

Long-term variation of demographic parameters in four small game species in Europe: opportunities and limits to test for a global pattern

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Abstract

Long-term variation of demographic parameters in four small game species in Europe: opportunities and limits to test for a global pattern. For decades, decreases in several populations of some small sedentary game species have been reported in Europe. From the literature, we extracted mortality and reproductive rates that were available for European populations in four iconic species, the grey partridge (*Perdix perdix*), the black grouse (*Tetrao tetrix*), the capercaillie (*T. urogallus*) and the brown hare (*Lepus europaeus*), to examine how demographic parameters vary with time. Our study revealed the need to consider many confounding factors (age, sex, origin of studied individuals, season, country and methods) and the scarcity of recent demographic studies. Statistical analyses showed contrasted patterns of demographic traits with time within and between species. Our results highlighted that there may be consistency with a population decrease in grey partridge and black grouse that has been reported in the literature. However, analyses in capercaillie and brown hare showed less support for a population decrease at the European scale. The significant effects of interactions between time and age (in grey partridge, capercaillie and brown hare), method or origin of individuals on demographic traits and the emergence of contrasted patterns between short, intermediate and long monitoring periods (in grey partridge and black grouse) suggested that further studies should pay particular attention to potential confounding factors. Finally, the lack of recent data and doubts about the relative importance of reported causal factors indicate the need for further studies on the links between demographic traits, densities and environmental changes in the long term, and particularly on the role of predation and habitat change.

Key words: Grey partridge, Black grouse, Capercaillie, Brown hare, Demography, Population monitoring

Resumen

Variación a largo plazo de los parámetros demográficos en cuatro especies de caza menor en Europa: oportunidades y limitaciones. Durante décadas, se ha registrado la disminución de varias poblaciones de algunas especies sedentarias de caza menor. A partir de los estudios publicados, se extrajeron las tasas de mortalidad y reproducción documentadas para las poblaciones europeas de cuatro especies icónicas: la perdiz pardilla (*Perdix perdix*), el gallo lira (*Tetrao tetrix*), el urogallo (*T. urogallus*) y la liebre europea (*Lepus europaeus*), para examinar la variación de los parámetros demográficos con el tiempo. Nuestro estudio reveló la necesidad de considerar muchos factores que pueden confundir (edad, sexo, origen de los individuos estudiados, estación, país y métodos) y la escasez de estudios demográficos recientes. Los análisis estadísticos mostraron diferentes patrones de variación de los parámetros demográficos con el tiempo dentro de cada especie y entre ellas. Nuestros resultados subrayaron que estos patrones pueden ser coherentes con la disminución de las poblaciones de perdiz pardilla y gallo lira que han sido documentadas en las publicaciones especializadas. No obstante, los análisis sobre el urogallo y la liebre europea mostraron menos indicios que apuntaran a una disminución de las poblaciones a escala europea. El efecto significativo de las interacciones entre el tiempo y la edad (en la perdiz pardilla, el urogallo y la liebre europea), los métodos o el origen de los individuos en los parámetros demográficos y la aparición de patrones distintos entre los períodos de seguimiento a corto, medio y largo plazo (en la perdiz pardilla y el gallo lira) sugieren que los nuevos estudios deberían dedicar una atención especial a los factores que pueden confundir. Por último, la falta de datos recientes sobre la

importancia relativa de los factores causales conocidos y las dudas que ello genera indican la necesidad de realizar más estudios sobre los vínculos entre los parámetros demográficos, las densidades y los cambios ambientales a largo plazo, en particular sobre la función de la depredación y el cambio del hábitat.

Palabras clave: Perdiz pardilla, Gallo lira, Urogallo, Liebre europea, Demografía, Seguimiento de poblaciones

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Introduction

For decades, decreases in several populations of farmland and woodland species have been highlighted in different areas of geographical Europe by various stakeholders (Comolet–Tirman et al., 2015), including hunting associations (Tapper, 2001; Vallance et al., 2008) and academic researchers (Sumption and Flowerdew, 1985; Smith et al., 2005; Storch, 2007; Inger et al., 2014). Wide-scale analyses controlling for the effects of, for instance, heterogeneity in studied areas and methods and individuals used as biological models would be useful to investigate whether demographic parameters might be used as proxy for variation in the abundance of small game species in Europe.

