in a way not good for the Black Grouse (Loneux & Vandiepenbeeck 2002, 2003).

The modelling gives much better estimated numbers when using crucial 1-week periods without overlap for variables related to the breeding time. It points to smaller crucial periods, which are a mean for the breeding time over the whole period of study: the first 2 weeks of June in Belgian Hautes-Fagnes.

In the previous analyses, all of the final models fitted very well and there was no indication of overdispersion (Lindsey 1999a). Here, the global model for all sub-populations combined shows some indication of overdispersion (residual deviance almost twice the degrees of freedom, Table 1). We shall come back to this point in the Discussion (Table 6).

DISCUSSION

The years with poor fit of the estimated number could be those with exceptional meteorological conditions during the mean crucial time periods considered. But neither the climate does explain all! Some extreme climatic events, or some other events not climatic at all, may have more affected the population in those years.

In the results obtained for each of the three sub-populations (Table 2, 3, 4), certain explanatory variables are not the same, even when the meteorological data are identical in the three cases. We have not yet found a satisfactory biological interpretation for such differences two by two among the variables taken into account. Another analysis with variables without overlap should be performed as well to allow comparison without any dodged issue.

AIC (Akaike Information Criterion), Null Deviance, Residual Deviance are criteria of evaluation of the quality of the modelling. They are not familiar and well understood, and not easily accepted by most of biologists. These know and prefer 'R²', which they believe

allows comparison of the quality of results obtained by different methods. 'R²' does not measure the variability explained by the model but they believe that the higher it is, the better is the model. It measures improvement over the null model, not goodness of fit. From our results, we can calculate R² (Table 5). Results show a larger value of R² for the model with 1-week periods. Note that the model with only previous cock numbers (2 years before), and no climatic variables, gives values which are commonly accepted by biologists as good result.

By comparison, a classical χ^2 goodness of fit test applicable on Poisson distribution (Table 6) gives the model for 3-4-week periods worse than that for 1-week periods. In 1999, the models fitted acceptably well. Now, in 2003, both models are rejected by the goodness of fit test ($P < 0.05$), indicating possible overdispersion. Thus climatic variables were sufficient to explain the series of grouse numbers from 1966 to 1999; but are no longer sufficient for the following 4 years.

In contrast to these approaches, the

Table 2. Explanatory variables in the best model for the main subpopulation 'Fagnes de la Baraque Michel', number 1 (Fig. 1), with P-values referring to partial effects of each variable. See Methods for the explanation of the variable names. Dispersion parameter for Poisson family taken to be 1. Null deviance: 175.217 on 29 df, residual deviance: 17.125 on 19 df, AIC: 203.62.

coefficients	estimate	std. error	z-value	P-value
(intercept)	3.0289418	0.2870887	10.551	
noFBM1	0.0144594	0.0028242	5.120	<0.001
noFBM2	-0.0054658	0.0029660	-1.843	<0.01
twinter	-0.0604980	0.0252725	-2.394	<0.05
twinter1	-0.1150495	0.0288731	-3.985	<0.001
ppSept	-0.0012659	0.0006752	-1.875	<0.1
pp4w25.5	0.0080353	0.0026230	3.063	<0.01
pp4w19.5	-0.0055746	0.0015941	-3.497	<0.01
t3w16.6	0.0658246	0.0164730	3.996	<0.001
pp3w01.6	-0.0080908	0.0017172	-4.711	<0.001
ppNov	-0.0011207	0.0006488	-1.727	<0.02

AIC only provides a relative measure of the value of a model as compared to others. It penalises for complex models by incorporating the number of param-

eters estimated. The best model among a series of formula tried on the same data set should have the lowest AIC.

Table 3. Explanatory variables in the best model for the subpopulation 'Fagnes du Nord-Est', number 2 (Fig. 1), with P-values referring to partial effects of each variable. See Methods for the explanation of the variable names. Dispersion parameter for Poisson family taken to be 1. Null deviance: 496.33 on 29 df, residual deviance: 25.84 on 19 df, AIC: 178.29. Deviance residuals: min -2.072161, Q -0.47625, median -0.01101, 3Q 0.57237, max 1.86633.

coefficients	estimate	std. error	z-value	P-value
(intercept)	1.326490	0.511814	2.592	
noFNE1	0.039028	0.004947	7.889	<0.001
noFNE2	-0.005426	0.005334	-1.017	>0.2
twinter	-0.072700	0.046918	-1.550	<0.2
twinter1	-0.103745	0.056928	-1.822	<0.1
ppSept	-0.003191	0.001201	-2.656	<0.01
pp4w25.5	0.003666	0.002571	1.426	<0.2
t3w16.6	-0.226434	0.136113	-1.664	<0.2
pp3w01.6	-0.007772	0.002502	-3.107	<0.01
t3w10.6	-0.346019	0.109127	-3.171	<0.01
t3w13.6	0.658990	0.188452	3.497	<0.01

