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

3

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25

26 **Abstract**

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

42

43 **Keywords:** Climate Packages, Galliforms, Mountain Avifauna, NAO, Reproductive Success,
44 *Tetrao tetrix*.

45

46 **Zusammenfassung**

47 **Kurzfristige Antwort auf die Nordatlantische Oszillation, aber keine Langzeiteffekte von**
48 **Klimawandel auf den Fortpflanzungserfolg eines alpinen Vogels**

49

50 Die Folgen der Klimaverhältnisse auf die Populationsdynamik zu entschlüsseln ist von größter
51 Wichtigkeit, um zu verstehen, wie sich Klimaveränderungen wahrscheinlich auf Organismen
52 auswirken werden. Mittels Daten aus umfassenden jährlichen Zählungen zwischen 1990 und 2007

53 zeigen wir, dass Nordatlantische Oszillationen in Winter und Sommer mehrere Anzeiger von
54 Bruterfolg bei Birkhühnern (*Tetrao tetrix*) in den französischen Alpen beeinflussen. Wir fanden
55 keinen Trend in den Zahlen von Hühnern oder in Brutanzeigern während des Untersuchungszeitraums.
56 Wir zeigen, dass Birkhühner ihre Fortpflanzungsleistung für positive Winter-NAOs (bezogen auf den
57 durchschnittlichen NAO-Index der letzten 30 Jahre) optimieren, was für einen an ein kaltes Klima
58 angepassten Vogel überraschend ist. Extreme NAOI-Werte führen zu niedrigerem Bruterfolg, was
59 darauf hindeutet, dass Birkhühner besser in der Lage sein könnten, Klimatrends zu folgen, als eine
60 Zunahme der Häufigkeit extremer Jahre zu bewältigen. Unsere Ergebnisse zeigen, dass zumindest aus
61 kurzfristiger Sicht die Produktivität der Birkhühner nicht durch einen Trend zu wärmeren
62 Klimaverhältnissen in den Alpen bedroht ist, jedoch durch eine erhöhte Häufigkeit extremer Jahre
63 beeinträchtigt sein dürfte. Wir empfehlen, für Studien, die sich auf die großflächige, globale Antwort
64 auf das Klima konzentrieren, die NAO als Klimamaß zu verwenden und nicht stark störanfällige und
65 verzerrte lokale Klimadeskriptoren.

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71

72 **Introduction**

73

74 Global climate change (IPCC 2007) has already been associated with shifts in
75 phenology, population dynamic, communities' composition and distribution of organisms
76 throughout the world (*e.g.* Walther et al. 2002; Parmesan and Yohe 2003). Cold-climate
77 ecosystems, in particular, might be especially sensitive to the rapid rise of temperatures and
78 changes in rainfalls regime anticipated under most future climate models because many
79 species living in such ecosystems have narrow thermal ranges or high habitat specialization
80 (*e.g.* Krajick 2001; Krajick 2004; Thuiller et al. 2005; Sekercioglu et al. 2008). Their
81 conservation thus requires a careful assessment of their population dynamics in response to
82 climate variations. Birds constitute a promising model for such studies because their
83 demography has often been shown to be closely related to climate variability (Saether et al.
84 2004).

85 Birds specialized in high latitude or altitude habitats should be particularly at risk
86 (Pimm et al. 2006) because they are expected to exhibit a weak resilience to rapid warming
87 (Martin and Wiebe 2004), especially if their dispersal abilities are limited. However, some
88 avian species show adaptive responses to climate changes, particularly in their phenology or
89 migration behaviour, suggesting that they can track at least to a certain extent climate and
90 associated habitat changes within short time lags (*e.g.* Jonzén et al. 2006; Charmantier et al.
91 2008).

