Monitoring black grouse *Tetrao tetrix* in Isère, northern French Alps: cofactors, population trends and potential biases

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Abstract

Monitoring black grouse Tetrao tetrix *in Isère, northern French Alps: cofactors, population trends and potential biases.* Wildlife management benefits from studies that verify or improve the reliability of monitoring protocols. In this study in Isère, France, we tested for potential links between the abundance of black grouse (*Tetrao tetrix*) in lek–count surveys and cofactors (procedural, geographical and meteorological cofactors) between 1989 and 2016. We also examined the effect of omitting or considering the important cofactors on the long–term population trend that can be inferred from lek–count data. Model selections for data at hand highlighted that the abundance of black grouse was mainly linked to procedural cofactors, such as the number of observers, the time of first observation of a displaying male, the day, and the year of the count. Some additional factors relating to the surface of the census sector, temperature, northing, altitude and wind conditions also appeared depending on the spatial or temporal scale of the analysis. The inclusion of the important cofactors in models modulated the estimates of population trends. The results of the larger dataset highlighted a mean increase of +17 % (+5.3 %; +29 %) of the abundance of black grouse from 1997 to 2001, and a mean increase in population of +47 % (+16 %; +87 %) throughout the study period (1989–2016). We discuss the hypothesis of plausible links between this past increase in the number of black grouse and the ecological impact of the winter storm 'Vivian'. Findings from our study and the ecological phenomena that were concomitant with the observed population trend provide opportunities to strengthen the monitoring and management of black grouse in the Alps.

Key words: Abundance estimates, Protocol cofactors, Lek–count, Wildlife management, Alpine bird, Galliformes

Resumen

Seguimiento del gallo lira, Tetrao tetrix*, en Isère, en el norte de los Alpes franceses: factores, tendencias demográficas y posibles sesgos*. La gestión de la fauna silvestre se beneficia de estudios que verifican o mejoran la fiabilidad de los protocolos de seguimiento. En este estudio, realizado en Isère (Francia) entre 1989 y 2016, hemos analizado la posible relación entre la abundancia de gallo lira (*Tetrao tetrix*), determinada en estudios de conteo en cantaderos, y una serie de factores (geográficos, meteorológicos y de procedimiento). Después, hemos examinado también el efecto de omitir o considerar los factores importantes que inciden en la tendencia demográfica a largo plazo que puede ser inferida de los datos sobre conteos en cantaderos. Los modelos seleccionados para los datos disponibles subrayaron que la abundancia de gallo lira estaba principalmente relacionada con factores de procedimiento, como el número de observadores, la hora de la primera observación de un macho exhibiéndose, el día y el año del conteo. Según la escala espacial y temporal de los análisis, también se observó alguna relación con otros factores relacionados con la superficie del sector censado, la temperatura, la orientación respecto al norte, la altitud y las condiciones de viento. La inclusión de los factores importantes en los modelos modificó las estimaciones de las tendencias demográficas. Los resultados del conjunto de datos más grande indicaron un incremento medio de +17 % (+5,3 %; +29 %) y de +47 % (+16 %; +87 %) de la abundancia de gallo lira durante el período 1997–2001 y el período del estudio completo (1989–2016), respectivamente. Analizamos la hipótesis de que pudiera existir una relación entre este incremento pasado del número de gallos lira y el impacto ecológico del temporal de invierno "Vivian". Nuestro estudio, y el fenómeno ecológico que fue concomitante con la tendencia demográfica observada, son una oportunidad de reforzar las iniciativas de seguimiento y gestión del gallo lira en los Alpes.

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Palabras clave: Estimaciones de abundancia, Factores de protocolo, Conteo en cantaderos, Gestión de fauna silvestre, Ave alpina, Galliformes

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Introduction

Evidence–based management of wild species requires reliable monitoring protocols and accessible scientific information (Walsh et al., 2004; Walsh et al., 2015). Many census methods have been developed, some to provide abundance estimates and others to measure population trends (Gregory et al., 2004; Meriggi et al., 2008; Schwarz and Seber, 1999). Trend evaluations may give some advantages in reducing interpretation biases that are sometimes associated with using abundance indices (Thompson, 2002). However, abundance estimates are still essential in standard management practices of many exploited species, such as evaluating the level of sustainable harvesting in game species. The methods producing abundance estimates are nonetheless based on key assumptions. They commonly assume that all individuals of a given territory are counted, which represents a detection probability equal to 1, constant over time. It is widely agreed that such a probability is nearly impossible to reach in standard monitoring fieldwork (Walsh et al., 2004; Simons et al., 2007; Jacob et al., 2010; Fremgen et al., 2016; Baumgardt et al., 2017).

The black grouse (*Tetrao tetrix*) has a wide distribution range, being found in numerous countries (Storch, 2007). When present, it is a flagship species in the mountainous and boreal habitats of Europe, such as the Alps and Scandinavia, although some populations are also present in lowland habitats like Belgium, the Netherlands, Great Britain, Poland and north–west Germany (Storch, 2000). Population decreases were recorded in the last half–century, particularly in lowland habitats and in its south–western distribution range (e.g. Belgium: Keulen et al., 2005; Netherlands: Larsson et al., 2008; Great Britain: Baines and Hudson, 1995; Sim et al., 2008; Poland: Merta et al., 2009; Germany: Ludwig et al., 2008, 2009). Although some local recoveries have recently been described (Scridel et al., 2017), in Europe, the available estimates of several demographic traits, such as survival rates and fledglings per hen, are consistent with these previous population decreases (Jahren et al., 2016; Gée et al., 2018).

Male lek–count is a widespread method for monitoring bird species such as the black grouse where males display for females during the breeding season (Cayford and Walker, 1991; Baines, 1996; Gregory et al., 2004; Chamberlain et al., 2012). Population monitoring of black grouse using lek–count data in the French Alps started in the late 1970's for management purposes (Ellison et al., 1988; Gehin and Montadert, 2016). Data from this standard monitoring of tetraonid species in France are managed by the 'Observatoire des Galliformes de Montagne' (Mountain Galliformes Observatory; e.g. Gehin and Montadert 2016). The monitoring of black grouse in the French Alps suggests contrasted results, i.e. sectors with decreasing, stable or increasing abundance of birds, depending on the considered local area (Ellison and Magnani, 1985; Bernard–Laurent, 1994; Amblard and Montadert, 2017). However, these patterns of abundance of birds are based on ambitious methodological assumptions and implicitly rule out residual links between the number of counted males and cofactors (procedural, geographical and meteorological cofactors, detailed hereafter).

Some studies of Galliformes and other species have emphasized that the results of counts were affected by cofactors due to links between a visibility bias and the detection probability of the focal species (Baumgardt et al., 2017). These cofactors may be, for example, meteorological factors such as wind (Baines, 1996; Simons et al., 2007; Drummer et al., 2011; Sadoti et al., 2016), precipitation (Anderson et al., 2015; Baines, 1996), temperature (O'Connor and Hicks, 1980; Zimmerman and Gutiérrez, 2007) and snow (Brubaker et al., 2013; Fremgen et al., 2016). Cofactors affecting the results of counts in wild species may also include procedural factors such as the number of observers (Sarasa and Sarasa, 2013), the observers' experience (Alldredge et al., 2007; Garel et al., 2005; Hancock et al., 1999; Jiguet, 2009), timing organization of counts (Cayford and Walker, 1991; Sim et al., 2008; Monroe et al., 2016; Baumgardt et al., 2017), count day (Baines, 1996; Cayford and Walker, 1991; Gregersen and Gregersen, 2014), count year (Hovi et al., 1996) and count site (Anderson et al., 2015; Baines and Richardson, 2007). Under–estimating key cofactors might thus expose the interpretations derived from count data to potential bias in abundance and trend estimates (Simons et al., 2007; Monroe et al., 2016), particularly when tracking population changes across annual intervals (Blomberg et al., 2013).

