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ORIGINAL ARTICLE

Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird

Jean-Yves Barnagaud · Pierre André Crochet · Yann Magnani · Ariane Bernard Laurent · Emmanuel Menoni · Claude Novoa · Olivier Gimenez

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Abstract Deciphering the effects of climatic conditions on population dynamics is of major importance in understanding how organisms are likely to be affected by climate changes. Using data from broad-scale annual censuses between 1990 and 2007, we show that winter and summer North Atlantic Oscillations affect several breeding success indicators of the Black Grouse (*Tetrao tetrix*) in the French Alps. We did not find any trend in hen counts or breeding indexes over the study period. Surprisingly for a bird specialised in cold climates, we show that Black Grouse optimise their reproductive output for positive values of the winter NAO corresponding to the average NAO index of the last 30 years. Extreme NAO values lead to lower breeding success, indicating that the grouse may be more able to track trends in climate than an increase in the frequency of extreme years. Our result show that, at least from a short-term perspective, Black Grouse productivity is not threatened by a trend towards warmer climatic conditions in the Alps, but may be affected by an increased frequency of extreme years. We advocate the use of the NAO as a climate proxy rather than using heavily noised and biased local climate descriptors in studies focusing on the global response to climate over a large spatial scale.

Keywords Climate packages · Galliforms · Mountain avifauna · NAO · Reproductive success · *Tetrao tetrix*

Zusammenfassung Die Folgen der Klimaverhältnisse auf die Populationsdynamik zu entschlüsseln ist von größter Wichtigkeit, um zu verstehen, wie sich Klimaveränderungen wahrscheinlich auf Organismen auswirken werden. Mittels Daten aus umfassenden jährlichen Zählungen zwischen 1990 und 2007 zeigen wir, dass Nordatlantische Oszillationen in Winter und Sommer mehrere Anzeiger von Bruterfolg bei Birkhühnern (*Tetrao tetrix*) in den französischen Alpen beeinflussen. Wir fanden keinen Trend in den Zahlen von Hühnern oder in Brutanzeigern während des Untersuchungszeitraums. Wir zeigen, dass Birkhühner ihre Fortpflanzungsleistung für positive Winter-NAOs (bezogen auf den durchschnittlichen NAO-Index der letzten 30 Jahre) optimieren, was für einen an ein kaltes Klima angepassten Vogel überraschend ist. Extreme NAOI-Werte führen zu niedrigerem Bruterfolg, was darauf hindeutet, dass Birkhühner besser in der Lage sein könnten, Klimatrends zu folgen, als eine Zunahme der Häufigkeit extremer Jahre zu bewältigen. Unsere Ergebnisse zeigen, dass zumindest aus kurzfristiger Sicht die

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J.-Y. Barnagaud (✉) · P. A. Crochet · O. Gimenez
Centre d'Ecologie Fonctionnelle et Evolutive,
Campus CNRS, UMR 5175, 1919 route de Mende,
Montpellier Cedex 5 34293, France
e-mail: jy.barnagaud@gmail.com

Y. Magnani
Office National de la Chasse et de la Faune Sauvage,
90 Impasse des Daudes, Route du col de Leschaux,
74320 Sevrier, France

A. Bernard Laurent
Office National de la Chasse et de la Faune Sauvage,
CNERA Faune de montagne, CADAM, Préfecture Est,
06286 Nice Cedex 3, France

E. Menoni
Office National de la Chasse et de la Faune Sauvage,
Impasse la Chapelle, 31800 Villeneuve de Rivière, France

C. Novoa
Office National de la Chasse et de la Faune Sauvage,
Direction des Etudes et de la Recherche,
Espace Alfred Sauvy, 66500 Prades, France

Produktivität der Birkhühner nicht durch einen Trend zu wärmeren Klimaverhältnissen in den Alpen bedroht ist, jedoch durch eine erhöhte Häufigkeit extremer Jahre beeinträchtigt sein dürfte. Wir empfehlen, für Studien, die sich auf die großflächige, globale Antwort auf das Klima konzentrieren, die NAO als Klimamaß zu verwenden und nicht stark störanfällige und verzerrte lokale Klimadeskriptoren.

Introduction

Global climate change (IPCC 2007) has already been associated with shifts in phenology, population dynamics, community composition and distribution of organisms throughout the world (e.g. Walther et al. 2002; Parmesan and Yohe 2003). Cold-climate ecosystems, in particular, might be especially sensitive to the rapid rise of temperatures and changes in rainfall regime anticipated under most future climate models, because many species living in such ecosystems have narrow thermal ranges or high habitat specialisation (e.g. Krajick 2001, 2004; Thuiller et al. 2005; Sekercioglu et al. 2008). Their conservation thus requires a careful assessment of their population dynamics in response to climate variations. Birds constitute a promising model for such studies because their demography has often been shown to be closely related to climate variability (Saether et al. 2004).