92 Several recent attempts to assess the effects of climate on birds have used large-scale
93 climate indices such as the North Atlantic Oscillation (NAO) (Stenseth et al. 2003). The
94 NAO, a large scale atmospheric oscillation over the North Atlantic, strongly influences
95 climate variability over Western Europe in winter (Hurrell et al. 2003) and, to a lesser extent,
96 in summer (Folland et al. 2009). The NAO has fruitfully been used as a “climate package” to

97 relate climatic variations with life history traits or population dynamics (Coulson et al. 2001;
98 Cotton, 2003; Grosbois and Thompson 2005; Stenseth and Mysterud 2005; Lewis et al. *in*
99 *press*). One of its main advantages is to summarize climate variations in a single index
100 encompassing interactions sometimes too complex to be captured by a simple model, whereas
101 the use of standard local climate descriptors such as temperatures or precipitations requires
102 numerous variables (Hallet et al. 2004). The NAO has exhibited more positive values for the
103 last 30 to 40 years than in the previous century, a trend which has been related to the current
104 climate change over the Northern Hemisphere (Hurrell 1996; Visbeck et al. 2001). The NAO
105 thus not only reflects inter-annual climatic variability but also long term climate changes.

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

113 Among boreal and alpine species, European mountain Galliforms (*Aves*, *Galliformes*)
114 are under close monitoring by wildlife management agencies due to their value as emblematic
115 wildlife and gamebirds (Lindström 1994; Sandercock et al. 2005) and the recent population
116 declines exhibited by several species (Storch 2007). While the main causes of such declines
117 appear to be hunting, tourism and habitat loss or degradation (*e.g.* Kurki et al. 2000; Patthey
118 et al. 2008; Storch 2007), climate variations were found to noticeably affect Galliform's
119 reproductive success in several studies (Swenson et al., 1994; Moss et al, 2001; Klaus, 2007;
120 Novoa et al., 2007). Current climate changes in particular cause mismatches between timing
121 of hatching and optimal climatic conditions in Finnish populations of Black Grouse (*Tetrao*

122 *tetrix*) (Ludwig et al. 2006). Loneux and Lindsey (2003) also found negative effects of hot
123 and dry climatic conditions on Black Grouse's demography in the Ardennes (Belgium),
124 raising concerns about the ability of these lowland populations of the species to track climate
125 changes. In Scandinavia, Spidsö et al. (1997) have shown the positive role of snowfalls and
126 cold weather for Black Grouse's survival through better thermoregulation and protection
127 against predation in winter. Moss et al. (2001) found that climate changes have a negative
128 effect on the reproductive output of Capercaillies (*Tetrao urogallus*) in Scotland, casting
129 doubts on the long-term persistence of the species under warmer future climatic conditions in
130 this area.

131 Alpine populations of Galliforms lie at the southern edge of the species distribution
132 and have declined for at least thirty years (Storch 2007). Given the results obtained in other
133 areas (see above), the substantial elevation of temperature and increase in frequency of dryer
134 conditions that are occurring over the Alps as a consequence of climate changes (Beniston
135 2006) could explain part of these populations declines. However, no study has addressed to
136 date the response of alpine populations of *Tetraonidae* to climatic variability and climate
137 changes.

138 In this paper, our aim was to investigate how alpine populations of Black Grouse, a
139 typical boreo-alpine species at the southern edge of its distribution, are affected by global
140 warming. We choose to concentrate on reproductive success, a demographic trait that has
141 already been shown to be highly sensible to climate change in other avian species (Jiguet et
142 al. 2007). Early spring weather conditions, usually corresponding to the snow melting period
143 in the Black Grouses' habitat, influences the nutritive values of available food (essentially
144 young seedlings) just before the breeding period, and strongly affects the reproductive success
145 through the quality of the eggs (Siivonen 1957, Moss et al, 1975; Moss et al, 1981). Further,

146 winter climate influences the health state and reserve storage of hens, which in turn accentuate
147 the effects of weather and food conditions just before breeding (Thompson & Fritzel 1988).

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

156

157 **Materials and Methods**

158

159 **Data**

160

161 - Count data

162

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

166 The study area covers all the French Alps, which we divided into four bioclimatic regions,
167 based on a more precise partition by Ozenda (1981), Ascencio (1983) and Chassagneux et al.
168 (1992) to account for geographic variation in habitat and local climate variability: Pre-Alps,
169 Northern Alps, Inner Alps, and Southern Alps (fig.1). Hens and chicks were counted once a
170 year in August by systematic censuses using pointing dogs. The counts were performed on the

