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RESEARCH

Fifty years of spring censuses in black grouse (*Lyrurus tetrix*) in the High Fens (Belgium): did the rabies vaccination has a negative impact on a fox prey population?

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Abstract

Since 2017, a reinforcement programme was developed to save the last, endangered, Belgian population of black grouse (*Lyrurus tetrix*), in the High Fens Natural Park. To improve the success of this programme, an analysis of past data of this population was undertaken to understand the causes of its past decline. A time series analysis was applied, using annual spring male census data recorded between 1967 and 2016. In the period 1967–1993, there was a fluctuation around an equilibrium of a population of ca. 40–45 males. The peak of 85 males observed in 1971 was probably due to a succession of several favourable years in terms of environmental conditions, albeit without an exceptional annual growth rate. It seems that fox density, by using the occurrence of rabies as a proxy, has an impact on the black grouse population. After 1993, the population dynamic changed drastically, decreasing continuously until finally reaching quasi-extinction. On average, the population lost 15.4% of its size each year. Climate models, applied in previous studies to explain these population trends in the High Fens, failed to describe this major modification in this population's dynamic and its recent decline. We suggest that this negative effect was mainly induced by a significant increase in predation by red fox (*Vulpes vulpes*), whose abundance has increased considerably since the 1990s, in particular, as a consequence of the eradication of fox rabies. We also discuss alternative hypotheses, such as the impact of other predator species, modification of the natural environment and climatic modifications.

Keywords Lek · Predation · Rabies · Tetraonid · Dynamic of populations · Fox

Introduction

The European avifauna has known major modifications during the twentieth century, and this is particularly true for open-field species. In moorlands and heathlands, many European species of ground-nesting birds are declining. The changes in land use, and more particularly, the loss and the fragmentation of their habitats, and the increases of predator density are thought to be the major causes of these trends (Fletcher et al. 2010; Douglas et al. 2017; McMahon et al. 2020). Therefore, understanding the factors affecting the survival of the avifauna is a major concern for conservation.

Among these threatened species, the Western lowland continental European black grouse (*Lyrurus tetrix*) have seen its populations severely reduced since World War II through hunting as well as habitat deterioration and fragmentation. Most lowland populations of Western Europe went extinct (Denmark, NE France) or near extinct (Germany, The Netherlands, Belgium) (Ciach 2015; Keller et al. 2020). In Belgium, black grouse were mainly found in moorlands and heathlands, from low altitudes (close to sea level) to the higher regions (up to 694 m in the High Fens). Over the last few decades, the Belgian populations decreased dramatically. Since the 1980s, they have been limited to higher elevations (above 500 m), on the high plateaus of Croix-Scaille, Baraque de Fraiture and the High Fens. By the 1990s, the High Fens sheltered the last remaining Belgian population (Loneux and Ruwet 1997a, b).

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The High Fens population has been intensively studied, notably through continuous censuses since 1967 (e.g. Ruwet 1982; Ruwet et al. 1997). The core population located around the Baraque Michel, despite seeing large variations in size year after year, appeared to be near equilibrium during a long period, until the middle of the 1990s (Fig. 1). From this point, the population saw a dramatic and stable decline, despite the implementation of strict protection measures (notably, the instauration of no-man's-land areas during the spring and early summer, channelling tourism) since the end of 1980s, as well as habitat (peatland and heathland) restoration (e.g. High Fens LIFE Project) since the 2000s. In the 2010s, the most suitable habitats and the highest carrying capacity since several decades were obtained thanks to the finalization of restoration projects (Frankard 2012; Plunus et al. 2012). However, quasi-extinction was reached, with only 1 and 2 males respectively in 2016 and 2017. Since then, a population reinforcement programme, by translocation of individuals captured in Sweden, has been launched.

Previous studies have explored the impact of weather and climate on the High Fens population (Loneux and Ruwet 1997a, b, Loneux and Lindsey 2003; Loneux 2000; Loneux and Lindsey 2003). Several weather parameters, i.e. spring and summer rainfall, snowfall and seasonal mean temperatures, were significant factors in explaining the fluctuation of the population size observed until the middle of the 1990s. However, these models were unable to explain the population size trajectory after this period. As with many ground-nesting species, the black grouse is vulnerable to predation by avian and mammalian predators and, particularly, by generalist predators such as foxes and crows (Fletcher et al. 2010; Policht et al. 2019). Other native predators (mustelids, felids, wild boar) can also predate eggs and chicks (Kämmerle and Storch 2019). For adult black grouse, the goshawk (*Accipiter gentilis*) and red fox (*Vulpes vulpes*) were identified as being the two main predators (e.g. Angelstam et al. 1984; Tornberg et al. 2011; Policht et al. 2019; Kämmerle and Storch 2019). Nowadays, it is established that generalist and/or invasive predator populations have increased markedly during the last decades in many European countries (McMahon et al. 2020; Tedeschi et al. 2021). Raccoons, recently introduced in Western Europe, are undergoing a demographic explosion (Salgado 2018). European fox and carrion crow populations have also markedly increased (McMahon et al. 2020). Moreover, the fox populations have benefited from a successful rabies vaccination programme in the 1980–1990s, after 30 years of the epidemic maintaining their population density below the habitat's carrying capacity (Chautan et al. 2000; Delcourt et al. 2022).