Birds specialised in high latitude or altitude habitats should be particularly at risk (Pimm et al. 2006), because they are expected to exhibit a weak resilience to rapid warming (Martin and Wiebe 2004), especially if their dispersal abilities are limited. However, some avian species show adaptive responses to climate changes, particularly in their phenology or migration behaviour, suggesting that they can track at least to a certain extent climate and associated habitat changes within short time lags (e.g. Jonzén et al. 2006; Charmantier et al. 2008).

Several recent attempts to assess the effects of climate on birds have used large-scale climate indices such as the North Atlantic Oscillation (NAO) (Stenseth et al. 2003). The NAO, a large-scale atmospheric oscillation over the North Atlantic, strongly influences climate variability over western Europe in winter (Hurrell et al. 2003) and, to a lesser extent, in summer (Folland et al. 2009). The NAO has been fruitfully used as a “climate package” to relate climatic variations with life-history traits or population dynamics (Coulson et al. 2001; Cotton 2003; Grosbois and Thompson 2005; Stenseth and Mysterud 2005; Lewis et al. 2009). One of its main advantages is to summarise climate variations in a single index encompassing interactions sometimes too complex to be captured by a simple model, whereas the use of standard local climate descriptors such as temperature or precipitation requires numerous variables (Hallett et al. 2004). The NAO has exhibited more positive values for the last 30–40 years than in the previous century, a trend which has been related to the current climate change over the northern hemisphere (Hurrell 1996; Visbeck et al. 2001). The NAO thus not only reflects inter-annual climatic variability but also long-term climate changes.

To assess the risks that alpine and boreal ecosystems face under current climate changes, the response of many alpine and boreal species to climate variations needs to be assessed. However, investigating the relationship between climate and population dynamics in mountain areas faces the issue of high fine-grained variability in local climatic parameters due to local variations in altitude and topography (Beniston 2006). The NAO might thus be a valuable tool to settle this problem in the Alps, where it explains from 56 to 80% of the variations in local winter atmospheric pressure or temperature (Beniston and Jungo 2002).

Among boreal and alpine species, European mountain Galliforms (Aves, Galliformes) are under close monitoring by wildlife management agencies due to their value as emblematic wildlife and gamebirds (Lindström 1994; Sandercock et al. 2005), and because of the recent population declines exhibited by several species (Storch 2007). While the main causes of such declines appear to be hunting, tourism and habitat loss or degradation (e.g. Kurki et al. 2000; Patthey et al. 2008; Storch 2007), climate variations were found to noticeably affect Galliform reproductive success in several studies (Swenson et al. 1994; Moss et al. 2001; Klaus 2007; Novoa et al. 2008). Current climate changes in particular cause mismatches between timing of hatching and optimal climatic conditions in Finnish populations of Black Grouse (*Tetrao tetrix*) (Ludwig et al. 2006). Loneux and Lindsey (2003) also found negative effects of hot and dry climatic conditions on Black Grouse demography in the Ardennes (Belgium), raising concerns about the ability of these lowland populations of the species to track climate changes. In Scandinavia, Spidsö et al. (1997) have shown the positive role of snowfalls and cold weather for Black Grouse survival through better thermoregulation and protection against predation in winter. Moss et al. (2001) found that climate changes have a negative effect on the reproductive output of Capercaillies (*Tetrao urogallus*) in Scotland, casting doubts on the long-term persistence of the species under warmer future climatic conditions in this area.

Alpine populations of several Galliforms lie at the southern edge of the species distribution and have declined for at least 30 years (Storch 2007). Given the results obtained in other areas (see above), the substantial elevation of temperature and increase in frequency of drier conditions that are occurring over the Alps as a consequence of climate changes (Beniston 2006) could explain part of these population declines. However, no study has to date addressed the response of alpine populations of Tetraonidae to climatic variability and climate changes.

In this paper, our aim was to investigate how alpine populations of Black Grouse, a typical boreo-alpine species at the southern edge of its distribution, are affected by global warming. We chose to concentrate on reproductive success, a demographic trait that has already been shown to be highly sensible to climate change in other avian species (Jiguet et al. 2007). Early spring weather conditions, usually corresponding to the snow melting period in the Black Grouse habitat, influence the nutritive values of available food (essentially young seedlings) just before the breeding period, and strongly affect the reproductive success through the quality of the eggs (Siivonen 1957, Moss et al. 1975, 1981). Further, winter climate influences the health state and reserve storage of hens, which in turn accentuate the effects of weather and food conditions just before breeding (Thompson and Fritzel 1988).

We used broad scale annual censuses of adult and young Black Grouse in the French Alps between 1990 and 2007 to test whether the breeding success of the species is affected by inter-annual climatic variation and long-term climate change. We first looked for global temporal trends in hen numbers and parameters of breeding success during the study period. We then assessed the effects of winter and summer climate variability on the reproductive success through the NAO. This allowed us to assess the effects of recent changes in average NAO values on reproductive success by comparing indices of breeding success for values of the NAO corresponding to its long-term average or to its means over shorter time lags.