In this study we tested for potential links between lek–count data from black grouse monitoring and several recorded cofactors in the northern French Alps. As the guidelines for standard monitoring of black grouse are partly focused on minimizing heterogeneity associated with meteorological and procedural cofactors (Leonard, 1989), only weak and negligible links between lek–count data and cofactors might be expected. Alternatively, if the goal of minimizing the heterogeneity linked to the procedural, geographical and meteorological cofactors is not fully met when applying the guidelines for standard monitoring of black grouse, substantial links between lek–count data and cofactors might be observed. Abundance trends that are inferred from lek–counts may also be affected if cofactors are not controlled for in models.

Material and methods

Study area

We analysed data from spring counts of black grouse in Isère, France, between 1989 and 2016. Isère is a department in the French Alps, located at the south–west limit of the distribution area for black grouse in Europe (Bernard–Laurent, 1994). It is one of the nine departments where black grouse are monitored in France (Bernard–Laurent, 1994; Amblard and Montadert, 2017). To our knowledge, this is the only study area combining two crucial points: first, the availability of detailed raw data over a long period in numerous sectors and conserved for years in a standardized format after counts, and second, the financial support required to enable the development of this study.

The sectors for monitoring black grouse were designed according to the topography within the altitudinal limits of black grouse distribution recorded in the French Alps (1,400 to 2,300 m a.s.l.; Bernard–Laurent, 1994). This altitudinal range is the subalpine zone where black grouse males display reproductive behaviour in open microhabitats such as ridges, clearings and meadows with few or no trees (Magnani, 1988; Bernard–Laurent, 1994). The mean size (± SD) of the monitored sectors was 230 ha (± 10.6; n = 133). Their size and delimitation combine the need for their surveillance within the two first hours of the males' display (OGM, 2004) and the accessibility and natural barriers of the sectors. The sectors were assumed to reveal the abundance of black grouse (OGM, 2004) and showed highly variable abundances, suggesting they may also have highly variable quality for black grouse, within the theoretical black grouse distribution in Isère.

Lek–count data

All the prospected sectors were monitored by applying the usual protocols for black grouse monitoring in France (described in Leonard, 1989; Montadert, 2016). Counts were conducted between the last week of April and the end of May. One or more observers, assumed to be the 'right' number of observers to survey the considered area (Ellison and Magnani, 1985), patrolled the sector, or remained in a fixed position if the layout of the area allowed, performing the count from early morning, before sunrise, and until no later than two hours after sunrise (Montadert, 2016). Male black grouse are known to arrive at lek site in the Alps at about three quarters of an hour before sunrise (Couturier and Couturier, 1980). In practice, logistical constraints resulted in some variability in some sectors during the study period. The spread of observers over the sectors aimed to ensure a survey of the entire area, although exact details were not available in a standardized format after counts. Neither was information available on the experience of observers. All cocks seen and/or heard were counted to obtain a total estimate of the number of male black grouse, each associated with a monitored sector on a monitoring day. At the end of the counts, the location and time of each display were noted to reduce or avoid the risk of double counting of birds, although the spatial information of displays was not conserved in a standardized format after counts. Spatially joined sectors were generally counted on the same day (Montadert, 2016) to minimize the risk of double counting at the edge of sectors. Counting was avoided during bad weather conditions i.e. heavy rain, strong winds, or dense fog (Leonard, 1989; Baines, 1996; Montadert, 2016). All the lek–count surveys considered in this study were organized and performed by the hunter's federation of Isère (FDC 38).

Cofactors

Procedural cofactors

Several procedural cofactors were noted on summary sheets during the lek–count: identification of the monitored sector (to connect the data to geographical cofactors; detailed hereafter), day and year, hour of first observation of a displaying male, counting time, and number of observers. The diversity of the cofactor values revealed the variability of fieldwork in practice (see results).

Geographical cofactors

Using the identification of the monitored sectors, GIS layer and Quantum GIS software (QGIS Development Team, 2017), we associated geographical cofactors with the lek–count data: surface of the sector, latitude, longitude, altitude, and exposure of the centroid of each sector. Exposure was included by two cofactors in the models (Pedersen et al., 2014): (1) northing, which was expressed as an index of 'north–facing–ness' (Nor) using the formula Nor = cos[radians(angle)], such that Nor varied from 1 (due north) to –1 (due south); and (2) easting, which was expressed as an index of 'east–facing–ness' (Ea) using the formula Ea = sin[radians(angle)], such that Ea varied from 1 (due east) to –1 (due west). The centroid of each sector was a square of 30 x 30 m.

Meteorological cofactors

Meteorological data from Météo France was also added to our database. Detailed local meteorological data were not available because not all monitored sectors have a meteorological station. Nevertheless, two meteorological stations of Météo France are located within the altitudinal stratum of the distribution of black grouse in Isère and have been recording data since 1989: Saint Christophe (1,570 m a.s.l.; 44º 56' 41.971200'' N, 6º 11' 16.764000'' E, WGS84) and Alpe d'Huez (1,860 m a.s.l.; 45º 5' 13.189200'' N, 6º 5' 5.960400'' E, WGS84). The available data from these meteorological stations was averaged per day to obtain a mean value, proxies of the meteorological parameters at the altitudinal stratum of the distribution of black grouse in Isère. For both meteorological stations, the available data are from 1989 to 2016 for the following meteorological parameters: accumulated daily rainfall (in mm), minimum daily temperature (in ºC), accumulated daily fresh snow (in cm), and total snow depth (in cm). For temperature, we used the minimum daily temperature, first, because it usually occurs just before sunrise (Reicosky et al., 1989), the period of the day at which the display of black grouse starts (Couturier and Couturier, 1980), and second, because the time spent displaying is negatively correlated with temperature (Baines,

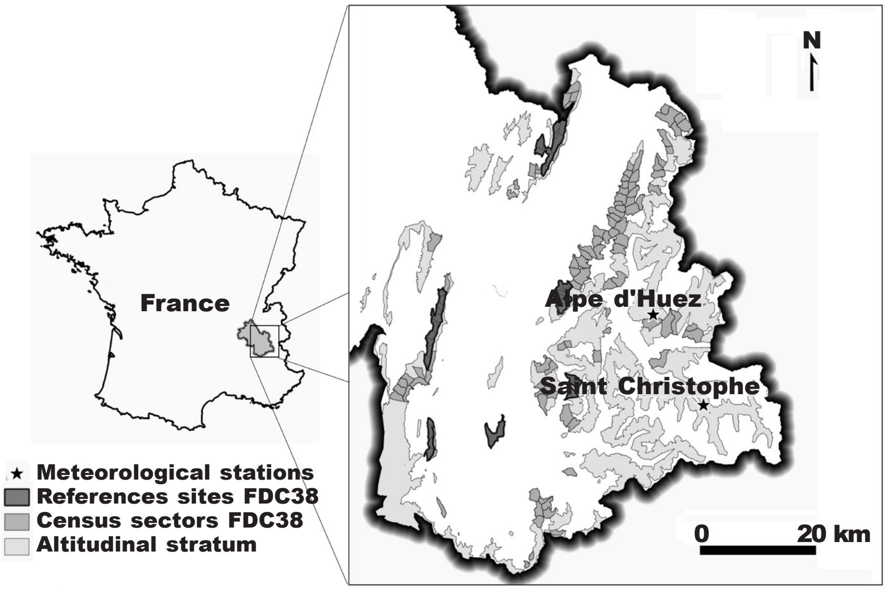


Fig. 1. The study area in Isère France (right panel), with the census sectors, the reference sites and the meteorological stations considered in this study, within the altitudinal range of the black grouse (1,400–2,300 m a.s.l.; Bernard–Laurent, 1994).