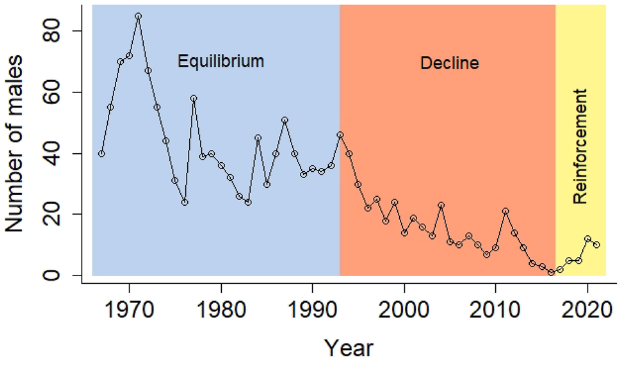

Fig. 1 Spring censuses of the black grouse cocks of the 'Baraque Michel' population in the High Fens between 1967 and 2021. Coloured periods highlight different dynamical population trajectories: relative stability (blue), decline (red) and the beginning of the reinforcement measures (orange)

The most precise understanding of the causes of the decline of the 'Baraque Michel' black grouse population appears necessary to help it reach a sustainable state and lead to successful translocation operations. With the removal of those factors well known to provoke the constant decline of the population (i.e. hunting, habitat deterioration and fragmentation), and as climate cannot in itself explain the decline, we examined the hypothesis that an additional factor may be limiting the recovery of this black grouse population: the increase of predation pressure. To this end, we first analysed the non-stationarity in male spring census trends in the High Fens. We then tested whether the supposed change since the middle 1990s is significant, or just a stochastic scenario in the range of population dynamic parameters, using time series analysis. We also analysed whether this population was really in equilibrium in the 1967–1993 period or whether this population has known a decline after an exceptional period of population abundance. Finally, we examined the hypothesis of predator impact, and in particular, whether the decline of the last Belgian black grouse population is a collateral impact of the vaccination campaign against fox rabies, through the increase in fox density since the 1990s.

Material and methods

Study area

The High Fens (Hautes Fagnes) is a plateau region in High Ardenne, in Eastern Belgium (Fig. 2). They include the largest terrestrial nature reserve of Belgium, covering an area of 6210 ha, which lies within the High Fens-Eifel Natural Park. The reserve has a subalpine climate, with strong winds and fierce winters, the wettest and coldest climate of Belgium, frequently shrouded in mist and low clouds (e.g. Mormal and Tricot 2004). The High Fens are characterized by large areas of moorlands and heathlands, with numerous relictual boreo-montane species. The natural reserve has benefited

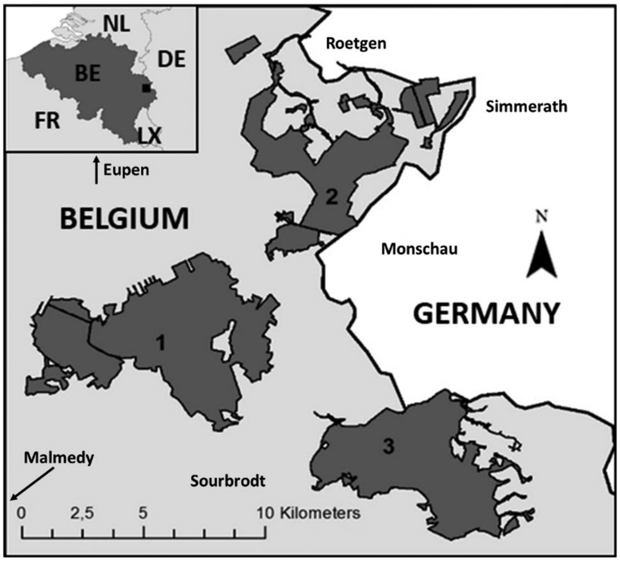

Fig. 2 Map of the three major sectors of the High Fens (Eastern Belgium) which were still occupied by black grouse in the recent past (1: Southwest High Fens with the 'Baraque Michel' (BM) population; 2: Northeast Fens with the NE population; 3: Fens of Sourbrodt-Elsenborn with the SE population). The BM population is the only survival population today and is the population studied in this paper

from LIFE projects in 2007–2012 aimed at restoring up to 1800 ha of degraded habitats of great biological interests (Frankard 2012; Plunus et al. 2012).

Study population

Three populations were present in the natural park (Fig. 2). Two small populations lived respectively in the Fens of Sourbrodt-Elsenborn (2564 ha, mainly within a military camp) (the 'SE population') and in the Northeast Fens (2.363 ha) (the 'NE population'). They disappeared respectively in the mid-1990s and in the 2000s (Suppl. Fig. 1), supposedly due to the disturbances induced by military activities for the SE population and due to the closing of the habitats by the forest for the NE population. Finally, the Baraque Michel (BM) population is found in the Southwest High Fens (c. 3000 ha). This remaining population has known a more limited impact of human activities and modifications of habitat. Focusing on the BM population would allow to explore the impact of predation without the major impacts of habitat evolution and fragmentation, and human disturbance.