Methods

Data

Count data

Breeding success was quantified by annual counts of Black Grouse hens and chicks carried out by the French Mountain Galliforms Observatory (Observatoire des Galliformes de Montagne (OGM) 2003) on 58 counting sites.

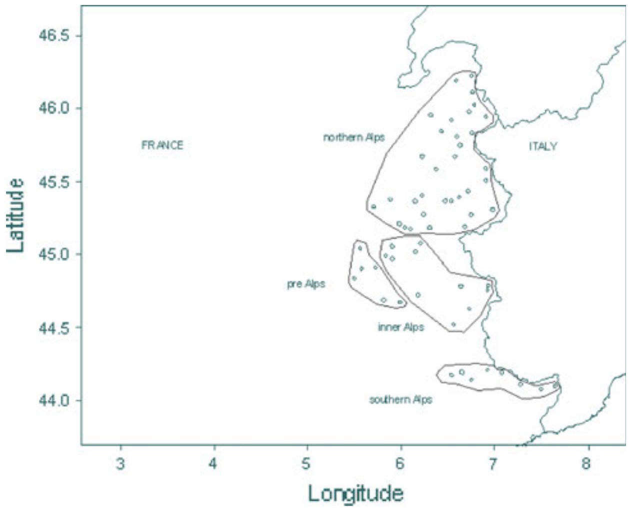

Fig. 1 Locations of the 58 count sites for Black Grouse (*Tetrao tetrix*) available over the period 1990–2007, used for our analyses. The France–Italy border is indicated. *Polygons* correspond to bioclimatic regions (see text for further details)

The study area covers all the French Alps, which we divided into four bioclimatic regions, based on a more precise partition by Ozenda (1981), Ascencio (1983) and Chassagneux et al. (1992) to account for geographic variation in habitat and local climate variability: Pre-Alps, Northern Alps, Inner Alps, and Southern Alps (Fig. 1). Hens and chicks were counted once a year in August by systematic censuses using pointer dogs. The counts were performed on the same sites and areas from one year to another, with the same operators, and the exact date of each count was adjusted for each site so that counting took place when the chicks were in similar development stages, able to fly but still dependent of the hen. Each dog and operator had an area of 10–30 ha to ride through, starting from below and walking up following parallel contour lines spaced out from each other by 15–20 m (Leonard 1992). Data were available over an 18-year period (1990–2007), but not every year for all sites. The number of available counts per year ranged from 7 (year 1990) to 52 (year 2006) (mean = 28 sites/year, SE = 3.89); and 1–18 counts were available for each site over the 18-year period (mean = 8.6 counts/site, SE = 0.62) (Fig. 2). Three reproduction indices were derived from the data: “proportion of hens with brood” was the

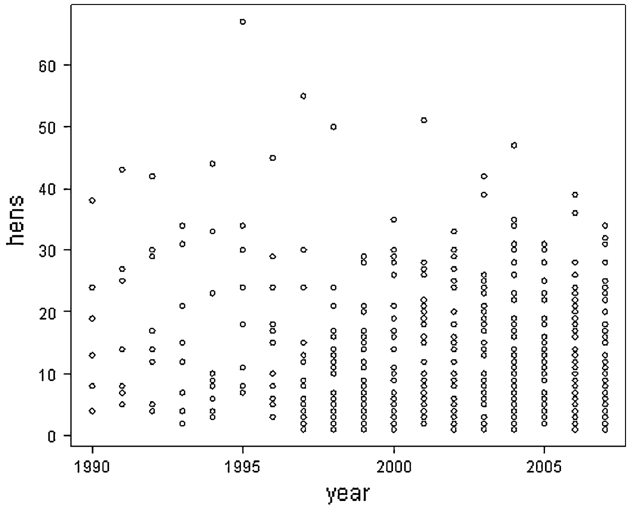

Fig. 2 Number of hens counted plotted against years. Each *point* correspond to 1 count site

proportion of hens with at least one chick; “brood size” was the mean number of chicks per successful hen (hen with brood); the product of these two measures gave a standard overall measure of the breeding success, the “number of chicks per hen” (Moss et al. 2001).