Fig. 1. Zona del estudio en Isère (Francia) (panel derecho) donde se muestran los sectores censados, las zonas de referencia y las estaciones meteorológicas consideradas en este estudio, en el rango altitudinal del gallo lira (1.400–2.300 m s.n.m.; Bernard–Laurent, 1994).

1996). During the period of black grouse lek–count, more than 99 % of the data for snow was equal to zero. Thus, the analysis of a potential link between the snow factor and the monitoring of black grouse was beyond the scope of our dataset. Wind data from the considered meteorological stations was only available from 2005 onwards. In our analysis we considered the maximum mean wind speed recorded in a 10–minute period between 6 a.m. and 7 a.m., the time of sunrise at which the first observations of black grouse generally occurred in our study. Strong windy days were avoided in accordance with the methodological recommendations (Leonard, 1989; Montadert, 2016). Wind data thus express breeze conditions but not windy weather.

Analysis

Standardization of data

To facilitate data analysis, the days were converted into Julian days (number of days after January first), the hour of first observation of a displaying male was converted into number of minutes after midnight, and counting time was converted into minutes. Data were not available for at least one parameter required for analysis on nearly half of the summary sheets. As the number of complete summary sheets was high (57 %) and to avoid the use of potentially questionable inferences of missing data, incomplete summary sheets were removed from our database. Thus, our database contains data from 1,040 counts made in 133 sectors monitored by the FDC 38, with a mean of 4.56 counted cocks per sector (SD = ± 3.38). Thirty–eight of these 133 sectors, constitute six reference sites that are used in Isère for the usual monitoring of black grouse (fig. 1).

To assess the potential effects of the spatial scale and the abundance of available information on inferred biological signals and thus on the monitoring of black grouse, we built two datasets, allowing direct comparison of the results between two spatial scales. The first, 'Total Isère', included the complete information of lek–count available, monitored by FDC 38 in Isère from 1989 to 2016 (n = 1,040). The second, 'Reference Sites', included only the complete information of lek–counts available from 1992 to 2016 for the sectors located in the six reference sites monitored by FDC 38 (n = 349).

Statistical analysis

For both databases (Total Isère and Reference sites) we built and compared generalized additive mixed models (GAMMs, Wood, 2006) of the number of counted cocks using the variables listed in table 1. Sectors were included as random effect (Wood, 2006). Lindsey (1999) highlighted that one should

Table 1. List of factors (F), with available data, potentially associated with lek–counts of black grouse in Isère, France.

Tabla 1. Lista de factores (F), con disponibilidad de datos, potencialmente asociados con los recuentos en cantaderos de gallo lira en Isère, Francia.

F	Description	F	Description
Y	Year of the count	Alt	Altitude of the prospected sector's centroid (m)
D	Julian day of the count (number of days after first January)	Ea	Easting: cos of the exposition of the sector's centroid (rad)
H	Hour of first observation of the count (min after midnight)	Nor	Northing: sin of the exposition of the sector's centroid (rad)
CT	Count time (min)	R	Daily rainfall (mm)
NO	Number of observers during the count	T	Daily minimal temperature (°C)
S	Surface of the prospected sector (ha)	Br	Maximum mean wind speed between 6 a.m. and 7 a.m. (m/s)
La	Latitude of the prospected sector's centroid (WGS84)		
Lo	Longitude of the prospected sector's centroid (WGS84)		

only look for overdispersion if the deviance is at least twice the number of degrees of freedom. In our case study, the ratio estimating the degree of overdispersion was 1.66, thus lower than 2. We therefore used Poisson distribution models without problematic overdispersion and the analyses displayed an acceptable fit to the data. Model selection was based on Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002). The relative importance (RI) of explanatory variables was estimated to quantify the importance of each factor within the set of models (Burnham and Anderson, 2002; Anderson and Burnham, 2002). Analysis, including breeze (Br), was performed using a short–term subset of the data because this factor has only been available since 2005.

The main variables and their links with the counts of black grouse in our study area were already identified in the results from this first analytical step (Wood, 2006; see results). Nonetheless, to provide the results on the trends in a more reader–friendly format, for illustrative purposes we performed a trend analysis (Knape, 2016) as a second analytical step, once the best model was identified. We used the long–term dataset of counted black grouse and the default parameters of the models (Knape, 2016) to focus the illustration on the most reliable signs of population change (Knape, 2016) and not on short–term stochastic fluctuations that are beyond the scope of this study. More specifically, it allowed a graphic comparison of the population trends that would be inferred considering, or not, the factors underlined by the best model for the data at hand. All analysis were performed using the 'R' statistical software (R Core Team, 2017), the 'mgcv' (Wood, 2006), and 'poptrend' (Knape, 2016) packages.

Results

Total Isère

For Total Isère, the number of black grouse counted was linked to procedural and meteorological factors. Model selection suggested that the best model for the long–term data at hand should include as explanatory factors: the surface of the sector, the counting time, the number of observers, the hour of first observation of a displaying male, the day of the count, the year, the daily minimum temperature and the 'north–facing–ness' (R^2 = 0.32; table 2; fig. 2). The estimates of cocks increased with the surface of the considered sector up to a threshold of between 350 ha to 400 ha, beyond which it remained averagely stable (fig. 2F). The estimates also increased with counting time (fig. 2E) and with the number of observers up to a threshold of five or six observers, beyond which it appeared averagely stable (fig. 2A). The number of counted cocks decreased when the hour of first observation increased (fig. 2B) and when 'north–facing–ness' increased (fig. 2G). The estimates of cocks appeared to decrease from the 10^{th} to the 20^{th} of May and then to increase up to the end of May (fig. 2C). The observed abundance of cocks varied non–linearly with the year (fig. 2D) and increased with

Table 2. Model selection for factors associated with the number of black grouse *Tetrao tetrix* counted during lek–count surveys for Total Isère between 1989 and 2016: n, sample size; K, number of estimated parameters; AICc, Akaike's Information Criterion corrected for small sample size; ΔAICc, difference of AICc between the model and the most–parsimonious model of the set; L(gi/x), likelihood of the model to be the best model of the tested models; Wi, Akaike weight of the model; R^2, proportion of the variance in the data explained by the model; RI, relative importance of each factor. Only the ten best models are reported (Burnham and Anderson, 2002). (For abbreviations see table 1).