Population census data

Black grouse leks are traditional display areas, usually located in open areas, where males gather annually to attract female mates. The consistent location of lek sites makes them ideal sites for population monitoring and counting the males (i.e., lek counts). As females are homochromic, behave more discreetly and visit the display arenas for a shorter period of time, female censuses are not used because female numbers are clearly underestimated (Ruwet 1982). Therefore, male censuses have been used by wildlife agencies as an index of population abundance for this species. In Belgium, the Behaviour Biology Unit of the University of Liège and the 'Service Public de Wallonie' (DEMNA and DNF) have been organizing censuses of the BM population since 1967. These occur in the spring (a couple of days in April, at a week interval) around dawn, while the males exhibit display activities and are carried out by a team of trained observers (ca. 20 people). The days are chosen according to weather conditions (good visibility, no fog or heavy precipitation). For the BM population, the census data covers the period 1967–2021 without missing values.

Statistics

To test whether the mid-1990s change in the data from the male spring censuses was significant or just a stochastic scenario within the range of normal population dynamics' parameters, we analysed the logarithm of censuses using autoregressive modelling combined with the interrupted time series analysis method (Gage and Lewis 2013; Hartmann et al. 1980), also called intervention analysis (Box and Tiao 1975). This method allows to test the relationship between a time series and an explanatory variable. The shape of the explanatory variable could be chosen to test a particular hypothesis suggested by the data to be analysed. Here, we choose the explanatory variable as equalling 1 between 1967 and 1993, then decreasing constantly to reach 0 in 2022. This allows us to confirm the suspicion that the time series is stationary between 1967 and 1993, then manifests a decreasing trend. First, we fitted a first-order autoregressive model, i.e. the values at time t were regressed against the values at time $t-1$ and time (year) to allow a linear time trend. We checked with the Durbin-Watson test (function *dwt* of the R {car} package; Fox and Weisberg 2019) that the residuals of this model were not significantly autocorrelated. Secondly, we tested the inclusion of the explanatory variable in the model, comparing the models with the Fisher test and the AIC. For the analysis of the annual growth rate $\lambda_i = N_{i+1}/N_i$, we applied the usual method used in PVA (Morris and Doak 2002) with the R package {*popbio*}, version 2.4 (Stubben et al. 2015). This linear regression approach in the estimation of the parameters provides a way to test if the mean (μ) and the variance (σ^2) of $\log(\lambda_i)$ significantly differ in distinct segments of the time series; in other words, it allows to test for changes in μ and σ^2 before vs. after a pivotal census (Dennis et al. 1991; Morris and Doak 2002). We used the unidirectional t test (with Welch correction) and a Fisher test, respectively, to compare the μ and σ^2 values of two analysed time segments. For each time segment, we applied a

Pearson *t* test to evaluate the effect of the population size on the log(λ_i). We also used the geometric mean growth rate λ_G of λ_i values, $\lambda_G = e^\mu$ (Morris and Doak 2002).

Fox data

The red fox, present in the High Fens for a long time, was highly suspected to be the major predator here. For instance, in a recent yet-unpublished study of tracked individuals translocated in the High Fens, around 90% of predation (on 27 reported cases) was attributed with a high probability to the red fox. To test the hypothesis that the decline of black grouse's population in the High Fens is linked to fox abundance, the only available data are hunting statistics over the period of 1986–2003 for all Wallonia, provided by the hunting councils in Wallonia. The number of foxes culled annually is frequently used to monitor changes in fox abundance, even if this method can be directly affected by the hunting effort (e.g. Chautan et al. 2000; Sadlier et al. 2004; Delcourt et al. 2022). However, during this period, Delcourt et al. (2022) underline that neither the number of hunters (see also Massei et al. 2015) nor the high hunting pressure on foxes during the 1970–1990s, to try to control the rabies epidemic, is enough to explain the increasing of the European fox populations just after the vaccination campaigns; hunting data therefore seems to be an adequate enough proxy to highlight the increase in fox populations at a regional scale in the areas that have experienced a vaccination campaign. After 2003, the monitoring method in Wallonia changed and was from then on based on only a small number of hunting districts, which are far from covering the surface of Wallonia to a satisfactory extent (see Fig. 4b in Delcourt et al. 2022). The records of fox rabies cases in Wallonia are available for the entirety of the study period (the official data published in *Rabies Journal Europe*, available at https://rbe.fli.de/resource/journal; see also Brochier et al. 2001). To test if fox density could be causing the data variations of male black grouse censuses, we used the total fox rabies cases reported in Wallonia by year (ra) as a proxy for fox density and applied the Granger causality principle (Granger 1969). We added log(ra) (instantaneous causality) in the first-order autoregressive model on the log of censuses, then proceeded as with the interrupted time series analysis. Some previous works have considered (Anderson et al. 1981; Fowler 2000 in red fox) or shown (Simon et al. 2019 in Artic fox) the direct relation between fox density and occurrences of fox rabies.