Table 4. Explanatory variables in the best model for the subpopulation 'Fagnes de Sourbrodt-Elsenborn', number 3 (Fig. 1), with P-values referring to partial effects of each variable. See Methods for the explanation of the variable names. Dispersion parameter for Poisson family taken to be 1. Null deviance: 274.329 on 29 df, residual deviance: 31.041 on 19 df, AIC: 150.65.

coefficients	estimate	std. error	z-value	P-value
(intercept)	-0.569446	0.795574	-0.716	
noFFSE1	0.063121	0.013023	4.847	<0.001
noFFSE2	0.005475	0.012564	0.436	>0.2
twinter	-0.331237	0.086491	-3.830	<0.01
twinter1	-0.206959	0.074877	-2.764	<0.02
ppsept	-0.004317	0.001616	-2.671	<0.02
pp4w25.5	0.021450	0.008902	2.410	<0.05
pp4w19.5	0.013580	0.009006	1.508	<0.02
pp3w01.6	-0.018326	0.006066	-3.021	<0.01
t3w10.6	0.170278	0.062426	2.728	<0.02
pp4w16.5	-0.024466	0.008983	-2.724	<0.02

Table 5. R²-value of the models, given by (null deviance - residual deviance)/ null deviance, for two different lengths of observations.

years	1966-1999	1966-2003
model 3-4-week periods	96.1%	92.3%
model 1-week periods	97.1%	95.5%
model previous cocks number only	76.9%	76.0%

Table 6. Comparison of χ^2 P-values of the residual deviance of Poisson modelling for two lengths of observations and variables with two different periods of weeks.

years	1966–1999			1966–2003		
	residual deviance	df	P-value	residual deviance	df	P-value
3–4-week periods	28.5	18	0.055	72.5	23	4.9×10^{-7}
1-week periods	21.5	19	0.310	42.1	24	0.013

A comparison of the sum of squared residuals calculated for 12-year periods reveals that the model does not fit well for the last dozen years (Table 7). However, we have seen above that the lack of fit is in fact primarily for the last four years. (This is partially hidden by the coarser grouping into 12-year periods.)

The last 12-year period is when the global climate warming affects the most values of minimal temperature and sum of rainfall during crucial periods of the Black Grouse life cycle. Important trends revealed are warming of winter mean minimum temperature, taken as negative in the model, increasing rainfall during autumn (November), taken as negative in the model and increasing rainfall during spring (March) and during parts of the breeding season, taken as negative in the model (Loneux & Vandiepenbeek 2002, 2003). Thus, global climate change, perceptible since the end of the 1970s, seems to explain part of the decline observed among the isolated Black Grouse populations living in West European protected areas.

Table 7. Sum of squared residuals (proportion of residual deviance) for the model with 1-week periods, adjusted numbers from 1968 to 2003. The higher the sum, the less accurate the model.

time period	sum of squared residuals
1968 to 1979	8.94
1980 to 1991	9.64
1992 to 2003	23.52

Recently, few birds are involved in the modelling. Thus the variability of their behaviour could be greater, especially regarding the climate evolution. It could be a greater shift between the real yearly breeding period in the recent years and the mean breeding period estimated over more than 30 years from field observations in the 1970s and literature on foreign populations (cf. Loneux et al. 1997). Another factor is that in recent years, the small size of population implies that any chance stochastic event (predation, poaching, tourist disturbance, habitat perturbation, etc.) could disrupt the model and brings the grouse close to local extinction.

CONCLUSIONS

(1) As an exploratory tool, modelling allows identification of the value of the main factors acting on the long-term dynamics. Those are the explanatory variables giving the best model. (2) As a game, modelling allows testing any explanatory variables, even unrelated to the biology of the birds. (3) Sometimes, even with meaningful variables, the results are difficult to understand, because of the lack of (obvious) biological interpretation.

From the point of view of studying Black Grouse, because of the climatic nature of the explanatory variables, it is not possible to predict more than one year ahead. The results of our modelling are not useful to predict the spring cock census the following year. They allow

identification and verification of the accuracy of the variables used in the model. This method is a good exploratory tool.

In the case of the Belgian Hautes-Fagnes, the goodness of fit goes down in recent years showing that other explanatory variables than strictly climatic ones have become more important, or that the climatic ones have exceptional value the years with poor estimates, or both. This will be subject to further investigation.

From our experience in modelling these data, as they have accrued over the past decades, we would like to make the following suggestions to those who wish to apply the method to other populations/species:

(1) Demographic data should cover minimum 20 years continuously (the more the better), of course with the same census effort and method.

(2) Demographic data should represent the whole population and not a small part of it (not one arena only).

(3) The judicious climatic data should come from a local weather station: this is very important for rainfall and minimum temperature.

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