Tabla 2. Selección de modelos para los factores asociados con el número de gallos lira Tetrao tetrix *contados durante los estudios de seguimiento en cantaderos de todo Isère entre 1989 y 2016: n, tamaño muestral; K, número de parámetros estimados; AICc, criterio de información de Akaike corregido para pequeños tamaños muestrales; ΔAICc, diferencia de AICc entre el modelo y el modelo más parsimonioso del conjunto; L(gi/x), probabilidad de que el modelo sea el mejor modelo de los modelos estudiados; Wi: peso de Akaike del modelo; R^2, proporción de la varianza en los datos explicada por el modelo; RI, importancia relativa de cada factor. Solo se muestran los diez mejores modelos (Burnham y Anderson, 2002). (Para consultar las abreviaciones, véase la tabla 1).*

Model	n	K	AICc	ΔAICc	L(gi/x)	Wi	R^2	RI	
NO+H+Y+D+T+CT+S+Nor	1040	18	1804.92	0	1	0.33	0.32	NO	1
NO+H+Y+D+T+CT+S+Nor+R	1040	20	1806.79	1.87	0.39	0.13	0.32	H	1
NO+H+Y+D+T+CT+S	1040	16	1806.80	1.88	0.39	0.13	0.30	Y	1
NO+H+Y+D+T+CT+S+Nor+Ea	1040	20	1807.73	2.81	0.25	0.08	0.33	D	0.99
NO+H+Y+D+T+CT+S+R	1040	18	1808.66	3.74	0.15	0.05	0.30	T	0.99
NO+H+Y+D+T+CT+S+Nor+Alt	1040	20	1809.51	4.59	0.10	0.03	0.32	CT	0.97
NO+H+Y+D+T+CT+S+Nor+R+Ea	1040	22	1809.63	4.71	0.10	0.03	0.33	S	0.95
NO+H+Y+D+T+CT+S+Ea	1040	18	1810.04	5.12	0.08	0.03	0.31	Nor	0.72
NO+H+Y+D+T+CT+S+Nor+R+Alt	1040	22	1810.75	5.83	0.05	0.02	0.32	R	0.28
NO+H+Y+D+T+CT+S+Alt	1040	18	1810.80	5.88	0.05	0.02	0.29	Ea	0.19
								Alt	0.10
								La	0.01
								Lo	0.01

the daily minimum temperature (fig. 2F). The tested factors that were not included in the best model for the long–term data at hand were: daily rainfall, latitude, longitude, altitude and 'east–facing–ness', although the daily rainfall factor was included in the second best model with substantial evidence support (table 2). A simplified version of the best model without a 'north–facing–ness' was the third best model, with a ΔAICc lower than 2 units.

The analysis of the subset that included the breeze factor provided a nuanced version of these results. Model selection suggested that the best model for the short–term data at hand should include as explanatory factors the surface of the sector, the number of observers, the hour of first observation of displaying male, the day of the count, the year, the breeze factor and the 'north–facing–ness' (R^2 = 0.37; table 3). The patterns of counted cocks globally matched with those detailed above for long–term data (fig. 2–3). In addition, the number of counted cocks appeared positively linked to the breeze factor up to a threshold of 3–4 m/s, beyond which it remained stable (fig. 3G). The number of counted cocks decreased when 'north–facing–ness' increased (fig. 3F). The factors counting time and daily minimum temperature, among others, were not included in the best model for short term data at hand (table 3).

Reference sites

For the Reference Sites, the number of counted black grouse was also linked to procedural and meteorological factors. Model selection suggested that the best model for the long–term data at hand should include as explanatory factors the number of observers, the hour of first observation of the displaying male, the day of the count, the year, and the minimum temperature (R^2 = 0.41; table 4; fig. 2). The links between the number of counted cocks and the associated factors closely match those detailed above for long–term data in Total Isère (fig. 2I–2M). Nonetheless, the link to daily minimum temperature suggested a potential non–linearity associated with a larger confidence interval for the higher values of temperatures (fig. 2M). In addition, the abundance of cocks with years in Reference Sites exhibited stronger variations than those in Total Isère (fig. 2L, 2D).

Analysis of the subset for short–term data at hand that included the breeze factor provided a nuanced version of said results albeit with a lower capacity to distinguish the best model. The best model included as explanatory factors the number of observers, the hour of first observation of a displaying male, the day of the count, the year, the surface of the sector, the 'north–facing–ness', and altitude (R^2 = 0.63; table 5; fig. 3). Nevertheless, six simplified versions of this model, with and without the surface, the day, the ''north–facing–ness' and the altitude appeared as having substantial support for the data at hand (table 5; fig. 3).

Population trends

When omitting the important cofactors for the long–term dataset, the population trends for both Total Isère and Reference Sites appeared without any significant increase or decrease in abundance of counted cocks (fig. 4A, 4B). However, when considering the cofactors highlighted in the best models, different patterns emerged (fig. 4C, 4D). In Total Isère, the number of male black grouse showed two periods of overall stability separated by a significant mean increase in population of +17 % between 1997 and 2001 (CI 95 %: +5.3 % – +29 %). In Reference Sites, a decrease in the number of male black grouse appeared from 1992 to 1995 but this result is supported by the data that was recorded for 1992 only. Two periods of overall stability (1995–98 and 2001–16) were separated by a significant mean increase in population of +46% between 1998 and 2001 (CI 95 %: +18 % – +80 %). Over the entire period of the study (1989–2016), the larger dataset, on Total Isère, suggested a mean increase in population of +47 % (CI 95 %: +16 % – +87 %).