Results

Time series analysis

As anticipated, the time series modelling of the censuses (Table 1, model 1) revealed a significant serial autocorrelation, but the effect could be suppressed by a regression against lag1 values as indicated by the results of the Durbin-Watson test. The analysis highlighted a significant coefficient for time, indicating the occurrence of non-stationarity in the data. The interrupted time series analysis (Table 1, model 2), i.e. the inclusion of our explanatory variable, significantly improved the fit of model 2 compared to model 1 (Table 1, significant value of the Fisher test and lower AIC for model 2). We also noted that, in model 2, the coefficient of time was no longer significant, whereas the coefficient of the explanatory variable was. This result should be interpreted as the intervention variable being a better explanation of the time series' non-stationarity than a general linear trend. It can be concluded that the censuses were more or less stationary up to around 1993, and then decreased steadily (Suppl. Fig. 3).

The annual growth rates

In the early 1970s, the BM population had reached its maximum, with 85 cocks (Fig. 1). Despite the growth rate not being exceptional (and therefore not being considered a bonanza event as defined by Morris and Doak (2002), i.e. an exceptional positive outlier in the population growth rate), the succession of several years with a positive growth rate had induced an increased population size (Fig. 3a). The

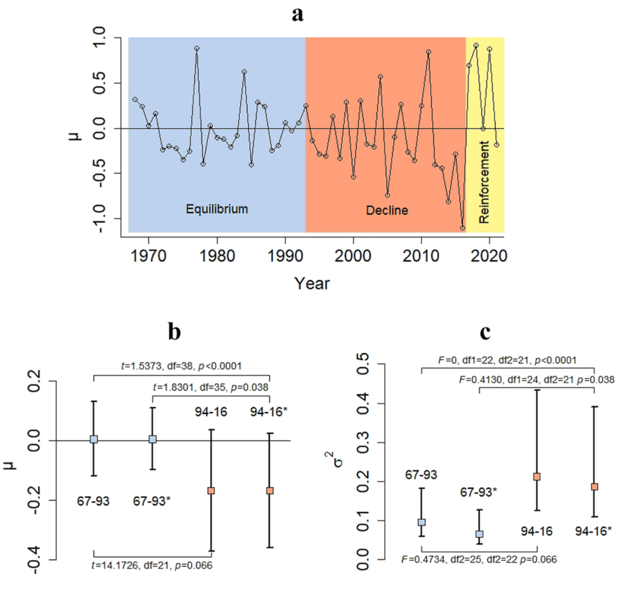

Fig. 3 **a** The annual log population growth rates of the BM population between 1967 and 2021. Coloured periods highlighted different dynamical population trajectory as defined in Fig. 1. **b** Comparison of the parameters μ, $\mu = \log(\lambda_G)$ (left), and **c** σ^2 (right), with 95% confidence intervals estimated from the annual growth rate (λ_i) for the periods 1967–1993, 1994–2016 and 1967–1993 (without the exceptional annual growth rate of 1977, indicated as '67–93*'), and 1994–2016 (without the exceptional annual growth rate observed in 2011, indicated as '94–16*'). The test values are based on a unidirectional *t* test and a Fisher test, respectively, for the μ and σ^2 values. Note that the comparison between 67–93* and 94–16 is not tested here

period of stability seems to cover from 1967 to circa 1993. The mean growth rate (λ_G) was equal to 1.005, with a variance (σ^2) of μ_t equal to 0.096 (Table 2).

The 1994–2016 period presents a more serrated log(λ_t) pattern than the first period, with a possible accentuation with years (Fig. 3a). The mean growth rate (λ_G) was equal to 0.846, i.e. on average, the population lost 15.4% of its size each year (Table 2). During this period, the fluctuations of the growth rates are amplified due to smaller population sizes and a larger value of variance (σ^2) of μ_t, with a value of 0.212. The comparison between segments of time series showed that the greatest difference is obtained in the pivot year set at 1993.

For the annual growth rate, there was no significant difference between the 1967–1993 and the 1994–2016 periods for both the parameters μ and σ^2. Nevertheless, if we removed the single exceptionally high value observed in 2011, the differences became highly significant (Fig. 3b, c; Suppl. Table 1). In fact, the growth rate was exceptional in 2011, probably due to exceptionally good seasonal conditions in 2010 for reproduction, with a 2.33 times increase in cock population size in 1 year (from 9 to 21 individuals). With only one such exception before, in 1977 (with $\lambda_t = 2.46$), never has the observed annual growth rate been so high. If this outlier value of 2011 is not included in the analysis, the differences between the two periods are very significant, with weaker values of μ and a larger value of σ^2 since 1994 (p values of < 0.0001), and if the value of 1977 is also excluded, the differences remain significant (Fig. 3b, c). The dynamics of the BM population are not significantly dependent on the population size in each of the two periods, but a tendency is observed between 1967 and 1993 (Fig. 4; Pearson *t* test: $p = 0.057$). Finally, between 2017 and 2019, three annual reinforcement operations were carried out using Swedish individuals; the planned reinforcement in 2020 and 2021 was unfortunately cancelled as a consequence of the COVID-19 crisis. More reinforcement operations are planned in the coming years. For the period of reinforcement, as the period is currently too short, it is too early to give any conclusions, even if the growth rates seem drastically better.