Climate data

Food intake in winter and early spring are decisive for the success of the reproduction in Galliforms (Novoa et al. 2008; Eiberle 1987) as in several other avian species, particularly geese (Dickey et al. 2009; Choinière and Gauthier 1995; Reed et al. 2004). Post-hatching survival of chicks in July is another major source of variation of the breeding success of the species (Ellison et al. 1987). Thus, relating grouse reproduction in the Alps to winter and summer NAO is biologically fully meaningful. The NAO time series were obtained from the Climate Analysis Section, NCAR, Boulder, USA, available at http://www.cgd.ucar.edu/cas/jhurrell/indices.html (Hurrell 1995). Beniston and Jungo (2002) showed a strong linear relationship between the winter NAO and surface pressure, precipitation or temperatures in the Swiss Alps, close to our survey area, and this was particularly true at high elevation areas (Giorgi et al. 1997) corresponding to the altitudinal distribution range of the Black Grouse in the area. We thus used the December to March seasonal PC-based NAO index (wNAO) to account for climate inter-annual variability in winter (Hurrell et al. 2003). Folland et al. (2009) recently showed that the summer NAO also has a significant effect on the European climate, although its explanatory power has not yet been tested. Hence, we also considered the June to August seasonal PC-based NAO index (sNAO; Hurrell 1995), as it covers the period over which chicks are most likely to be strongly affected by climate variations (Erikstad and Spidsö 1982), especially in the alpine range of the species (Zbinden and Salvioni 2004). Note that, while the NAO affects local climatic conditions in summer and winter, it has little influence on spring and autumn climates (Portis et al. 2001; Hurrell et al. 2003). Thus, we chose not to relate Black Grouse breeding success to the spring NAO, although spring also includes some critical periods for the reproduction of Black Grouse.

Statistical analyses

All the analyses were conducted with R (R Development Core Team 2007).

Temporal trends in hens numbers

We checked for linear trends in the number of hens during the study period on a subset of 9 sites on which it was certain that the surveyed area remained constant between years; 7–18 counts were available on these sites over the period considered. Using the R package lme4 (Bates and Sarkar 2008), we created a linear mixed model with the hen numbers as the response variable (log-transformed), year as an explanatory variable, and site as a random effect on both the intercept and the slope of the regression. We used a MCMC algorithm to obtain the posterior distribution of the year effect, then calculated its 95% posterior credible interval to test for the existence of a significant time trend (Bolker et al. 2009).

Effect of climate on reproduction

We used general linear mixed models with Poisson distribution and log-link function (mgcv R package; Wood 2006) to assess the effects of the NAO on number of chicks per hen or brood size. The models for the number of chicks per hen and the brood size included the number of chicks as the response variable, and, respectively, the number of hens or broods as an offset. The models for the proportion of hens with brood included the number of brood as the response variable, and the number of hens as an offset. For each season (winter and summer) and each reproductive index, the most complex model included a fixed effect for bioclimatic regions (BR), the NAO as simple and quadratic fixed effects, and interactions between regions and NAO. A random site effect, nested in regions, was included to accommodate the correlation of successive annual counts in the same sites.

When a quadratic response (that is, a function of the form $y = a + b\ x + c\ x^2$) appeared in the preferred model, we calculated the response optimum max as $\max = \frac{-\hat{b}}{2\hat{c}}$ where $\hat{b}$ and $\hat{c}$ are the maximum likelihood estimates of the regression parameters b and c. The associated standard error $SE_{\max}$ of max was obtained using the delta-method (Seber 1982):

$$SE_{\max} = \sqrt{\frac{1}{4} \times \left(\frac{\hat{b}}{\hat{c}}\right)^2 \times \left[\left(\frac{SE(\hat{b})^2}{\hat{b}^2}\right) + \left(\frac{SE(\hat{c})^2}{\hat{c}^2}\right) - \left(\frac{2 \times \mathrm{cov}(\hat{b},\hat{c})}{\hat{b} \times \hat{c}}\right)\right]}$$

where $\mathrm{cov}(\hat{b}, \hat{c})$ is the estimated covariance between the estimates of b and c. Finally, in order to check for winter climate-linked variations of hen survival, we performed a Poisson regression with hen counts as a response variable, wNAO as the explanatory variable, and random site effect, using the 9 sites retained for the temporal trend analysis.

Model selection

As our aim was to assess the effects of winter and summer climate separately, we built separate models for winter and summer NAO values. For each of them, we built the most complex model (see above), a null model including no effect but the site effect, and all possible intermediate models. Although it is recommended to use the Akaike

Information Criterion corrected for small sample size (AICc) as a routine selection method, the sample size of our dataset was large enough compared to the maximum number of estimated parameters to make the difference between AICc and AIC negligible; we thus retained the model with the lowest value of AIC (Burnham and Anderson 2002). If the retained model included a quadratic or an interaction effect, the corresponding single terms were systematically added (Mc Cullagh and Nelder 1989). When less than 2 AIC units separated models including the NAO as a quadratic or linear effect, the response pattern was examined graphically. If no sensible difference between the linear and quadratic curve appeared, we kept the linear model. We calculated AIC weights as $\mathrm{AIC}_{Wi} = \left(\frac{\exp(-0.5 \times \Delta AIC_i)}{\sum_{r=1}^{M} \exp(-0.5 \times \Delta AIC_r)} \right)$, where $\Delta\mathrm{AIC}_i$ is the difference between the AIC of model i and that of the best model, and M is the total number of compared models (Burnham and Anderson 2002). To assess the gain of explanatory power of a model when adding a variable, we calculated evidence ratios as $\mathrm{E}_{i,j} = \mathrm{AIC}_{wi}/\mathrm{AIC}_{wj}$, where i and j are two of the tested models.