Direct testing of populations decreases from abundance estimates might appear to be an intuitive approach to examine the temporal variations of small game species in Europe (European Environment Agency, 2014). However, reliable long-term series of abundance (or density) are available from very few study sites (Potts and Aebischer, 1995) and short-term estimates of abundance or density may be misleading because of the diversity of methods or the uneven probability of detection across habitats (Thompson, 2002). Furthermore, the restocking of game species might be a confounding factor of abundance estimates (Díaz–Fernández et al., 2013). An overall population decrease should theoretically be associated with a decrease in demographic traits, including survival and reproduction. However, a decrease in only one trait, particularly reproduction (Panek, 1992b; Lindström et al., 1997), might require complementary information as potential demographic trade-offs or density-dependent processes might be involved in population dynamics (Panek, 1992b; Lindström et al., 1997; Grimm and Storch, 2000; Sachot et al., 2006).

Variations in mortality and reproductive rates over the last half century might be difficult to highlight as some factors might have changed concomitantly, such as monitoring and estimation methods and the origin of birds. Captures, animal handling, and tracking equipment (including radio-transmitters or GPS) might affect animal mobility and behaviour and also reproductive and mortality rates (Bro et al., 1999; Mech and Barber 2002; Barron et al., 2010). The number of breeding black grouse hens (*Tetrao tetrix*), for instance, can be halved when they are equipped (Caizergues and Ellison, 1998). Furthermore, for restocking purposes, hunting associations have made many attempts to release captive-reared individuals. However, various studies have shown that these birds often have different foraging and anti-predator behaviour, and poorer body condition than wild birds (Parish and Sotherton, 2007; Rantanen et al., 2010; Rymešová et al., 2013), affecting mortality and reproductive rates (Birkan, 1977a, 1977b). The mortality of reared birds can be ten times greater than that of wild birds (Putala et al., 2001), reaching 90% in one study (Rymešová et al., 2013). Age and sex might also have a strong effect on mortality and breeding success. Yearling black grouse hens, for

instance, might have a lower clutch size and might be more likely to lose their entire brood than adults (Willebrand, 1992; Marjakangas and Törmälä, 1997). In the same way, mortality in summer in grey partridge males (*Perdix perdix*) has been reported to be lower than in females (Birkan et al., 1992) while sex and age effects have been reported in other grouse and age, sex and origin should thus be controlled when analysing patterns of mortality and reproductive estimates over time.

From the data available in the scientific literature, our aim was to explore whether estimates of mortality and reproductive rates might be used as empirical support of the demographic declines in four small game species in Europe: the grey partridge, the black grouse, the capercaillie (*Tetrao urogallus*), and the brown hare (*Lepus europaeus*). We assumed that an increase in mortality estimates associated with a decrease in reproduction estimates suggests population declines (Bro et al., 2000; Ludwig et al., 2006). However, uncertainty may exist if only one proxy (reproduction or survival) varies with time or if potential factors, such as methods, origin, or sex, significantly affect estimates of demographic traits. This question was studied in small game species by testing for the effect of year on estimates of reproductive and mortality rates. When possible, we controlled for the effect of the following confounding factors: sex, age and origin of individuals, method, season and country of monitoring.

Material and methods

Data collection

We identified all articles available up to May 2015 from the Web of Science and Science Direct reporting demographic traits (mortality and reproductive rates) in grey partridge, black grouse, capercaillie and brown hare. These articles were collected through a systematic search that included key-words related to demographic traits (e.g. survival, mortality, reproduction) and names of species. Articles on wild rabbit (*Oryctolagus cuniculus*), pheasant (*Phasianus colchicus*), red-legged partridge (*Alectoris rufa*), hazel grouse (*Tetrastes bonasia*) and rock ptarmigan (*Lagopus muta*) were not considered here as they were too rare to allow statistical analyses on the variation of estimates of demographic parameters with time. For a few studies, data were not directly accessible (e.g. studies in non-English languages) but were available from scientific reviews or comparative studies. Data were not considered when: 1) the estimation value revealed confounding factors (e.g. when estimates of winter mortality from counts showed a 'negative' mortality, meaning that the number of migrants was greater than the number of deaths and emigrants); and 2) data were missing for several factors that we wanted to test (e.g. the year in which rates were estimated) or control for (e.g. the country where the study was performed). Some data sets can be found in several articles (e.g. the Game and Wildlife Conser-

vation Trust's Count Scheme in England); these were therefore gathered only once to avoid double counting and were completed when additional information was available from a different article with the same data set. When data were presented as averages over several years, special attention was paid to using the raw data whenever possible.