171 same sites and areas from one year to another, with the same operators, and the exact date of
172 each count was adjusted for each site so that counting took place when the chicks were in
173 similar development stages, able to fly but still dependent of the hen. Each dog and operator
174 had an area of 10-30 hectares to ride through, starting from down and walking up following
175 parallel contour lines spaced out from each other by 15 – 20 meters (Leonard 1992). Data
176 were available over an 18-year period (1990 – 2007), but not every year for all sites. The
177 number of available counts per year ranged from 7 (year 1990) to 52 (year 2006) (mean = 28
178 sites / year, standard error = 3.89); and 1 to 18 counts were available for each site over the 18-
179 year period (mean = 8.6 counts / site, standard error = 0.62) (fig.2). Three reproduction
180 indices were derived from the data: “proportion of hens with brood” was the proportion of
181 hens with at least one chick; “brood size” was the mean number of chicks per successful hen
182 (hen with brood); the product of these two measures gave a standard overall measure of the
183 breeding success, the “number of chicks per hen” (Moss et al. 2001).

184

185 - Climate data

186

187 Food intake in winter and early spring are decisive for the success of the reproduction in
188 Galliforms (Novoa et al. 2008; Ebeirle 1987) as in several other avian species, particularly
189 geese (Dickey et al. 2009; Choinière and Gauthier 1995; Reed et al. 2004). Post-hatching
190 survival of chicks in July is another major source of variation of the breeding success of the
191 species (Ellison et al. 1987). Thus, relating grouse reproduction in the Alps to winter and
192 summer NAO is biologically fully meaningful. The NAO time series were obtained from the
193 Climate Analysis Section, NCAR, Boulder, USA, available at
194 <http://www.cgd.ucar.edu/cas/jhurrell/indices.html> (Hurrell 1995). Beniston and Jungo (2002)
195 showed a strong linear relationship between the winter NAO and surface pressure,

196 precipitation or temperatures in the Swiss Alps, close to our survey area, and this was
197 particularly true at high elevation areas (Giorgi et al. 1997) corresponding to the altitudinal
198 distribution range of the Black Grouse in the area. We thus used the December to March
199 seasonal PC-based NAO index (wNAO) to account for climate inter-annual variability in
200 winter (Hurrell 2003). Folland et al. (2009) recently showed that the summer NAO also has a
201 significant effect on the European climate, although its explanatory power has not been tested
202 yet. Hence, we also considered June to August seasonal PC-based NAO index (sNAO, Hurrell
203 1995), as it covers the period over which chicks are most likely to be strongly affected by
204 climate variations (Erikstad and Spidsö 1982), especially in the alpine range of the species
205 (Zbinden and Salvioni 2004). Note that, while the NAO affects local climatic conditions in
206 summer and winter, it has little influence on spring and autumn climates (Portis et al. 2001,
207 Hurrell et al. 2003). Thus, we chose not to relate Black Grouses' breeding success to the
208 spring NAO, although spring also includes some critical periods for the reproduction of Black
209 Grouse.

210

211 **Statistical analyses**

212

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

214

215 - Temporal trends in hens numbers

216

217 We checked for linear trends in the number of hens during the study period on a subset
218 of 9 sites on which it was certain that the surveyed area remained constant between years; 7 to
219 18 counts were available on these sites over the period considered. Using the R package lme4
220 (Bates et al, 2008), we created a linear mixed model with the hens' numbers as the response

221 variable (log-transformed), year as an explanatory variable, and site as a random effect on
 222 both the intercept and the slope of the regression. We used a MCMC algorithm to obtain the
 223 posterior distribution of the year effect, then calculated its 95% posterior credible interval to
 224 test for the existence of a significant time trend (Bolker et al 2009).

225

226 - Effect of climate on reproduction

227

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

238 When a quadratic response (that is, a function of the form $y = a + b x + c x^2$) appeared in the
 239 preferred model, we calculated the response optimum \max as $\max = \frac{-\hat{b}}{2\hat{c}}$ where \hat{b} and \hat{c} are the

240 maximum likelihood estimates of the regression parameters b and c. The associated standard
 241 error SE_{\max} of \max was obtained using the delta-method (Seber 1982):

242
$$SE_{\max} = \sqrt{\frac{1}{4} \times \left(\frac{\hat{b}}{\hat{c}}\right)^2 \times \left[\left(\frac{SE(\hat{b})^2}{\hat{b}^2}\right) + \left(\frac{SE(\hat{c})^2}{\hat{c}^2}\right) - \left(\frac{2 \times \text{cov}(\hat{b}, \hat{c})}{\hat{b} \times \hat{c}}\right) \right]}$$
 where $\text{cov}(\hat{b}, \hat{c})$ is the estimated covariance

243 between the estimates of b and c. Finally, in order to check for winter climate-linked
 244 variations of hen survival, we performed a Poisson regression with hen counts as a response

245 variable, wNAO as the explanatory variable, and random site effect, using the 9 sites retained
246 for the temporal trend analysis.