Fox rabies and spring censuses

Figure 5 illustrates the possible connection between reported fox rabies cases, the rabies vaccination campaign, the number of hunted foxes in Wallonia (South Belgium) and the spring census of male black grouses in the High Fens. Wallonia has known a rabies epidemic between 1966 and 1999, and the High Fens Natural Park has been case-free since circa 1992, with the last epidemic peak (1994–1998) being reported in a limited area far from the High Fens (Brochier et al. 2001). The vaccination campaign in Wallonia from 1986 until the 2000s eradicated rabies from Belgium. The number of hunted foxes showed a low level until the mid-1980s, but then underwent an exponential increase until it reached a plateau at the end of the 1990s. During the epidemic period, the number of rabies cases could be associated with fox abundance, as a

Table 1 Interrupted time series analysis of the male black grouse censuses (pop) of the BM population (High Fens, Belgium), Fisher goodness-of-fit test (*F* statistic), R^2 and Durbin-Watson test (D-W statistic)

Predictors	Estimate	SE	*t* value	*p* value
First-order autoregressive model of log(pop) (model 1, pop_{t-1} = observed census in $t-1$)				
Model 1: $\log(\text{pop}_t) \sim 1 + \log(\text{pop}_{t-1}) + \text{yr}$ [a]				
Intercept	39.779110	13.458238	2.956	*0.00486***
$\log(\text{pop}_{t-1})$	0.695348	0.111912	6.213	*1.28e − 07****
Year	−0.019510	0.006606	−2.954	*0.00489***
Model including the intervention variable (I_t model 2)				
Model 2: $\log(\text{pop}_t) \sim 1 + \log(\text{pop}_{t-1}) + I_t + \text{yr}$ [b]				
Intercept	17.143771	15.897077	1.078	0.28647
$\log(\text{pop}_{t-1})$	0.525546	0.127817	4.112	*0.00016****
I_t	1.166703	0.484535	2.408	*0.02011**
Year	−0.008345	0.007816	−1.068	0.29127

Model comparison with the Fisher test

	Res.Df	RSS	*F* statistic	*p* value	AIC
Model 1	46	5.8131			48.23405
Model 2	47	6.5458	5.7979	*0.02011**	44.29865

Res.Df residual degree of freedom, *RSS* residual sum of squared, *yr* year

[a] Multiple $R^2 = 0.8439$, adjusted $R^2 = 0.8373$; *F* statistic = 127.1 on 2 and 47 DF, *p* value = *< 2.2e − 16****; D-W statistic = 2.046, *p* value = 0.924

[b] Multiple $R^2 = 0.8614$, adjusted $R^2 = 0.8523$; *F* statistic = 95.28 on 3 and 46 DF, *p* value = *< 2.2e − 16****; D-W statistic = 1.947, *p* value = 0.526

$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Table 2 Linear model analysis to test the relation between the occurrence of rabies in Wallonia and the male black grouse censuses (pop$_t$) of the BM population (High Fens, Belgium) during the period 1967–1993, with Fisher goodness-of-fit test (F statistic), and R^2

Predictors	Estimate	SE	*t* value	*p* value
First-order autoregressive model of $\log(\mathrm{pop}_{t-1})$ (model 1, pop_{t-1} = observed census in $t-1$)				
Model 1: $\log(\mathrm{pop}_t) \sim 1 + \log(\mathrm{pop}_{t-1}) + \mathrm{yr}$ [a]				
Intercept	27.938537	17.198199	1.625	0.1179
$\log(\mathrm{pop}_{t-1})$	0.429860	0.190868	2.252	*0.0342**
Year	−0.013032	0.008486	−1.536	0.1383
Model including the log(ra) (ra = number of rabies cases), used as a proxy of the fox densities				
Model 2: $\log(\mathrm{pop}_t) \sim 1 + \log(\mathrm{pop}_{t-1}) + \log(\mathrm{ra}) + \mathrm{yr}$ [b]				
Intercept	35.149769	15.984001	2.199	*0.0387**
$\log(\mathrm{pop}_{t-1})$	0.215276	0.196250	1.097	0.2845
log(ra)	−0.075609	0.031876	−2.372	0.0269*
Year	−0.016116	0.007851	−2.053	0.0522
Model comparison with the Fisher test				

	Res.Df	RSS	*F* statistic	*p* value	AIC
Model 1	22	1.3750			11.275273
Model 2	23	1.7267	5.6264	*0.02686**	7.354279

[a] Multiple $R^2 = 0.4045$, adjusted $R^2 = 0.3527$; F statistic = 7.812 on 2 and 23 DF, p value = *0.002576*

[b] Multiple $R^2 = 0.5258$, adjusted $R^2 = 0.4611$; F statistic = 8.131 on 3 and 22 DF, p value = *0.0007926*

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

higher rabies prevalence could be observed when foxes are abundant. Unfortunately, we cannot prove this link, as data for the hunted numbers of foxes by year, used here as an indicator of fox abundance, is available only since 1986, and the last rabies peak did not affect the majority of Wallonia. If this link exists, the number of rabies cases could be a predictor of the predation pressure by fox on the black grouse population, and in fact, during the period 1967–1993, we put in evidence a significant prediction effect of the log of fox rabies occurrence on the spring censuses ($p = 0.0269$; Table 2, model 2); taking account the occurrence of rabies improves significantly the neutral model (ANOVA test: $p = 0.027$). Supplementary Fig. 3 illustrates the contribution of the occurrence of rabies on the prediction of spring censuses. Our interpretation is when the fox density is high, the black grouse population tends to decrease.