From all indicators of mortality rates that were used in the literature, we extracted an individual's probability of dying during the monitoring period considered in the study. Back-transformation from partial estimates (e.g. for data presented in a fragmented format linked to predation) to overall mortality was carried out when possible (i.e. when the total population size was given) (discarded otherwise). Similarly, several reproductive traits were reported in the literature, including clutch and brood size, the proportion of nests in which at least one egg hatched or in which at least one young survived, the proportion of females with a nest or with young, the probability of re-nesting, the number of chicks, young or fledglings per hen, per adult, or per couple. The estimates of reproductive parameters are presented as rates (e.g. proportion of breeding hens) or real numbers (e.g. brood size, clutch size). We studied the variation in mortality rates and reproduction through the post-hatching brood size, the number of fledglings per hen, and the proportion of hens with fledglings; this provided enough data from the literature to run statistical analyses.

Finally, we noted the year and season of the study. For studies exceeding one year and presenting pooled data, the median year was considered. We dealt with the marked heterogeneity in the monitoring periods by considering three classes: (1) one season or less; (2) from one season to less than one year; and (3) one year or more. To control for potentially confounding effects, we also noted the age, sex and origin (reared or wild) of the studied individuals, the monitoring method, and the country of the study, although a detailed presentation of their effects is beyond the scope of this study.

Data analysis

For each species, we ran linear models to test for the long-term effect of time on mortality and reproductive rates (Tx) that were logit-transformed to fulfil statistical requirements related to the homogeneity of variances and linearisation.

We started our procedure by performing a model (Eq. 1) including time (x_1) and its square (i.e. time², x_2) to investigate the nonlinear relationship between time and demographic traits:

$$\text{Logit}(Tx) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \varepsilon \quad (\text{Eq. 1})$$

with β , the model parameters and ε , the residual error. As it is hazardous to compare estimated mortality rates from 3-month studies with those calculated over several years, we ran different sets of separate models for each species when the duration of the study was: (1) one season or less, (2) from one season to less than one year, and (3) one year or more. To

include a reasonable number of degrees of freedom in each procedure, we tested controlling factors such as method, sex, age, origin and country separately. Within each model set, each controlling factor (x_n) was included in the procedure (i.e. in Eq. 1) and the deviance between the model with and without the controlling factor was tested using *F*-tests. Two-way interactions were also tested with the same procedure. When the deviance between the two models was significant, this factor (or the interaction) was kept throughout the procedure. Once all significant controlling factors and interactions were determined, we tested the effect of time and time².

Concerning mortality in capercaillie and brown hare, the limiting number of data required a specific statistical procedure. The effect of time was tested using a forward selection procedure that compared deviance between a null model and a model including time only. This was then compared with a model that included time and time² using the *F*-test. Then, we tested for the effect of the controlling factors using the same procedure, and we also tested two-way interactions.

The structural limits of the data set hindered mixed-effect models, including the identity of the publication as a random effect. However, we checked that residuals fulfilled statistical requirements including a normal distribution of residuals, a lack of heterogeneity of variance when plotting residuals against fitted values, and a lack of temporal correlation of residuals when using a partial autocorrelation function (pacf). All statistical procedures were performed using R software (R Development Core Team, 2015).

Results

Data collection

The available data highlighted a large difference between the four studied species in the number of studies in the literature. The number of studies on grey partridge was considerably higher than that for the other three species (tables 1 and 2).

Grey partridge

For grey partridge we collected data for mortality rates from 30 papers and data for reproductive traits from 26 papers. The lowest mortality rate was 0.012 (in a short monitoring period; Kaiser, 1998) while the highest rate was 0.99 (in a long monitoring period; Buner et al., 2011). Variation in reproduction with time was analysed using post-hatching brood size, which ranged from 0.66 to 20.00 (Rands, 1985; Rymešová et al., 2013), and the proportion of hens with fledglings, which ranged from 0.17 to 0.66 (Buner et al., 2011).

Mortality rates

Analysis showed a significant association between time and mortality rate estimates in grey partridge, but this link differed between the temporal scales at which it was assessed (table 3).