247

248 - Model selection

249

250 As our aim was to assess the effects of winter and summer climate separately, we built
251 separate models for winter and summer NAO values. For each of them, we built the most
252 complex model (see above), a null model including no effect but the site effect, and all
253 possible intermediate models. Although it is recommended to use the Akaike Information
254 Criterion corrected for small sample size (AICc) as a routine selection method, the sample
255 size of our data set was large enough compared to the maximum number of estimated
256 parameters to make the difference between AICc and AIC negligible; we thus retained the
257 model with the lowest value of AIC (Burnham and Anderson 2002). If the retained model
258 included a quadratic or an interaction effect, the corresponding single terms were
259 systematically added (Mc Cullagh and Nelder 1989). When less than 2 AIC units separated
260 models including the NAO as a quadratic or linear effect, the response pattern was examined
261 graphically. If no sensible difference between the linear and quadratic curve appeared, we

262 kept the linear model. We calculated AIC weights as $AIC_{wi} = \exp\left(\frac{-0.5 \times \Delta AIC_i}{\sum_{r=1}^M -0.5 \times \Delta AIC_r}\right)$, where

263 ΔAIC_i is the difference between the AIC of model i and that of the best model, and M is the
264 total number of compared models (Burnham and Anderson, 2002). To assess the gain of
265 explanatory power of a model when adding a variable, we calculated evidence ratios as $E_{i,j}$
266 $= AIC_{wi} / AIC_{wj}$, were i and j are 2 of the tested models.

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

272

273 - Autocorrelation

274

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

280

281 **Results**

282

283 **Trends**

284

285 The slope of the year effect (-0.005, SD= 0.030) on hens numbers was not different
286 from 0 (posterior 95% credible interval [-0.07 0.02]). There was thus no significant
287 temporal trend in the number of female Black Grouse during the study period in the
288 monitored sites, and no indication of a decline at all (estimated slope positive). Similarly, no
289 temporal trend was detected for any of the 3 reproduction indices for the period considered
290 (1990 – 2007) (fig.3). Neither spatial nor temporal autocorrelations were found in the selected
291 regression model residuals (all p-values > 0.05). Nevertheless, an effect of bioclimatic regions

292 appeared in all the preferred models for the number of chicks per hen and the brood size
293 (tab.1), but not the proportion of hens with brood (fig. 4b), indicating differences in breeding
294 success linked to regional variations in the Alps.

295

296 **Summer NAO**

297

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

304

305 **Winter NAO**

306

307 According to the AIC model ranking, the best models for the number of chicks per hen
308 and the proportion of hens with brood included a quadratic effect of wNAO (tab. 1). For both
309 indices, the estimate of the linear term was positive, and the estimate of the quadratic term
310 was negative (tab.2), corresponding to a convex response shape (fig. 4), with a maximum for
311 a particular value of wNAO. For the number of chicks per hen, the difference with the model
312 without a wNAO effect was slightly less than 2 AIC units. The shape of the response to the
313 wNAO showed a clear quadratic curve however (fig. 4a, see tab. 2 for the values of the
314 explanatory variables estimates) so our retained model includes this wNAO effect. For the
315 brood size however, no effect of the wNAO was detected. wNAO did not either affect the

316 total number of hens counted in the following summer ($\Delta AIC = 0.0498$ between model with
317 wNAO ($AIC = 133.2962$) and null model ($AIC = 133.2464$))

318 The highest numbers of chicks per hen and of hens with broods were reached for
319 wNAO values of $0.40 (\pm 0.34$ standard error) and $0.39 (\pm 0.25$ standard error) respectively (fig.
320 5). These values are above zero, so above the long-term average of wNAO over the 20th
321 century but correspond to the mean wNAO values observed since 1970 (mean wNAO 1970-
322 2007 = 0.32 ± 0.34 ; mean wNAO 1980 – 2007 = 0.49 ± 0.39 ; fig. 5).