Discussion

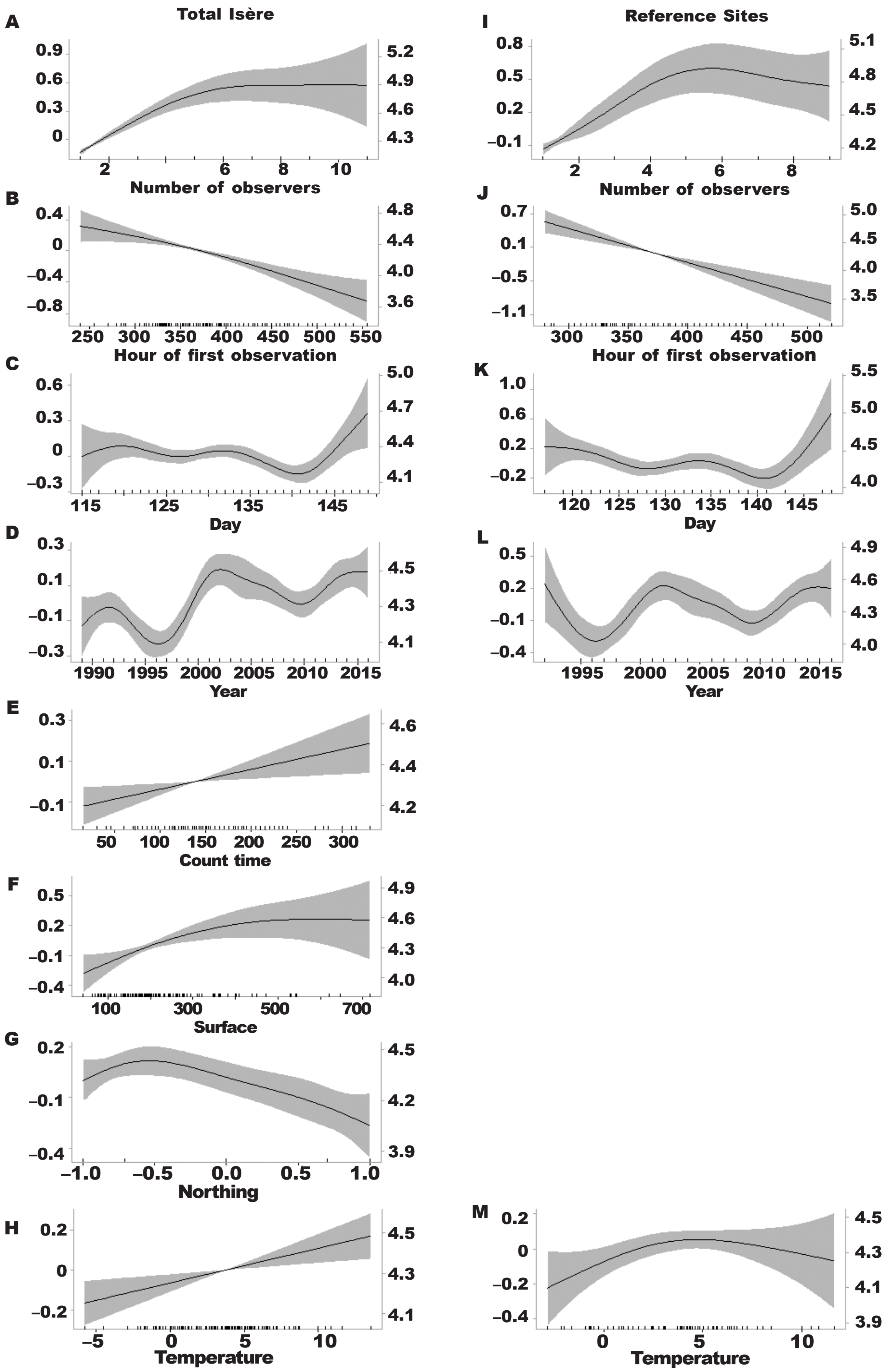
This study provides the first quantitative evidence, based on standard monitoring, that procedural and environmental cofactors modulate the estimates of abundance and population trends of the black grouse, a flagship species of alpine and northern environments.

Black grouse monitoring and cofactors

On the basis of the available information, our models suggest that the numbers of counted males in Isère are predominantly associated with procedural factors, and more specifically, with the number of observers, the hour of first observation of a displaying male, and the day of count, in addition to the year of the count. Additional details appeared, depending on the available information, the temporal scale and the spatial scale of the analysis. The analysis with the larger data set on Total Isère suggests that counting time, surface of the monitored sector, northing and temperature are also associated with the number of counted males. Nevertheless, the role of counting time, northing and the surface of sectors was not detected when using the smaller data set on Reference Sites. Furthermore, when considering the breeze factor, available on a smaller temporal scale, the relationships with counting time and temperature were not highlighted while the breeze factor was included in the best model of Total Isère, and altitude in the best model of Reference Sites. The amount of available information, the spatial scale and the temporal scale are thus important determinants of links between variables and of observed trends. When the sample size (n) is small compared to the number of estimable parameters in the approximating model (K) (see Burnham and Anderson, 2002), secondary, although important, cofactors are not necessarily detected, in accordance with the smaller spatial and temporal scales in our case study. Thus, sufficient data must be collected for a considered question so as to integrate a reasonable number of potential cofactors in the analyses and to analyze data at the

Fig. 2. Evolution of the number of black grouse cocks counted for Total Isère (left) and in Reference Sites (right) between 1989 and 2016, in relation to each cofactor of their respective best models (models with the lowest AICc, see tables 2 and 4). The solid lines represent the estimated patterns and shaded areas indicate 95% confidence intervals. The left–hand y–axis represents the centred values and the right–hand axis represents the estimated abundance of male black grouse. Mean of predicted values: Total Isère = 4.32 birds; Reference Sites = 4.32 birds.

Fig. 2. Evolución del número de machos de gallo lira contados en Total Isère (izquierda) y en las zonas de referencia (derecha) entre 1989 y 2016, en relación con cada cofactor de sus respectivos mejores modelos (modelos con el menor AICc, véanse tablas 2 y 4). Las líneas continuas representan los patrones estimados y las zonas sombreadas en gris indican el intervalo de confianza del 95%. El eje de las Y de la izquierda representa los valores centrados y el de la derecha, las abundancias estimadas de machos de gallo lira. Media de los valores previstos: Total Isère = 4,32 aves; Zonas de Referencia = 4,32 aves.



A
Total Isère
Number of observers
B
Hour of first observation
C
Day
D
Year
E
Count time
F
Surface
G
Northing
H
Temperature
I
Reference Sites
Number of observers
J
Hour of first observation
K
Day
L
Year
M
Temperature

appropriate spatial and temporal scale. Nonetheless, as in other species (Sarasa and Sarasa, 2013; Monroe et al., 2016), our results underlined that the counts of black grouse are associated with procedural, meteorological and geographic cofactors, in addition to the expected links to the interannual variations of birds. These results complement those of previous studies on counts of black grouse (Baines 1996). It should be noted that in this study, the time of first observation might be a cofactor more connected to the timing count and logistical constraints than to the timing of the bird's behaviour. The high estimates of counted males are preponderantly associated with counts performed by 6–7 observers per sector, with an early–morning first observation (between 4 a.m. and 5 a.m.), during long counting times (2h 30'–3h), in moderately large sectors (300–400 ha) and usually on days with mild temperatures (5°C or above) or a light breeze (3–5 m/s). The high estimates of counted males were usually recorded early in the counting season (during the last days of April) although a few counts occurred in the late counting season (later than 20th of May). These few counts in the late season might be too scarce to accurately reflect the range values of this procedural cofactor, highlighting a need for further studies on the phenology of reproductive displaying of black grouse in the Alps. The results referring to time and day mainly agree with those described in Sweden and Wales (Cayford and Walker, 1991; Borecha et al., 2017) even though the premating and peak mating periods of black grouse in the Alps must be further studied (perhaps in relation to the Normalized Difference Vegetation Index) and compared to northern populations. The predominant importance in our results of procedural cofactors rather than meteorological cofactors suggests that the methodological recommendations to observers (who must avoid adverse meteorological conditions during lek–counts) might successfully reduce potential noise related to meteorology in lek–count data. Another hypothesis suggests that the meteorological data available (only at two meteorological stations within the altitudinal range of the black grouse) may reveal macro–variations at the scale of Isère but might be too limited to allow a full analysis of the potential effects of very local weather on lek–count estimates. The fact that most of the geographical cofactors (altitude, longitude, latitude, easting) were not selected in the best models also suggests a predominant role of procedural and very local factors on local estimates of black grouse rather than biogeographical factors. The negative link observed between 'north–facing–ness' and the number of black grouse cocks might appear paradoxical in a flagship species of mountainous and boreal habitats. However, further studies are required to explore potential associations to key resources at a very local level, as already reported in other grouse species (Storch, 1993). Although beyond the scope and the potentiality of our dataset, further studies might go into other factors able to induce over–estimations (e.g. double counting) or sub–estimations of abundance (e.g. variable experience and age of observers, Hancock et al., 1999; Farmer et al., 2014; variable male lek count attendance in black grouse, Baines, 1996; acoustic limitations, Simons et al. 2007; low or variable probability of detection in tetraonids, Zimmerman et al., 2007, Fremgen et al., 2016). Several observers are often required for fieldwork and current protocols already tend to minimize or avoid double counts (see Method section). However, the potential problems related to the incomplete probability of detection or to the variability of observers are to date unmitigated. The relative importance of the heterogeneity of the sites, in particular to local weather and microhabitats that modulate the probability of detection and the suitability of the habitat for birds is also an open question. Thus, in addition to integrating the important cofactors that were highlighted in our results into monitoring programs, further studies on other potential cofactors might be required to continue improving the monitoring program of the black grouse.