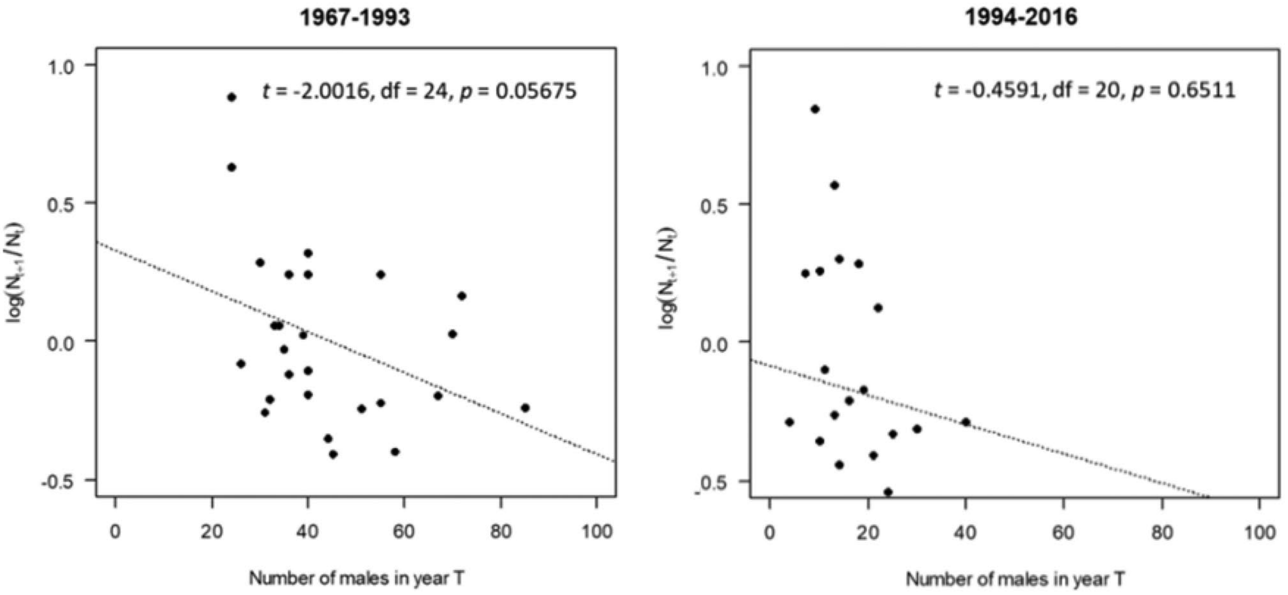

Fig. 4 Linear regressions to test the density dependence of the black grouse population (left) during the 1967–1993 period and (right) during the 1994–2016 period, with correlation line and Pearson t test

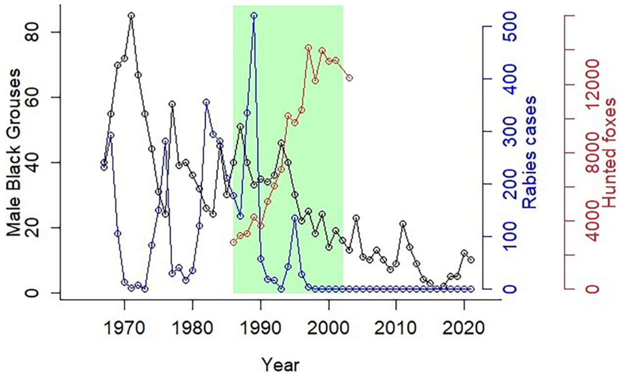

Fig. 5 Number of reported rabies cases in Wallonia (blue curve), number of reported hunted foxes in Wallonia (red curve) and lek census of male black grouses in the BM population in the High Fens (black curve) by year (1967–2021). The light green period (1986–2002) corresponds to the intensive fox rabies vaccination campaign

Discussion

The statistical analysis of the censuses between 1967 and 2016 led to a congruent conclusion with our hypothesis. The census data was more or less stable up to around 1993, then decreased first steadily, then exponentially. The analysis of the annual growth rate derived from the censuses let suppose that, on average, it was lower after 1993 than before.

