DYNAMICS OF A BLACK GROUSE (*TETRAO TETRIX*) POPULATION IN THE FRENCH MARITIME ALPS

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ABSTRACT

The populations of the Eurasian black grouse *Tetrao tetrix* show different patterns of variability in different parts of Europe, at cause of the complex interplay between endogenous and exogenous factors on the regulation of population growth rates. In this study, a black grouse population was censused annually during autumn by the same observer in southern Alps, within the Tende's shooting ground (French department of Alpes Maritimes). During the 31-year study period (1967 – 1997), the population abundance index remained constant as assessed by TRIM (Trends and Indices from Monitoring Data) analysis. In addition, this population did not show signs of regular cyclicity (i.e. statistically periodicity), as it has been observed in other southern populations of black grouse. Simulation tests and autoregressive moving average (ARMA) modeling showed that direct density dependence was responsible for about 40% of the variation in population growth rates, while the total amount of spring rainfall (April – June) explained 10% of the variability due to exogenous factors. The hunting pressure, that was reduced since 1974, and the creation of a national protected area adjacent to the study site in 1979, showed no significant effect on the black grouse population, that apparently was already fluctuating near its environmental carrying capacity.

KEY WORDS

ARMA modelling, density dependence, grouse, French Alps, time series analysis, TRIM software.

INTRODUCTION

The Eurasian black grouse *Tetrao tetrix* (Linnaeus, 1758) is a non-migratory bird belonging to the subfamily Tetraoninae of the family

Phasianidae (Drovetsky, 2002) found throughout Eurasia with a continuous distribution from Great Britain to south-eastern Siberia in the North, and from Kyrgyzstan, North Korea and French and Italian Maritime Alps in the South. In western and central Europe populations are fragmented and isolated and ongoing declines have been reported in most of European countries (e.g., Loneux and Ruwet, 1997; Ludwig et al., 2008), while the species became recently extinct in Denmark (BirdLife International, 2009). In the Alps, black grouse densities are declining mainly because of changes in land use practices (Bernard-Laurent, 1994; De Franceschi, 1994).

Black grouse populations show different levels of variability in different parts of the species distribution range. In general, in northern Europe there is evidence of regular and sometimes synchronous population cycles lasting 4-7 years (reviewed in Ranta et al., 2006), while in Southern Europe, and in particular in the Italian Alps, there is only a weak tendency to display regular fluctuations in abundance (Ellison et al., 1984; De Franceschi, 1985; Cattadori and Hudson, 1999; 2000). These different patterns of population variability are mainly due to different types of population regulation resulting from the complex interactions between endogenous (i.e. density dependent) and exogenous (i.e., climatic) factors (Cattadori and Hudson, 2000). In North Europe, black grouse populations appear regulated by the interaction between strong delayed density-dependence and spring or summer weather conditions, that induce regular high-amplitude fluctuations in abundance while, in Southern Europe and in particular in populations from the Italian and Swiss Alps, the prevalence of a strong first order direct density-dependent regulation upon growth rates coupled with a relatively high level of local environmental stochasticity are suggested as the causes of the absence of a clear cyclic dynamic patterns (Cattadori and Hudson, 1999; 2000).

In this study, a black grouse population from the southern French Alps of was counted within a reference area for 31 years, from 1967 to

1997, by the same observer. The dynamics of this population was analyzed be means of simulation tests and autoregressive moving average (ARMA) modeling, and the contributions to the observed population dynamics of climatic factors and local hunting regulations could be also evaluated. The results from the Tende population, which is the southernmost black grouse populations analyzed by autoregressive modeling (see, Cattadori and Hudson, 1999; 2000), were also compared with those from other regions such as the French and Italian Alps and northern Europe.

STUDY AREA

The study site is located in the Tende's shooting ground (French department of Alpes Maritimes, south-western Alps), that has a surface of about 11 600 ha and altitudes ranging from 1600 to 2200 m a.s.l. This shoot lies on the Roya Valley, between the Valley of Casterino (1567) and Col de Tende (1870 m). During the study period the shooting rules changed. Up to 1970, shooting occurred first at the beginning then at the end of September with only 4 shooting days per hunter and per week. Since 1991, hunting was further reduced and closure was set at the 11th of November with only one kill per day per hunter (only in year 2000, a shooting plan was implemented on the basis of annual spring and autumn censuses). Black grouse cocks and hens were counted annually within a 350 ha area characterized by a larch (*Larix decidua*) forest on the northern slopes and by pine woods (arolla pine *Pinus cembra* and mountain pine *Pinus uncinata*) on the southern slopes. Trees were interspersed with a shrub vegetation including rhododendron *Rhododendron ferruggineum*, bilberry *Vaccinium mirtillus* and belonging to the Rodoreto-Vaccinietum Br.-Bl. association. In this area the black cock density was estimated to be 4.95 individuals per 100 ha, by a previous long-term study (Spanò and Borgo, 1991).