Population trends

Our results on the long–term population trends of abundance of counted males highlight that omitting cofactors creates a bias in population trends. When considering cofactors, a marked increase of +17 % (CI 95 %: +5.3 %; +29 %) of the counted black grouse appeared between 1997 and 2001, followed by a period

Fig. 3. Evolution of number of black grouse cocks counted for Total Isère (left) and in Reference Sites (right) between 2005 and 2016 in relation to each cofactor of their respective best models (models with the lowest AICc, see tables 3 and 5). The solid lines represent the estimated patterns and shaded areas indicate 95 % confidence intervals. The left–hand y–axis represents the centred values and the right–hand axis represents the estimated abundance of male black grouse. Mean of predicted values: Total Isère = 4.54 birds; Reference Sites = 4.64 birds.

Fig. 3. Evolución del número de machos de gallo lira contados e Total Isère (izquierda) y en las Zonas de Referencia (derecha) entre 2005 y 2016, en relación con cada cofactor de sus respectivos mejores modelos (modelos con el menor AICc, véanse las tablas 3 y 5). Las líneas continuas representan los patrones estimados y las zonas sombreadas en gris indican el intervalo de confianza del 95 %. El eje de las Y de la izquierda representa los valores centrados y el de la derecha, las abundancias estimadas de machos de gallo lira. Media de los valores previstos:Total Isère = 4,54 aves; Zonas de Referencia = 4,64 aves.

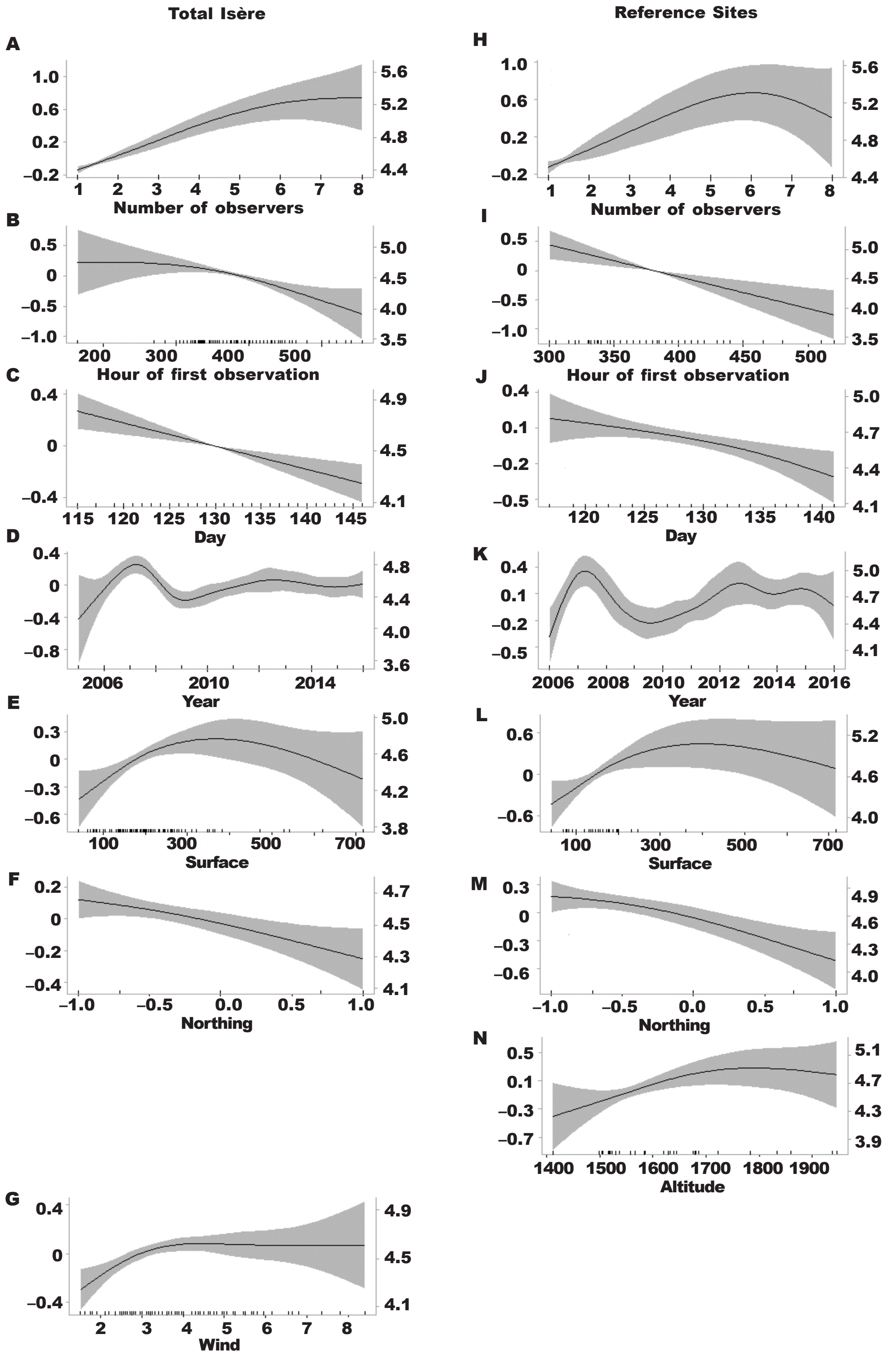

Total Isère
Reference Sites
A
H
Number of observers
B
I
Hour of first observation
C
J
Day
D
K
Year
E
L
Surface
F
M
Northing
N
Altitude
G
Wind

Table 3. Model selection for factors associated with the number of black grouse *Tetrao tetrix* counted during lek–count surveys for Total Isère between 2005 and 2016. Only the ten best models are reported (Burnham and Anderson, 2002). (For abbreviations see tables 1 and 2).