When a model included an effect of the NAO, we also built the corresponding generalised additive mixed model (Wood 2006), which uses splines functions as non-parametric smoothers of the explanatory variables, to ensure by checking response curves visually that no complex response other than linear or quadratic (for instance, breakpoints or thresholds) was missed.

Autocorrelation

To assess potential spatial trends that could have biased our analyses, we checked whether spatial autocorrelation remained in the residuals of the preferred models (e.g. Selmi et al. 2003), using correlograms based on Moran's I tests calculated over 12 classes of distance (Legendre and Legendre 1984). Similarly, we looked for temporal autocorrelation (Brockwell and Davis 1991) in the residuals of the models, using the acf function in R.

Results

Trends

The slope of the year effect (−0.005, SD = 0.030) on hen numbers was not different from 0 [posterior 95% credible interval (−0.07 0.02)]. There was thus no significant temporal trend in the number of female Black Grouse during the study period in the monitored sites, and no indication of a decline at all (estimated slope positive). Similarly, no temporal trend was detected for any of the 3 reproduction indices for the period considered (1990–2007) (Fig. 3). Neither spatial nor temporal autocorrelations were found in the selected regression model residuals (all P values >0.05). Nevertheless, an effect of bioclimatic regions appeared in all the preferred models for the number of chicks per hen and the brood size (Table 1), but not the proportion of hens with brood (Fig. 4b), indicating differences in breeding success linked to regional variations in the Alps.

Summer NAO

For all the reproduction indices, a positive linear effect of sNAO appeared in summer (Table 1). Based on the AIC values, it was not possible to determine if a quadratic term should be incorporated in the preferred models (ΔAIC < 2 between linear and quadratic models). However, the response curves of the quadratic models for each index did not depart visually from straight lines. Indeed, quadratic terms estimates were close to 0 and were thus not retained in the final models.

Winter NAO

According to the AIC model ranking, the best models for the number of chicks per hen and the proportion of hens with brood included a quadratic effect of wNAO (Table 1). For both indices, the estimate of the linear term was positive and the estimate of the quadratic term was negative (Table 2), corresponding to a convex response shape (Fig. 4), with a maximum for a particular value of wNAO. For the number

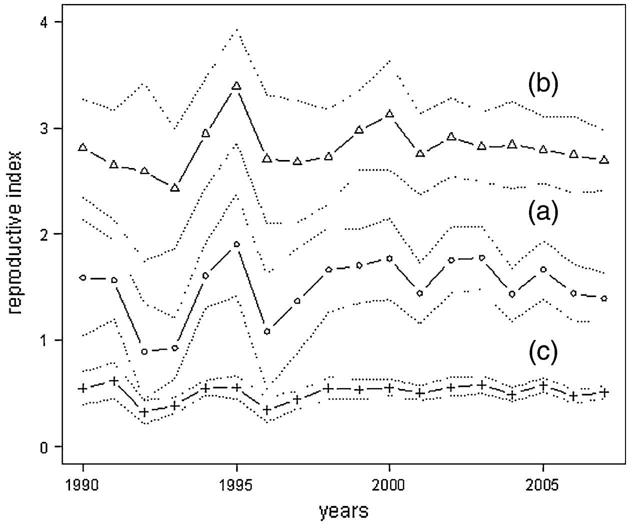

Fig. 3 Mean values of the reproductive indices of the Alpine Black Grouse over the period 1990–2007. **a** Number of chicks per hen ($r = -0.05$, $P = 0.69$); **b** brood size ($r = 0.01$, $P = 0.28$); **c** proportion of hens with brood ($r = -0.02$, $P = 0.43$); *dotted lines* correspond to 2 × standard error

Table 1 Model selection and evidence ratios for the model relating breeding success to the NAO. *A*. Model selection for the response to the NAO (winter: December to March;summer: June to August) of the number of chicks per hen Black Grouse (*Tetrao tetrix*), the brood size and the number ofhens with brood. *B*. Evidence ratio calculated as Ei,j = AIC weight$_j$/AIC weight$_i$ where j arecolumns and i are rows