MATERIALS AND METHODS

During the period 1967-1997, from the end of September to the end of October, the same observer (S. Spanò) walked inside the reference area of 350 ha with a pointing dog (English Setter) and noted all black grouses by sex and age. Each sampling surveyed about ¼ of the reference area and lasted about six hours. The mean number of sampling days per year was six. The black grouse annual population index was obtained as the mean number of animals (cocks plus hens) observed per day (Spanò and Borgo, 1991). This index does not consider the possible effects of juvenile mortality during winter, however the sampling method was highly consistent over the entire period and thus may generate adequate data to understand the local dynamics of the black grouse population.

STATISTICAL ANALYSES

The overall population trend was assessed by Trends and Indices for Monitoring Data (TRIM), a software that uses a log-linear regression model with Poisson error terms and that takes into account over-dispersion and serial correlation in the data (Pannekoek and van Strien, 2005). Models with different change points (i.e., with significant changes in slope at different years) based on Wald test may be tested, and the most parsimonious model selected trough AIC index (Pannekoek and van Strien, 2005). This is of particular interest, since in 1974 the hunting effort (i.e. the number of hunting days per hunter) was reduced by the reserve managers, while in 1979, the Mercantour national Park (Parc national du Mercantour) was created in proximity of the study site. Thus it was also possible to evaluate the effects of two events on black grouse population abundance and dynamics.

The presence of density dependence in the time series was assessed by simulation by means of the parametric bootstrap likelihood ratio test (Dennis and Taper, 1994) and randomization test (Pollard et al., 1987), with 10000 replications in both cases. The black grouse population dynamics was analyzed by a linear autoregressive moving average (ARMA) modeling. These models take into consideration both the effect of abundances in previous years (AR) and of lagged random external shocks (MA). This method is considered more performing than just fitting the autoregressive term AR to explain lagged environmental effects, because the MA term accounts for direct and indirect effects of stochasticity on the population dynamics (Abbott et al., 2009). The ARMA was fitted by the general model (Royama, 1992; Chatfield, 2004):

$$ln(N) = a + b_1 ln(N_{t-1}) + \ldots\ldots + b_p ln(N_{t-p}) + c_1 U_{t-1} + \ldots\ldots + c_p U_{t-p} + \varepsilon_t$$

where *a* is the maximum per capita growth rate, *b* and *c* are the autoregressive parameters, *N* is the population abundance, *p* and *q* are the order of autoregressive parameters, *t* is the sampling interval, *U* is the external shock and ε is random variation. The dimension of the feedback structure was analyzed by autocorrelation (ACF) and partial rate correlation (PRCF) functions (Berryman and Turchin, 2001) and statistical significance of both ACF and PRCF was assessed by Bartlett's 95% confidence intervals: $\pm 2/\sqrt{n}$, where n is the number of years in the time series (Berryman and Turchin, 2001). The most parsimonious ARMA model was selected by the minimum Akaike's information criterion corrected for small samples (AIC_c) and model residuals were checked for autocorrelation by the Ljung-Box test (Chatfield, 2004). Climate variables were selected in order to describe environmental conditions that could influence black grouse mortality and reproduction. The North Atlantic Oscillation Index, measured from December to March (NAO_w, www.cru.uea.ac.uk), was used as a large-scale climatic variable describing winter climate. NAO_w is calculated from the normalized pressure difference between Azores and Iceland. NAO_w positive values determine dry winter conditions, while negative values correspond to a humid climate in the Mediterranean region (Stenseth et al. 2003). Local weather during brooding, hatching and chick raising has been reported an important environmental factor influencing grouse dynamics in different black grouse populations in Central Europe (e.g. Loneux, 2001; Loneux and Linsday, 2003), and in particular in the Italian Maritime Alps (Provenzale, 2008). Thus monthly rainfall during April, May and June ($Rain_{April}$, $Rain_{May}$ and $Rain_{June}$), the first two weeks of July ($Rain_{July}$) and the entire spring period ($Rain_{Spring}$) were considered. Rainfall data were obtained from two stations near Limone Piemonte, located about 12-14 km from the study site. Unfortunately, no temperature data were available from these stations. Local rainfall data and NAO_w were regressed on the residuals of the selected ARMA model to obtain insights on the role of exogenous factors in addition to endogenous feedback (Lima et al. 2002; Bommarco et al. 2007). The software Poptools 3.1 was used in simulation tests, all other analyses were performed by means of Minitab 15.1 software.