Tabla 3. Selección de modelos para los factores asociados con el número de gallos lira Tetrao tetrix *contados durante los estudios de seguimiento en cantaderos de todo Isère entre 2005 y 2016. Solo se muestran los diez mejores modelos (Burnham y Anderson, 2002). (Para consultar las abreviaciones, véase las tablas 1 y 2).*

Model	n	K	AICc	ΔAICc	L(gi/x)	Wi	R^2	RI	
NO+H+Y+D+Br+S+Nor	447	16	744.92	0	1	0.47	0.37	NO	1
NO+H+Y+D+Br+S	447	14	747.64	2.73	0.26	0.12	0.34	Y	1
NO+H+Y+D+Br+CT+S+Nor	447	18	749.16	4.25	0.12	0.06	0.37	H	1
NO+H+Y+D+Br+CT+S	447	16	750.01	5.09	0.08	0.04	0.34	D	1
NO+H+Y+D+Br+S+Nor+Alt	447	18	750.20	5.29	0.07	0.03	0.37	Br	0.98
NO+H+Y+D+Br+Nor	447	14	750.56	5.64	0.06	0.03	0.30	S	0.92
NO+H+Y+D+Br+T+S	447	16	750.77	5.85	0.05	0.03	0.34	Nor	0.72
NO+H+Y+D+Br+S+Nor+Ea	447	18	751.25	6.33	0.04	0.02	0.37	CT	0.17
NO+H+Y+D+Br+S+Ea	447	16	751.65	6.74	0.03	0.02	0.34	T	0.08
NO+H+Y+D+Br+S+R	447	16	751.91	7.00	0.03	0.01	0.34	Ea	0.07
								Alt	0.07
								R	0.06
								La	0.01
								Lo	0.01

Table 4. Model selection for factors associated with the number of black grouse *Tetrao tetrix* counted during lek–count surveys in Reference Sites between 1992 and 2016. Only the ten best models are reported (Burnham and Anderson, 2002). (For abbreviations see tables 1 and 2).

Tabla 4. Selección de modelos para los factores asociados con el número de gallos lira Tetrao tetrix *contados durante los estudios de seguimiento en cantaderos de las zonas de referencia entre 1992 y 2016. Solo se muestran los diez mejores modelos (Burnham y Anderson, 2002). (Para consultar las abreviaciones, véase las tablas 1 y 2).*

Model	n	K	AICc	ΔAICc	L(gi/x)	Wi	R^2	RI	
NO+H+Y+T+D	349	12	628.32	0	1	0.21	0.41	NO	1
NO+H+Y+T+Nor	349	14	629.61	1.29	0.53	0.11	0.43	H	1
NO+H+Y+T+D+Ea	349	14	630.99	2.67	0.26	0.05	0.42	Y	1
NO+H+Y+D	349	10	631.14	2.81	0.24	0.05	0.41	D	1
NO+H+Y+T+D+Nor+Alt	349	16	631.20	2.88	0.24	0.05	0.48	T	0.79
NO+H+Y+T+D+S+Nor	349	16	631.61	3.29	0.19	0.04	0.52	Nor	0.40
NO+H+Y+T+D+S	349	14	631.83	3.50	0.17	0.04	0.47	Alt	0.20
NO+H+Y+T+D+CT	349	14	632.16	3.84	0.15	0.03	0.41	S	0.20
NO+H+Y+T+D+R	349	14	632.34	4.01	0.13	0.03	0.41	Ea	0.19
NO+H+Y+D+Nor	349	12	632.36	4.04	0.13	0.03	0.42	CT	0.13
								R	0.11
								La	0.02
								Lo	0.02

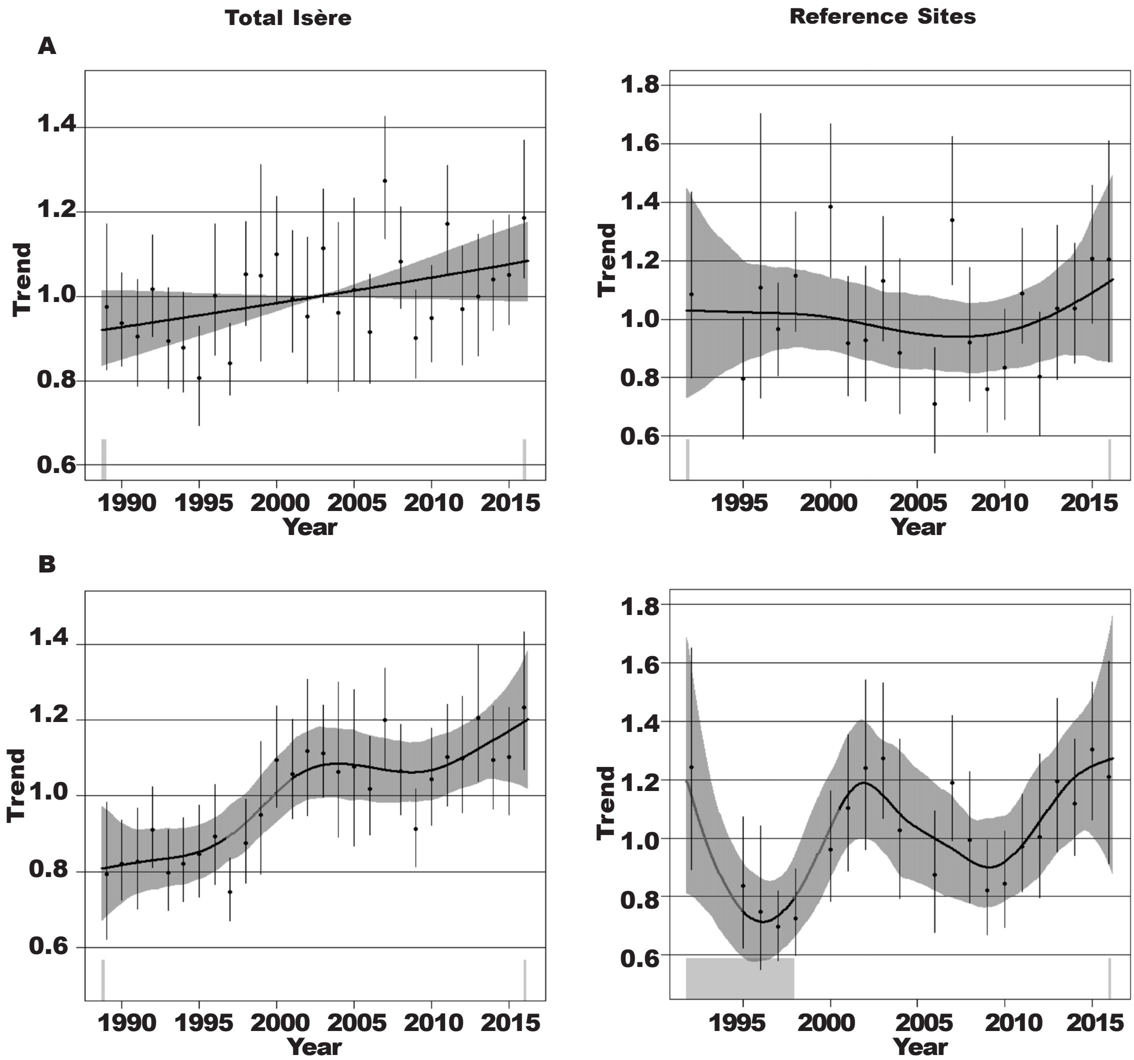


Fig. 4. Estimated long–term trends for black grouse from lek–count surveys between 1989 and 2016. A, omitting potential cofactors; B, the best model including cofactors.The solid line in these panels is the estimated long–term component of the trend, while the points are estimates of the trend with estimates of the random year effects superimposed. Estimates with random year effect and automatic degree of freedom, standardized with respect to the mean of the long–term component of the trends; confidence intervals (shaded area and vertical lines) are computed from the 2.5% and 97.5% quantiles of the bootstrap distributions; for periods where there is a significant increase or decrease in the trend at the 5% level, the trend line is colored, respectively, in green and orange; periods where the curvature is significantly positive or negative are marked by green and orange rectangles at the bottom of the panels (Knape, 2016). For instance, an increase in the value from 1.0 to 1.2 suggests an increase of 20% with respect to the mean.