Model	K	Chicks per hen			Brood size			Proportion of hens with brood		
		AIC	ΔAIC	AIC weight	AIC	ΔAIC	AIC weight	AIC	ΔAIC	AIC weight
A. Model selection for the response to the NAO[a]										
Winter										
Null	2	838.4	9.3	0.006	483.4	15.3	0.000	524	13.5	0.001
Regions	6	830.7	1.6	0.268	468.2	0	0.664	524.5	13.9	0.000
NAO	3	839.8	10.7	0.003	485.4	17.3	0.000	525.1	14.6	0.000
Regions + NAO	7	832.4	3.3	0.115	470.2	2	0.245	525.8	15.2	0.000
NAO + NAO^2	4	837.2	8.1	0.010	487.3	19.2	0.000	510.6	0	0.499
Regions + NAO + NAO^2	8	829.1	0	0.598	472.2	4	0.090	510.6	0	0.499
Summer										
Null	2	838.4	74.8	0.000	483.4	42.6	0.000	524	2.7	0.000
Regions	6	830.7	67.1	0.000	468.2	27.3	0.000	524.5	2.8	0.000
NAO	3	768.8	5.2	0.051	451.9	11	0.003	496.7	0	0.459
Regions + NAO	7	763.6	0	0.681	440.8	0	0.698	498.8	2.1	0.161
NAO + NAO^2	4	770.9	7.2	0.018	453.4	12.5	0.001	497.7	1	0.278
Regions + NAO + NAO^2	8	765.6	1.9	0.251	442.5	1.6	0.298	499.7	3	0.102

Response	Model	Null	Regions	NAO	Regions + NAO	NAO + NAO^2
B. Evidence ratio[b]						
Chicks per hen	Regions	0.02				
	NAO	2.00	89.33			
	Regions + NAO	0.05	2.33	0.03		
	NAO + NAO^2	0.60	26.80	0.30	11.50	
	Regions + NAO + NAO^2	0.01	0.45	0.01	0.19	0.02
Brood size	Regions	0.00				
	NAO	0.00	–			
	Regions + NAO	0.00	2.71	0.00		
	NAO + NAO^2	0.00	–	0.00	–	
	Regions + NAO + NAO^2	0.00	7.38	0.00	2.72	0.00
Proportion of hens with brood	Regions	–				
	NAO	–	0.00			
	Regions + NAO	–	0.00	0.00		
	NAO + NAO^2	0.00	0.00	0.00	0.00	
	Regions + NAO + NAO^2	0.00	0.00	0.00	0.00	1.00

[a] The fixed effects included are shown under *Model*; *K* gives the total number of estimated parameters (including the intercept, residual variance term and site random effect). The ΔAIC is the difference between the AIC of the best model and the AIC of the model shown in the "model" column. See text for the calculation of the AIC weights

[b] The higher is $E_{i,j}$, the lower is the difference of explanatory power between two models

of chicks per hen, the difference with the model without a wNAO effect was slightly less than 2 AIC units. The shape of the response to the wNAO showed a clear quadratic curve, however (Fig. 4a; see Table 2 for the values of the explanatory variables estimates), so our retained model includes this wNAO effect. For the brood size however, no effect of the wNAO was detected. wNAO did not either affect the total number of hens counted in the following summer (ΔAIC = 0.0498 between model with wNAO (AIC = 133.2962) and null model (AIC = 133.2464)).

The highest numbers of chicks per hen and of hens with broods were reached for wNAO values of 0.40 (±0.34SE) and 0.39 (±0.25SE), respectively (Fig. 5). These values are above zero, so above the long-term average of wNAO over the twentieth century but correspond to the mean wNAO values observed since 1970 (mean wNAO