RESULTS AND DISCUSSION

The black grouse relative abundance index displayed moderate interannual variations, ranging from 3 to 14.5 cocks per year (Fig. 1) with a mean value of 5.77 ± 2.23 standard deviation, and a coefficient of variation of 0.39. According to TRIM analysis, the most parsimonious models were those with a change point in 1994 or 1995 (slope becoming positive according to Wald test with $P < 0.001$ in both cases, AIC_c = –45,02 and –45.47 respectively). There was no effect of the reduction of hunting effort in 1974 (AIC_c = –38.47), or of the Institution of the Mercantour national Park in 1979 (AIC_c = –39.02) or of the combination of these two events (AIC_c = –38.00). The time series overall multiplicative slope was 1.0068 with standard error 0.0052, and the black cock population trend remained constant over the 31-study period.

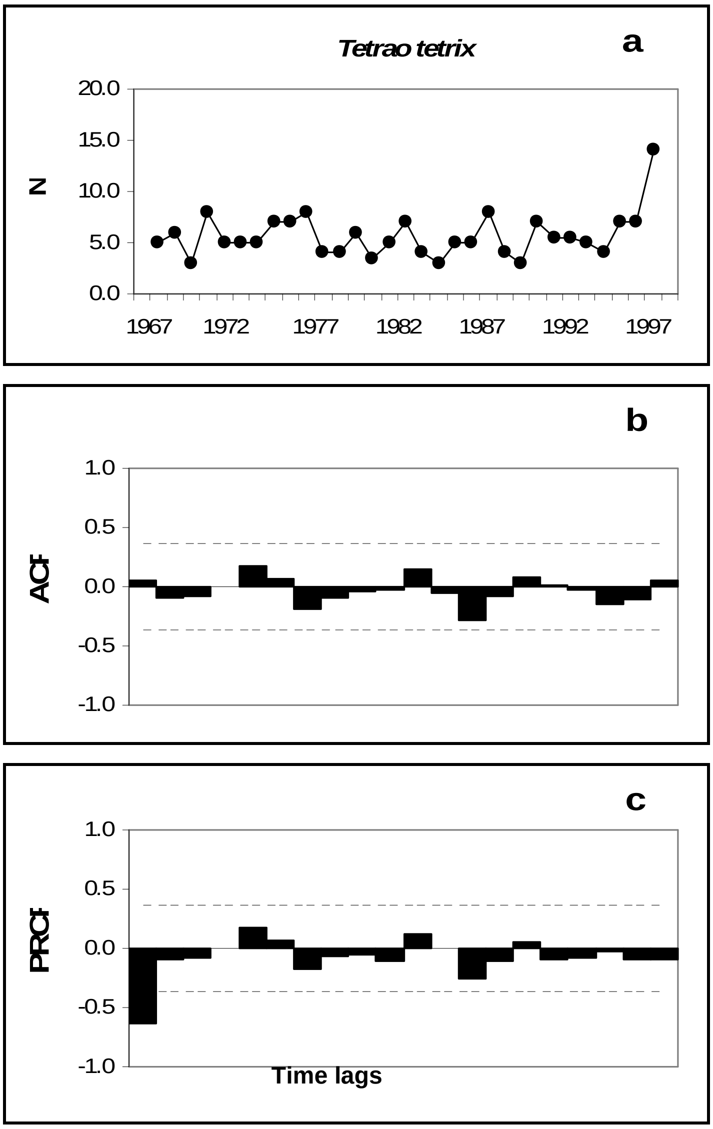

Fig. 1. a) Black grouse population time series; b) autocorrelation function (ACF) of the time series; c) partial rate correlation function (PRCF) of the time series, see text for explanation. Stippled lines in b) and c) are 95% confidence intervals.

Both simulation tests showed the presence of a strong density-dependent regulation in the black grouse population: Pollard's test P = 0.003 and Dennis and Taper test P = 0.001. The ACF of the $\log_e$-transformed time series was not significant (P > 0.10), while the PRCF indicated that only the first-order negative feedback influenced significantly the population growth rate [$PRCF_{(1)} = -0.64$, d.f. = 30, P < 0.05, $r^2 = 0.41$]. The two most parsimonious ARMA models were both first-order autoregressive models: ARMA(1,0) and ARMA(1,1) with $AIC_c = -62.604$ and -61.3460 respectively. These models wad no autocorrelation in the residuals (Ljuing-Box test, P > 0.05, in both cases). The climatic variables were normally distributed (Anderson-Darling test, P > 0.05, in all cases) and did no show any significant autocorrelation (P > 0.05, in all cases). The regression analyses using the residuals from both the selected ARMA models and the climatic variables evidenced that only the total amount of rainfall fallen during spring showed a significant negative correlation: $r = -0.468$, $P = 0.018$, $r^2 = 0.19$ and $r = -0.506$, $P = 0.010$, $r^2 = 0.22$ for ARMA(1,0) (Fig. 2) and ARMA(1,1) respectively.