Table 1. Mortality data collected from the scientific literature.

Tabla 1. Datos de mortalidad recolectados en publicaciones científicas.

Species	Numer of studies	Number of data	Period
References			
Grey partridge	30	403	1917–2011
Middleton (1935), Jenkins (1961), Birkan et al. (1975), Potts (1980), Montagna and Meriggi (1991), Birkan et al. (1992), Nösel (1992); Panek (1992a), Potts and Aebischer (1995), Boatman and Brockless (1998), Kaiser (1998), Sotherton (1998), Bro et al. (2000, 2001), Faragó (2001), Putaala et al. (2001), Reitz and Mayot (2001), Aebischer et al. (2002), Panek (2002), Aebischer and Ewald (2004), Panek (2005, 2006), Parish and Sotherton (2007), Watson et al. (2007), Aebischer and Baines (2008), Besnard et al. (2010), Rantanen et al. (2010), Buner et al. (2011), Draycott (2012), Ryměšová et al. (2012)			
Black grouse	8	77	1933–2008
Angelstam (1984), Baines (1991), Caizergues and Ellison (1997), Warren and Baines (2002), Baines et al. (2007), Bowker et al. (2007), Wegge and Rolstad (2011), Pekkola et al. (2014)			
Capercaillie	7	49	1984–2002
Gjerde and Wegge (1989), Schroth (1991), Storch (1994), Moss et al. (2000), Wegge and Kastdalen (2007), Wegge and Rolstad (2011), Åhlen et al. (2013)			
Brown hare	7 (+1*)	52	1959–2008
Broekhuizen (1979), Frylestam (1979), Wasilewski (1991), Hansen (1992), Marboutin and Peroux (1995), Marboutin and Hansen (1998), Misiorowska and Wasilewski (2012)			
* Abildgard et al. (1972) in Broekhuizen (1979), Marboutin and Hansen (1998)			

Controlling for the effects of age, sex, origin, method, country and season, mortality rates from short monitoring periods (equal to or less than one season) showed a significant decrease between 1917 and 2010 (time: $\beta \pm SE = -0.02 \pm 0.01$; fig. 1A; table 3), while this link was affected by age, method and origin (fig. 1s in supplementary material). Adult mortality showed a high increase with time ($\beta \pm SE = 0.77 \pm 0.38$) while chick mortality decreased ($\beta \pm SE = -0.72 \pm 0.34$; fig. 1s in supplementary material). Mortality increased with time when the methods used in the studies were by radio-collar and census ($\beta \pm SE = 0.77 \pm 0.38$), while the link of the modelling method was relatively stable (fig. 1s in supplementary material).

Controlling for the effects of age, method, season, sex, origin and country, mortality rates from intermediate monitoring periods showed a significant increase between 1933 and 2011 (time: $\beta \pm SE = 0.02 \pm 0.01$; fig. 1B; table 3) while this link was affected by the age of birds (fig. 2s in supplementary material). Mortality of adults showed the highest increase with time ($\beta \pm SE = 0.03 \pm 0.01$) while the dynamic of chick mortality did not differ significantly over time for the sample at hand (fig. 2s in supplementary material).

For long monitoring periods (greater than or equal to one year) and controlling for the effects

of method, age, sex, origin and country, mortality rates increased significantly with time from 1978 to 2010 (time: $\beta \pm SE = 0.04 \pm 0.14$; fig. 1C; table 3).

Thus, the apparent decrease in mortality rates between 1975 and 2010 from short monitoring studies contrasted with an apparent increase in mortality rates from longer monitoring studies. Adjusted R^2 of the three models (for short, intermediate and long-monitoring periods) was 0.33, 0.39 and 0.77, respectively.

Reproduction

Controlling for the effects of country, method and season, we found a strong overall decline in brood size estimates between 1910 and 2010 ($\beta \pm SE = -0.11 \pm 0.01$; fig. 2A; table 3) while this pattern interacted with method and season (fig. 3s in supplementary material). The few data in June suggested an increasing pattern in brood size ($\beta \pm SE = 3.60 \pm 1.30$) while the prevailing data in non-determined months suggested an overall decrease.

Similarly, our results showed that the proportion of hens with fledglings decreased linearly between 1968 and 2005 (time: $\beta \pm SE = -0.03 \pm 0.01$; fig. 2B; table 3) when the effects of country, method, season and origin were controlled for. Adjusted R^2 of the models of brood size and proportion of hens with fledglings were 0.80 and 0.23, respectively.