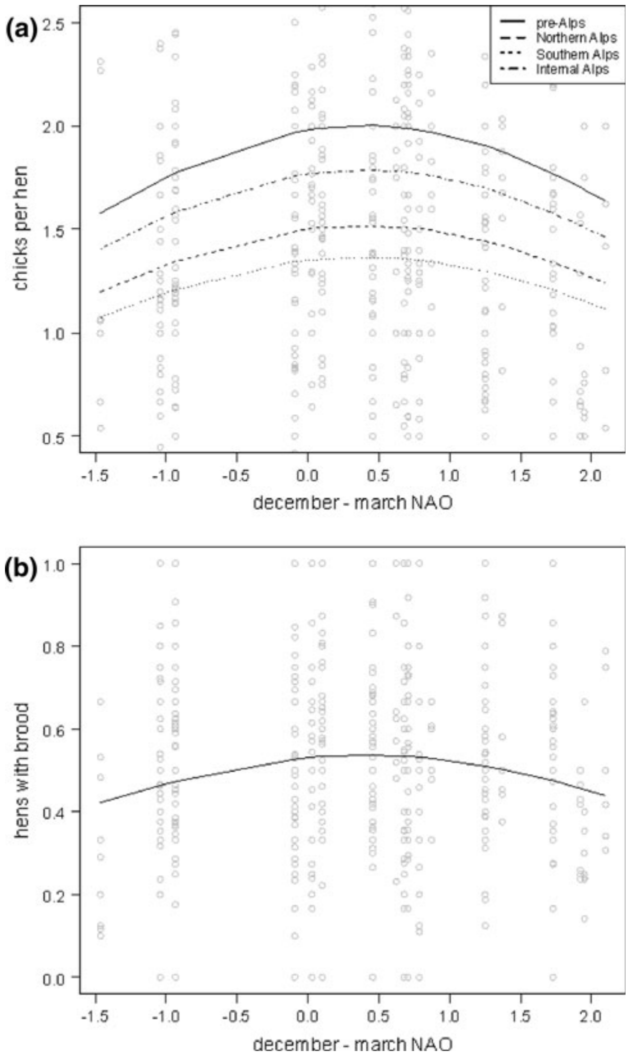

Fig. 4 Number of chicks per hen (**a**) and proportion of hens with brood (**b**) plotted against winter NAO values, and response *curves* as given by the preferred models. As an effect of regions appeared in the number of chicks per hen (see "Results"); 1 *curve* is plotted for each region

1970–2007 = 0.32 ± 0.34; mean wNAO 1980–2007 = 0.49 ± 0.39; Fig. 5).

Discussion

Response of reproductive parameters to summer NAO

The positive linear relationship between summer NAO and breeding parameters suggests that Black Grouse benefit from hotter and drier late spring and summer climates. Hot weather and dry conditions could directly enhance the survival of young chicks in their first week, when their thermoregulation performances are poor (Erikstad and Spidsö 1982). Conversely, heavy rains in early summer may compromise the survival of few-days-old chicks, which would result in a reduced number of chicks per hen or even complete losses of broods affecting number of hens with broods at the time of the count surveys. Indirect effects of cold and wet early summers also include reduced availability of Arthropod prey, on which young chicks rely most in their first weeks (Baines et al. 1996). Overall, these results are consistent with those of previous studies using local climate descriptors on the Black Grouse and other Galliforms (Ellison et al. 1987, Swenson et al. 1994; Slagsvold and Grasaas 1979).

Response of reproductive parameters to winter NAO

We found a quadratic relationship between chick productivity and the NAO of the previous winter. The absence of a relationship with brood size means that winter climate essentially affects breeding success through the proportion of hens with broods; this is supported by the fact that the latter has a similar response shape to the NAO as the global index "number of chicks per hen".

The convex shape (that is, positive linear NAO effect, negative quadratic effect; Table 2) suggests that both colder/wetter and hotter/drier than average winters have a negative influence on the number of hens that can reproduce. Cold and wet winters presumably constrain females to allocate more energy to survival than to reserve storage, diminishing the number of females able to reproduce the following spring. On the other hand, the reproductive success is also low after drier (i.e. with less snow) and warmer winters than normal (highly positive NAO). A too-thin snow layer could prevent grouse from using snow as a protection against predation or cold weather (Spidsö et al. 1997), depleting the birds' energy stocks. Alternatively, a decrease in quality and quantity of vegetal resources available because of seedlings being exposed directly to frost (e.g. Taulavuori et al. 1997) could also result in an altered reproduction after dry and warm winters. An earlier-than-usual spring could lead to discrepancies between plant growth and breeding initiation, as previously shown with Capercaillie by Moss et al. (2001), or a mismatch between prey availability and chick feeding periods due to earlier hatching without advance of summer conditions (Ludwig et al. 2006).

Effects of long-term climate warming

The Alps are currently undergoing a significant global change in climatic conditions, with warmer temperatures and drier conditions, especially in winter, that reflect particularly well such large scale processes as the NAO (Beniston et al. 1997; Beniston 2005, 2006; Giorgi et al. 1997). Among other consequences, changes in phenology

Table 2 Regression coefficients estimates of the models best supported by the data for each reproduction index (number of chicks per hen; brood size; proportion of hens with broods), and associated standard errors (SE) and *P* values

Reproduction index	Season	Variable	Estimate	SE	*t* value	*P* value
Number of chicks per hen	Winter	Intercept (Pre-Alps)	0.684	0.109	6.252	8.74E-10
		Northern Alps	0.407	0.117	−2.359	0.019
		Southern Alps	0.3	0.153	−2.497	0.012
		Inner Alps	0.57	0.134	−0.849	0.397
		NAO	0.055	0.026	2.077	0.038
		NAO^2	−0.069	0.023	−3.063	0.002
	Summer	Intercept (Pre-Alps)	0.626	0.11	5.715	1.98E-08
		Northern Alps	0.371	0.119	−2.144	0.033
		Southern Alps	0.205	0.161	−2.621	0.01
		Inner Alps	0.478	0.136	−1.087	0.278
		NAO	0.069	0.028	2.459	0.014
Brood size	Summer	Intercept (Pre-Alps)	1.185	0.048	24.447	2.00E-16
		Northern Alps	1.075	0.053	−2.091	0.0371
		Southern Alps	0.831	0.074	−4.819	1.97E-06
		Inner Alps	1.148	0.06	−0.627	0.531
		NAO	0.045	0.016	2.765	0.006
Proportion of hens with broods	Winter	Intercept	−0.632	0.031	−20.111	2.00E-16
		NAO	0.056	0.019	2.959	0.003
		NAO^2	−0.07	0.016	−4.271	2.33E-05
	Summer	Intercept	−0.675	0.031	−21.73	2.00E-16
		NAO	0.022	0.021	1.04	0.299