In 1967–1993, the population size seems to be at equilibrium, with relatively regular fluctuations, but with no evident long-term growth or decrease ($\mu \sim 0$ and $\lambda \sim 1$). Our analysis does not confirm the existence of a demographic explosion due to an exceptional growth rate at the end of the 1960s, the high population size values simply being a fortunate sequence of five good years. The same trend was observed in some other populations, notably in the Belgian SE and NE populations (with a maximum total of 198 males in 1971 in the High Fens s.l.—Ruwet 1982, 1997; Ruwet et al. 1997), but also in Germany, such as with the Thuringe and Lange Rhön populations (Bergmann and Klaus 1994; Loneux and Ruwet 1997a, b; Müller 1996). In the High Fens, the suggested explanations are as follows: (1) the ban on black grouse hunting (since 1967); (2) the decrease in poaching, following the establishment of the High Fens as a nature reserve (set in 1957, with a large extension in 1964); (3) the large gassing of fox populations to struggle the rabies epizootic, so decreasing a major predation pressure; and (4) a succession of good summers favourable for reproduction (Ruwet et al. 1997). Furthermore, the population decrease observed between 1971 and 1976 could be related to exacerbated competition on parade arenas due to high densities of males, which induced a mortality of older males (Ibidem). This hypothesis would imply a negative density effect on population size, but our analysis did not conclude that it was significant (Fig. 4). Another explanation for this decrease would be a weaker recruitment rate of new males due to a poor reproductive success, coupled with the progressive disappearance of older males born in the 1960s. In 1976, the exceptionally dry summer induced one of the highest population size increases the next year. Exceptional growth rates were also noted after dry and warm early summers in 1984, 2011 and 2020. The 1977–1993 period was relatively more stable in terms of census, with fluctuation between 25 and 60 males for the BM population.

After 1993, the dynamics' parameters changed, with a mean loss of 15.4% of the population size each year, bringing the population close to extinction in 2016. This was aggravated by an increase of the variance (σ^2) of growth rate. In fact, the probability of reaching low population size values, and thereby reaching the threshold of (quasi-)extinction, increases with higher σ^2 (Morris and Doak 2002). However, the increase of σ^2 was also certainly a consequence of the small population size: a slight change induces a larger variation of growth rate when the group size is small. This also explains why the annual growth rate curve becomes more and more serrated during this period of decline. In 2011, following the dry and warm summer of 2010, an increase in growth rate was observed, but unfortunately, this success was not confirmed the next year: a wildfire affecting 1300 ha and major sites for the species, such as arenas and reproductive sites, occurred in the end of spring 2011.

Fox predation hypothesis

The sudden change circa 1993 in the BM population's trends for census and dynamic parameters let us suspect a rapid change in the environment, able to potentially induce an increased mortality or a decreased reproduction rate, or both. Predation, affecting all stages of life, is able to induce these impacts. The red fox, a major predator of black grouse (e.g. Kämmerle and Storch 2019), has experienced large changes in its abundance in these last decades in Western Europa, notably due to a rabies epizootic which had induced a decrease in densities, both directly by the disease and indirectly by voluntary elimination of foxes by gassing and by hunting, in the hopes of controlling the epidemic which was dangerous for both humans and domestic animals (Delcourt et al. 2022). These methods were inefficient until the development and large-scale use of oral vaccines from the end of the 1980s in Wallonia (Brochier et al. 2001; Delcourt et al. 2022). As a consequence, and despite hunting pressure already certainly being high before vaccination campaigns, the number of foxes hunted strongly increased to reach a plateau at the end of the 1990s. If we assume that the number of foxes hunted is a decent indicator of fox density, it seems to have undergone a demographic explosion in the first part of the 1990s. In fact, many field observers in Wallonia observed the increase, but no one quantified or adequately reported the observation. Even if Wallonia and the High Fens are not really at the same scale of study, the change in fox population was probably similar in the Natural Reserve of High Fens as it was in the region surrounding it. Not only did the European fox population recover to its previous value, but its population has since increased remarkably to levels higher than before the rabies epidemic (Delcourt et al. 2022). Foxes have benefited notably from better accessibility to food provided by humans (garbage, landfill and gardens), the releasing of game birds (Pringle et al. 2019) and even from animal traffic casualties due to a large increase of traffic and the number of roads (Schwartz et al. 2018).

Here, the opposing trend between the fox and the black grouse populations supports the hypothesis that the decline of the BM population since 1993 might result from the increase of predation by foxes. In this scenario, the rabies vaccination would have led to the rarefaction of the last Belgian black grouse populations. In Norway, Lindström et al. (1987, 1994) have shown the same impact of foxes on black grouse populations where, during a period of severe mange epidemic in the 1980s affecting the fox population, black grouse populations significantly increased. However, once the fox population recovered to its pre-epidemic level, their prey's populations seriously decreased until reaching the level previously observed.

Other predator hypothesis

The fox is not the only black grouse predator. For adult birds, another major predator present in the High Fens is the goshawk. In the past, goshawk populations have declined due to the contamination of DTT and PCB, but they recovered in the 1980s (Doucet 2005; Rutz et al. 2006). In the 1990s, the goshawk was in expansion in Central Belgium (Fasol 2011) but in regression in South-western Belgium (Doucet 2005). In favourable habitats in Germany, close to the High Fens (Nordrhein-Westfalen), populations were stable (Rutz et al. 2006). Corvids are also potentially predators of eggs and young chicks. In the High Fens, magpies (*Pica pica*) are rare in the natural reserve. Ravens (*Corvus corax*) have returned to Wallonia in 1970, but their density remains low in the natural reserve. Carrion crows (*Corvus corone*) were rare in the High Fens in the past, but their populations have increased these last decades possibly due to the development of agricultures and farms around the reserve, as well as the development of tourisms (increasing of litter) (Keulen et al. 2005). The wild boar (*Sus scrofa*) is also known to be a predator of ground-nesting birds (both eggs and even occasionally nesting females) (Oja et al. 2017; Cukor et al. 2021). The wild boar population in Wallonia has increased steadily over recent decades (Licoppe et al. 2020). Other potential predators are the pine marten (*Martes martes*)—but the trend in its population is unknown in the High Fens—and the raccoon (*Procyon lotor*), an invasive American predator which can have a negative potential impact as an egg predator. However, raccoons mainly settled the region during the 2000–2010s (Libois 2006), around a decade after the beginning of the BM population's decline. Nevertheless, the raccoon is a species to keep under observation and control as a priority.