Table 2. Reproductive data collected from the scientific literature: * numbers in brackets (black grouse and capercaillie) correspond to data gathered in Jahren (2012).

*Tabla 2. Datos de reproducción recolectados en publicaciones científicas: * los números entre paréntesis (en el gallo lira y el urogallo) corresponden a los datos recopilados en Jahren (2012).*

Species	Number of studies	Number of data	Period
References			
Grey partridge	26	580	1910–2010
Middleton (1935, 1936, 1937), Jenkins (1961), Potts (1970, 1980), Rands (1985); Montagna and Meriggi (1991), Birkan et al. (1992), Nösel (1992), Panek (1992a), Thomaides and Papageorgiou (1992), Potts and Aebischer (1995), Tapper et al. (1996), Boatman and Brockless (1998), Bro et al. (2000), Aebischer and Ewald (2004), Bro et al. (2004), Panek (2006), Parish and Sotherton (2007), Besnard et al. (2010), Buner et al. (2011), Rymešová et al. (2013)			
Black grouse	16 (+ 7*)	304 (+ 7*)	1975–2009
Angelstam et al. (1984), Moss (1986), Baines (1991), Willebrand (1992), Caizergues and Ellison (1997), Kurki et al. (1997), Marjakangas and Törmälä (1997), Caizergues and Ellison (1998), Warren and Baines (2002), Summers et al. (2004), Baines et al. (2007), Bowker et al. (2007), Grant et al. (2009), Ludwig et al. (2010), Summers et al. (2010), Wegge and Rolstad (2011), Jahren (2012)			
* Siivonen (1953), Myrberget and Hagen (1974), Lindén (1981), Ellison et al. (1982), Angelstam (1983), Storaas and Wegge (1984), Brittas and Willebrand (1991) in Jahren (2012)			
Capercaillie	17 (+ 9*)	247 (+ 10*)	1975–2009
Moss (1986, 1987), Leclercq (1988), Storch (1994), Kurki et al. (1997), Picozzi et al. (1999), Moss et al. (2000), Proctor and Summers (2002), Saniga (2002), Summers et al. (2004), Wegge and Kastdalen (2007), Summers et al. (2009, 2010), Wegge and Rolstad (2011), Jahren (2012)			
* Höglund (1953), Siivonen (1953), Myrberget and Hagen (1974), Wegge and Grasaas (1977), Lindén (1981), Jones (1982), Klaus (1984), Spidsø et al. (1984), Storaas and Wegge (1984) in Jahren (2012)			

Black grouse

Mortality rates in black grouse were collected from eight papers and reproductive traits were collected from 23 papers. The lowest mortality rate was 0.003 (in a short monitoring period; Baines et al., 2007) and the highest was 0.97 (in a long monitoring period (Bowker et al., 2007)). The variation in reproductive rates over time was analysed using the post-hatching brood size, which ranged from 2.0 to 4.82 (Kurki et al., 1997; Caizergues and Ellison, 1998), and the number of fledglings per hen, which ranged from 0 to 6.3 (Moss, 1986; Caizergues and Ellison, 1998; Summers et al., 2010).

Mortality rates

Estimates of mortality rate decreased linearly with time (time: $\beta \pm SE = -0.31 \pm 0.04$; fig. 3A; table 4) for short monitoring periods between 1985 and 2005 when controlling for the effects of method, season, age, and country. The mortality rates appeared stable between 1980 and 2008 for intermediate monitoring periods, controlling for the effects of method, sex, age and country (fig. 3B). Estimates of mortality rate from

long monitoring studies increased between 1980 and 2008 (time: $\beta \pm SE = 0.05 \pm 0.03$; fig. 3C; table 4) when controlling for the effect of method, sex, age and country. Thus, the temporal pattern of black grouse mortality rates differed according to the temporal scale at which the rates were assessed. Adjusted R^2 of the three models was 0.77, 0.63 and 0.94, respectively.

Reproduction

We detected a significant nonlinear relationship between time and brood size. Controlling for the effects of country, method, and season, we found that average brood size increased from 1988 to 1995 (time: $\beta \pm SE = 50.78 \pm 30.58$; time²: $\beta \pm SE = 0.01 \pm 0.01$; fig. 4A; table 4). Nevertheless, this pattern seemed to depend greatly on the data heterogeneity with time, including one point at earlier and later periods.