323

324 **Discussion**

325

326 **Response of reproductive parameters to summer NAO**

327

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

339

340 **Response of reproductive parameters to winter NAO**

341

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

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

362

363 **Effects of long-term climate warming**

364

365 The Alps are currently undergoing a significant global change in climatic conditions, with
366 warmer temperatures and dryer conditions, especially in winter, that reflect particularly well
367 large scale processes such as the NAO (Beniston 1997; Beniston 2005; Beniston 2006; Giorgi
368 et al. 1997). Among other consequences, changes in phenology or altitudinal shifts in
369 vegetation have already been reported (Jolly et al. 2005; review *in* Theurillat and Guisan
370 2001).

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

383 Further, neither the numbers of hens nor the breeding indexes have declined during the
384 last 18 years. This result is consistent with recent reports (Storch 2007) suggesting that the
385 alpine populations of Black Grouse which declined during most of the 20th century (Magnani
386 1987) have stabilized in the past two decades, despite the climate warming threat. This
387 absence of decline agrees with community-level studies showing lower-than-expected effects
388 of climate change on alpine birds (Archaux 2004), and means that Black grouses have been be
389 able to track climatic trends towards a warmer and dryer climate until now. Interactions with

390 habitat modifications may also impact grouses' response to climate change. As the upper edge
391 of forests is shifting towards higher altitudes due to land use changes (Chauchard et al, 2010;
392 Gehrig-Fasel et al, 2007), grouses may be able to colonize higher, thus colder areas than in
393 past decades. This process could allow grouses to track the rise in altitude of their climatic
394 niche, maintaining the reproductive success. Altitudinal shifts in Black Grouse habitats have
395 not yet been observed in the Alps, so this issue remains fully hypothetical. However,
396 assessing the balance between habitat changes in altitude and climate change effects would be
397 valuable to assess conservation strategies of edge species such as Black Grouse.

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

404

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406

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414

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606 **List of tables**

607

608 **Table 1** (a) Model selection for the response to the NAO (winter: December to March;
609 summer: June to August) of the number of chicks per hen, the brood size and the number of
610 hens with brood. The fixed effects included are shown in the “model” column; the column
611 "K" gives the total number of estimated parameters (including the intercept, residual variance
612 term and site random effect). The ΔAIC is the difference between the AIC of the best model
613 and the AIC of the model shown in the “model” column. See text for the calculation of the
614 AIC weights. (b) Evidence ratio calculated as $E_{i,j} = AIC\ weight_j / AIC\ weight_i$ where j are
615 columns and i are rows. The higher $E_{i,j}$, the lower the difference of explanatory power
616 between two models is.

617

618 **Table 2** Regression coefficients estimates of the models best supported by the data for each
619 reproduction index (number of chicks per hen (a); brood size (b); proportion of hens with
620 broods (c)), and associated standard errors (SE) and p-values. The column “season” indicates
621 which NAO has been used (either winter or summer); and the column “variable” gives the
622 model variables

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631 **List of figures**

632

633 **Figure 1** Locations of the 58 count sites available over the period 1990-2007, used for our
634 analyses. The France – Italy border is indicated as a landmark. Polygons correspond to bio-
635 climatic regions (see text for further details)

636

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

638

639 **Figure 3** Mean values of the reproductive indices of the Alpine Black Grouse over the period
640 1990 – 2007: (a): number of chicks per hen ($r=-0.05$, $p=0.69$); (b): brood size ($r=0.01$,
641 $p=0.28$); (c): proportion of hens with brood ($r=-0.02$, $p=0.43$); the dotted lines correspond to 2
642 \times standard errors

643

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

648

649 **Figure 5** Response maximum of the number of chicks per hen and the number of hens with
650 brood to the winter (December to March) NAO over the period 1990 – 2007, with associated
651 confidence intervals ($\pm 2 \times SE_{\max}$, see “Statistical Analyses” in “Materials and Methods”); and
652 mean winter NAO index (with $2 \times$ standard errors) for 5 periods between 1900 and 2007

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