The temporal trend of the black cock population from Tende's shooting ground remained constant over the 31-year study period, as assessed by TRIM analysis. This evidence is of interest for different reasons. Firstly because the French populations over the Maritime Alps have been considered stable during the period 1990-2005 (Bernard-Laurant, 2007). Therefore, if the population from Tende can be considered indicative of the overall situation in this southern Alps sector, black grouse populations remained constant during almost 40 years (i.e., from 1967). Indeed, it seems that this black grouse population was apparently fluctuating near the environmental carrying capacity, within a highly favorable habitat well before the change in the hunting regulations adopted in 1994.

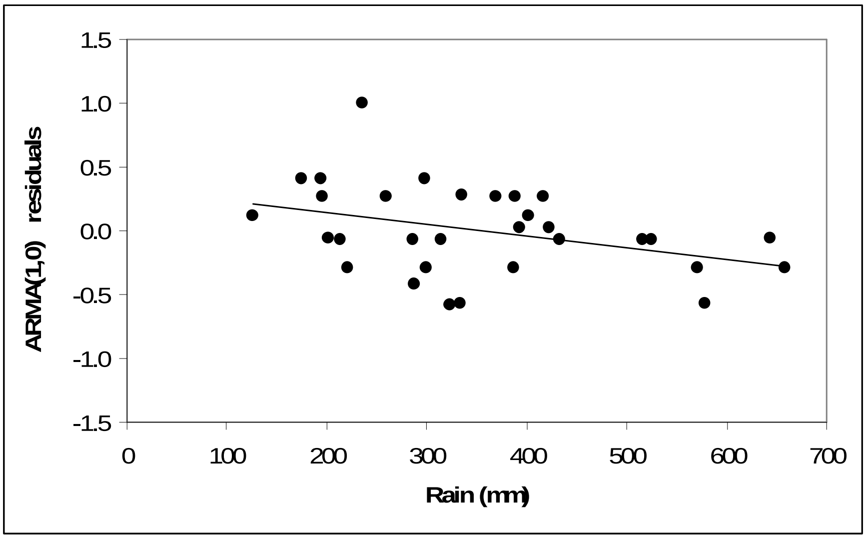

Fig. 2. Regression plot between residuals of the ARMA (1,0) model and total spring rainfall (mm), in the period April-June.

The black cock population from Tende showed no sign of statistical cyclic dynamics. Population cycles have been observed and analyzed in many northern and central European black grouse populations, in which delayed density dependent regulation is usually present (Lindström et al., 1995; Ranta et al., 2006). Conversely, black grouse populations from the Italians and Swiss Alps are regulated by a first order negative feedback of population density on their growth rates (Cattadori and Hudson, 1999; 2000; Provenzale, 2008). This is good news for conservation, because populations regulated by direct density dependence are less prone to extinction than fluctuating ones, at least in absence of catastrophic environmental perturbations (Royama, 1992). Indeed, the strong first order density dependent regulation observed in Tende's shooting ground was similar to the regulation reported for black grouse populations in the nature reserve of Orsiera-Rocciavré, in

Southern Piedmont Italy, during the period 1991-2006 (Provenzale, 2008). The Piedmont grouse population was sampled in the Cottian Alps, about 100 km northwards of the French population analyzed in this study. The dynamic structure of the Piedmont population, also analyzed by autoregressive modeling, showed a first order density dependent regulation that explained 31% of the total variability (in comparison to 41% in Tende), while rainfall during the first two weeks of June contributed significantly to the observed dynamics, explaining 55% of the variation (Provenzale, 2008). In Tende, the influence of local climate was apparently reduced, because rainfall contributed to about 22% of the environmental variability (13% of the total). Finally, winter climate, that plays a relevant role in population regulation in Central Europe (e.g., Loneaux, 2001; Loneaux et al., 2003; 2005), seemed to have a negligible role on the Tende population dynamics, which is located at the southern limit of the species distribution and probably benefits of the Mediterranean influence. This population seems more dependent on the complex interaction between population density in the previous year and local rainfall during the spring, when eggs are laid and chicks hatch.

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