Fig. 4. Tendencia a largo plazo del gallo lira, estimada a partir de estudios de seguimiento por recuento en cantaderos entre 1989 y 2016. A, omitiendo posibles factores; B, el mejor modelo que incluye factores. La línea continua en estos paneles es el componente estimado a largo plazo de la tendencia, mientras que los puntos son estimaciones de la tendencia con estimaciones de los efectos aleatorios del año superpuestos. Estimaciones con efecto anual aleatorio y grado de libertad automático, estandarizado respecto al promedio de la componente a largo plazo de la tendencia; los intervalos de confianza (área sombreada y líneas verticales) se calculan a partir de los cuantiles del 2,5% y del 97,5% de las distribuciones de bootstrap*; para los períodos donde hay un aumento o una disminución significativos de la tendencia en el nivel del 5%, la línea de tendencia se indica en verde y naranja, respectivamente; los períodos en los que la curvatura es significativamente positiva o negativa están marcados con rectángulos verdes y naranjas en la parte inferior de los paneles (Knape, 2016). Por ejemplo, un incremento del valor de 1,0 a 1,2 sugiere un incremento del 20% respecto al valor medio.*

Table 5. Model selection for factors associated with the number of black grouse *Tetrao tetrix* counted during lek–count surveys in Reference Sites between 2006 and 2016. Only the ten best models are reported (Burnham and Anderson, 2002). (For abbreviations see tables 1 and 2).

Tabla 5. Selección de modelos para los factores asociados con el número de gallos lira Tetrao tetrix *contados durante los estudios de seguimiento en cantaderos de las zonas de referencia entre 2006 y 2016. Solo se muestran los diez mejores modelos (Burnham y Anderson, 2002). (Para consultar las abreviaciones, véase las tablas 1 y 2).*

Model	n	K	AICc	ΔAICc	L(gi/x)	Wi	R^2	RI	
NO+H+Y+D+S+Nor+Alt	186	16	338.54	0	1	0.08	0.63	NO	1
NO+H+Y+D+S	186	12	338.63	0.09	0.95	0.08	0.51	Y	1
NO+H+Y+D	186	10	339.09	0.55	0.76	0.06	0.40	H	0.95
NO+H+Y+D+S+Nor	186	12	339.43	0.89	0.64	0.05	0.59	S	0.62
NO+H+Y	186	8	339.65	1.11	0.57	0.05	0.39	D	0.62
NO+H+Y+S	186	10	339.92	1.38	0.50	0.04	0.49	Nor	0.46
NO+H+Y+D+S+Nor	186	14	340.14	1.61	0.45	0.04	0.60	Alt	0.32
NO+H+Y+D+S+Nor+Br	186	16	341.12	2.58	0.28	0.02	0.59	Br	0.17
NO+H+Y+D+Nor+Alt	186	14	341.32	2.78	0.25	0.02	0.57	La	0.10
NO+H+Y+Nor+Alt	186	12	341.74	3.20	0.20	0.02	0.55	Lo	0.10
								CT	0.10
								T	0.08
								R	0.07
								Ea	0.07

of overall stability up to 2016. This trend differs from the trends reported in some parts of Italy (Viterbi et al., 2015), the UK (Warren and Baines, 2008; Summers et al., 2010; Scridel et al., 2017) and Finland (Ludwig et al., 2006) but corresponds to the trend highlighted in the Mont Avic Natural Park, Italy (Chamberlain et al., 2012). The increases in abundance of black grouse observed in Isère (France) and Mont Avic (Italy) during the second half of the 1990s were concomitant with a major ecological phenomenon that affected the habitat of the black grouse in the north–western Alps at this time. In February 1990, the winter–storm Vivian strongly affected the altitudinal range in the Alps, with gales of up to 270 km/h at the Italian–Swiss border (Schüepp et al., 1994). This storm was considered one of the most devastating wind–storms of the 20th century, causing about 100 million m^3 of wind throw damage in Europe (Cinotti, 1992), including about 8 million m^3 in France (Cinotti, 1992). Damage from Vivian also affected the Alpine forests in the northern French Alps (Dorren et al., 2004). Following the passage of Vivian, a proliferation of arthropods was reported in the Alps, mainly studied in Switzerland (e.g. Wermelinger et al., 2002). Arthropods, such as the saproxylic species, exhibited a boosted abundance that was observed as a successional phenomenon (Wermelinger et al., 2002). The increased abundance of several species that are associated with late stages of disturbed forest, such as Cerambycidae (Wermelinger et al., 2002, 2003), occurred during the second half of the 1990s. This corresponded to the period of increased abundance of black grouse that was highlighted in our results and in the Mont Avic Natural Park, Italy (Chamberlain et al., 2012). Ants are one group of the species associated with dead wood and the late stages of disturbed forests (Lempérière et al., 2002; Lempérière and Marage, 2010). They are also a key resource in habitat selection (Schweiger et al., 2012) and reproduction of black grouse (Ponce and Magnani, 1988; Ponce, 1992; Baines et al., 2017). Consequently, a plausible hypothesis for the marked increase in abundance of black grouse in Isère and other areas in the Alps, such as Mont Avic, at this time, would be a bottom–up stimulation of grouse abundance during the 1990s, induced by the cascading effects of the winter–storm Vivian. Although further studies might be necessary to verify this hypothesis, other factors with potentially positive links to abundance of grouse did not appeared as exhibiting noteworthy variations only during that period in the northern French Alps: forestry (Office National des Forêts, 2001); climate (Bigot and Rome, 2010); hunting (Magnani, 2009; Lauer and Magnani, 2013); and husbandry (Chatelier and Delatre, 2003). For instance, the hunting of black grouse was reduced in the French Alps, including our study area, to less than half, following a rather regular pattern between 2000–2011 (see page 18 of Lauer and Magnani, 2013). This decrease over a long period of time fits poorly with the marked increase in grouse numbers during 1997–2001 period only. Further analysis integrating additional demographic data could add to the understanding of the overall increase in grouse numbers during the full study period (1989–2016). Further studies in alpine habitats are needed to determine the cascading links between uncleared gaps of windthrow timber, abundance of arthropods –particularly ants– and abundance of grouse. Such studies could provide promising perspectives for the integrated management of black grouse and their habitat, as the management of dead wood in forests might be a key factor in the dynamics of birds such as the black grouse.

Conclusions

Several cofactors, in particular procedural cofactors, are linked to lek–counts of male black grouse, and the studied population exhibited an increase that was previously not detected in France. This corresponds, however, to an ecological phenomenon previously reported in the north–western Alps. Thus, these findings might stimulate substantial improvements in the monitoring and management of black grouse through greater integration of the important cofactors in monitoring protocols and models of abundance. The concomitance between the observed trends and other ecological phenomena in the Alps questions the need for integrated management of the habitat, specifically on the potential links between dead wood, arthropod populations and black grouse populations.

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