With the exception of the carrion crows, and perhaps recently the raccoon, no predator other than the red fox is able to, alone, explain the declining trend of the BM population after 1993 in the High Fens. However, the proportion of predation induced by foxes alone in comparison with predation from all other predators (or even other mortality causes) has yet to be evaluated.

The climate change hypothesis

Given that the black grouse has its distribution centred on high latitudes, in mountains and on high-plateau regions, it is regularly suggested that its decline in Belgium would be the consequence of climate change and particularly of global warming. However, this is forgetting that there were important lowland populations throughout Europe before the destruction and fragmentation of habitats and the intensive use of land for urbanization, as well as intensive agriculture, left little room for this bird. Moreover, most of the survival lowland populations are currently insularized. The natural reserve of the High Fens is one of the last vast protected areas in Belgium, where human pressure is thus limited. The temperature difference between the province of Antwerp (where black grouse populations were known until the 1980s), and the High Fens is still several degrees (3.5 °C in mean), and this difference already existed several decades ago when the low-altitude populations were still important (IRM data). However, weather does have a direct impact on mortality and reproductive success. We have already reported that dry and warm summers have had important positive effects on the reproductive success in our BM population. Through modelling, Loneux et al. demonstrated the negative effect of mild and rainy winters and rainy breeding periods, as well as the positive effect of warm temperatures during hatching (Loneux and Lindsey 2003; Loneux et al. 2003). Besides climate predictors, the model also included the population density of the two previous years (Loneux and Lindsey 2003; recent data are unpublished). However, applied to the most recent data (since the 1990s), the model was too optimist, which let suppose that these factors have evolved, or that additional factors are now constraining the population. Pearce-Higgins et al. (2019) show that, for black grouse, the negative effect upon reproduction of June rainfall was eliminated at sites where predator control occurred, and that productivity was maximized when predator control and habitat management were combined.

Other environmental changes

Habitat destruction is probably the major cause of decline of the black grouse in Belgium. The very small SE population disappeared in the 1990s. For this population, favourable habitat is present in the military camp, but military activities induced potential disturbance (military training, shellings and detonations). Yet, the modest NE population reached a peak of 80 males in 1971, followed by a large decline in the mid-1970s, then stabilization at 7–18 individuals until the 1990s, followed by further decline until extinction in the 2000s. The evident closing of its habitat these last decades seems an important factor in explaining the fate of this population (Keulen et al. 2005). Habitat restoration in the 2000s–2010s of this part of the natural reserve was probably too late, but it could welcome black grouses again in the future. The BM population is located in a more stable habitat, where the peatlands and heathlands were well maintained without significant closing of the habitat by the forest. However, moor grass (*Molinia caerulea*) has colonized large sections of these habitats, to the detriment of the Ericaceous areas. Another potential impact is the increasing of cervid grazing, which can affect the height of ericaceous shrubs. In fact, female black grouse choose the protection of a bush to nest on the ground. The increase in deer density observed these last decades may have induced a decrease of potential nesting areas by overgrazing. However, the colonization of moor grass and overgrazing did not suddenly appear in the beginning of the nineties, and cannot alone explain the population dynamics' changes of black grouse in the BM population.

Conclusions and perspectives

The time series analysis of male black grouse annual census in the Southwest High Fens over 50 years of continuous data has allowed to underline two distinct periods in population trends: one with a population at equilibrium with natural fluctuations and one of quasi-constant decline. Numerous explanations are suggested to explain this decline, notably climate, habitat modification and predation. One of them is particularly striking: this decline—since circa 1993–1994—seems to fit well with the red fox's demographic explosion at exactly the same moment, probably owing to the massive vaccination campaign against fox rabies, which eliminated the disease after 30 years of epidemic in Western Europe. In this scenario, the elimination of fox rabies by human intervention would have, indirectly and involuntary, induced the decline of the last Belgian black grouse populations. However, other additional causes may have played in the fox demographic growth, as fox population levels are largely higher after than before the rabies presence (Delcourt et al. 2022). Another remaining question is how predation on black grouse is impacted with their density: could a larger grouse population be less sensitive to loss due to predation, or is the intensity of predation proportional to black grouse density? Another interesting approach would be to determine population viability of a restored population on the basis of these environmental effects. Population viability analysis goes beyond the aims of this article, but will be the next working step to determine the probability of success of restoring a sustainable population in Belgium. A final question would be to determine what is the real carrying capacity for black grouse in the near future: this is an important parameter to determine whether the future High Fens population could be restored to the same population size observed in the 1970s and 1980s, or even at higher levels.

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Declarations

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

Conflict of interest The authors declare no competing interests.

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