Season indicates which NAO has been used (either winter or summer); *Variable* gives the model variables

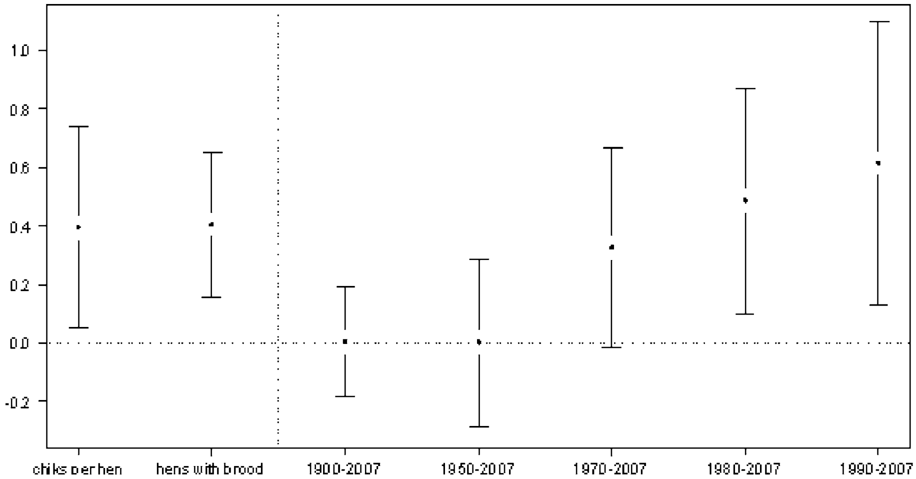

Fig. 5 Response maximum of the number of chicks per hen and the number of hens with brood to the winter (December to March) NAO over the period 1990–2007, with associated confidence intervals ($\pm 2\times \text{SE}_{\max}$, see "Statistical Analyses" in "Methods"); and mean winter NAO index (with 2× SE) for 5 periods between 1900 and 2007

or altitudinal shifts in vegetation have already been reported (Jolly et al. 2005; review in Theurillat and Guisan 2001.

The optimal weather conditions for the reproduction of the Black Grouse in the French Alps (as expressed by the maximum of the response of breeding parameters to winter NAO) correspond to average winter NAO values for the last 30 years (Fig. 5), clearly higher than the average for the last century. This suggests that the species has adapted to more frequent positive NAO anomalies in the last decades, i.e. to a warmer and drier climate. Assessing whether this adaptation is due to phenotypic plasticity or genetic changes under natural selection requires deeper studies at the individual level (see, e.g., Gienapp et al. 2008) that are not yet available in this case. The alternative hypothesis that the species has always had a maximum reproductive output for slightly positive NAO values, and thus was maladapted to previous colder and wetter climatic conditions, is highly unlikely given the long-term stability of previous climatic conditions (before the recent climate warming) and the fact that the Black Grouse is a typical cold-climate species.

Further, neither the numbers of hens nor the breeding indexes have declined during the last 18 years. This result is consistent with recent reports (Storch 2007) suggesting that the alpine populations of Black Grouse which declined during most of the twentieth century (Magnani 1987) have stabilised in the past two decades, despite the climate warming threat. This absence of decline agrees with community-level studies showing lower-than-expected effects of climate change on alpine birds (Archaux 2004), and means that Black Grouse have until now been able to track climatic trends towards a warmer and drier climate. Interactions with habitat modifications may also impact grouse response to climate change. As the upper edge of forests is shifting towards higher altitudes due to land use changes (Chauchard et al. 2010; Gehrig-Fasel et al. 2007), the grouse may be able to colonise higher, and thus colder, areas than in past decades. This process could allow the grouse to track the rise in altitude of their climatic niche, maintaining the reproductive success. Altitudinal shifts in Black Grouse habitats have not yet been observed in the Alps, so this issue remains fully hypothetical. However, assessing the balance between habitat changes in altitude and climate change effects would be valuable in assessing conservation strategies of edge species such as the Black Grouse.

Hence, alpine Black Grouse appear to be more threatened by declines in the availability of suitable areas and changes in habitat structure (Bernard-Laurent 1994; Kurki et al. 2000; Wilson et al. 2005) than by direct effects of climate warming on its reproduction. Overall, our findings highlight that even a highly specialised mountain species can track rapid climate changes without decreasing its productivity, at least within the limits of current climate changes.

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