When controlling for the effect of country, method, season and age, our data indicated that the number of fledglings per female decreased linearly with time between 1975 and 2009 (time: $\beta \pm SE = -0.02 \pm 0.01$; fig. 4B; table 4). Adjusted R^2 of the two models was 0.57 and 0.04, respectively.

Table 3. Results of the links between demographic traits and time in grey partridge *Perdix perdix*: factors, F -values and p -values.

Tabla 3. Resultados relativos a la relación entre los parámetros demográficos y el tiempo para la perdiz pardilla *Perdix perdix*: factores y valores F y p .

Mortality rates

Short monitoring periods

Time	$F_{1,115} = 5.81, p = 0.02$
Time x age	$F_{1,115} = 5.26, p = 0.02$
Time x method	$F_{2,115} = 3.55, p = 0.03$
Time x origin of birds	$F_{1,115} = 5.26, p = 0.02$
Age	$F_{2,115} = 51.61, p < 0.001$
Sex	$F_{2,115} = 1.34, p = 0.27$
Origin of birds	$F_{2,115} = 6.87, p < 0.01$
Method	$F_{2,115} = 42.69, p < 0.001$
Country	$F_{6,115} = 35.20, p < 0.001$
Season	$F_{1,115} = 16.79, p < 0.001$

Intermediate monitoring periods

Time	$F_{2,144} = 5.54, p < 0.01$
Time x age	$F_{2,144} = 5.54, p < 0.01$
Age	$F_{3,144} = 6.13, p < 0.001$
Sex	$F_{2,144} = 0.60, p = 0.55$
Origin of birds	$F_{2,144} = 11.47, p < 0.001$
Method	$F_{2,144} = 0.53, p = 0.59$
Country	$F_{6,144} = 4.87, p < 0.001$
Season	$F_{1,144} = 0.52, p = 0.47$

Long monitoring periods

Time	$F_{1,89} = 8.71, p < 0.01$
Age	$F_{3,89} = 7.25, p < 0.001$
Sex	$F_{2,89} = 10.88, p < 0.001$
Origin of birds	$F_{2,89} = 24.02, p < 0.001$
Method	$F_{1,89} = 13.52, p < 0.001$
Country	$F_{3,89} = 16.07, p < 0.001$

Reproduction

Brood size

Time	$F_{1,156} = 175.25, p < 0.001$
Time x method	$F_{1,156} = 8.70, p < 0.01$
Time x season	$F_{1,156} = 5.70, p = 0.02$
Method	$F_{1,156} = 79.64, p < 0.001$
Country	$F_{5,156} = 22.47, p < 0.001$
Season	$F_{2,156} = 46.96, p < 0.001$

Proportion of hens with fledglings

Time	$F_{1,24} = 5.26, p = 0.03$
Method	$F_{1,24} = 2.50, p = 0.13$
Country	$F_{1,24} = 2.50, p = 0.13$
Season	$F_{2,24} = 1.39, p = 0.27$
Origin of birds	$F_{2,24} = 3.41, p = 0.05$

Capercaillie

In capercaillie, mortality rates and reproductive traits were collected from seven and 26 articles respectively. The lowest mortality rate was 0.01 (in an intermediate monitoring period (Wegge and Rolstad, 2011) and the highest was 0.93 (in a long monitoring period; Moss et al., 2000). The proportion of hens with fledglings and the number of fledglings were considered to analyse the variation in reproductive rates with time. The former rose from 0.02 to 0.77 (Leclercq, 1988) and the latter from 0 to 7 (Leclercq, 1988; Saniga, 2002; Summers et al., 2004, 2010).

Mortality rates

Controlling for the effect of age, country, sex, and season, we found that estimates of mortality rate for intermediate monitoring periods decreased for a linear way with time (time: $\beta \pm SE = -0.10 \pm 0.05$; fig. 5A; table 5); this link was affected by the age of birds (fig. 4s in supplementary material). The few data on young birds suggested an increase in mortality with time ($\beta \pm E = 1.78 \pm 0.56$; fig. 4s in supplementary material) while data on adults suggested an overall decrease.

For long monitoring periods, mortality rates appeared stable between 1995 and 2002 (fig. 5B), and none of the control factors seemed to have a

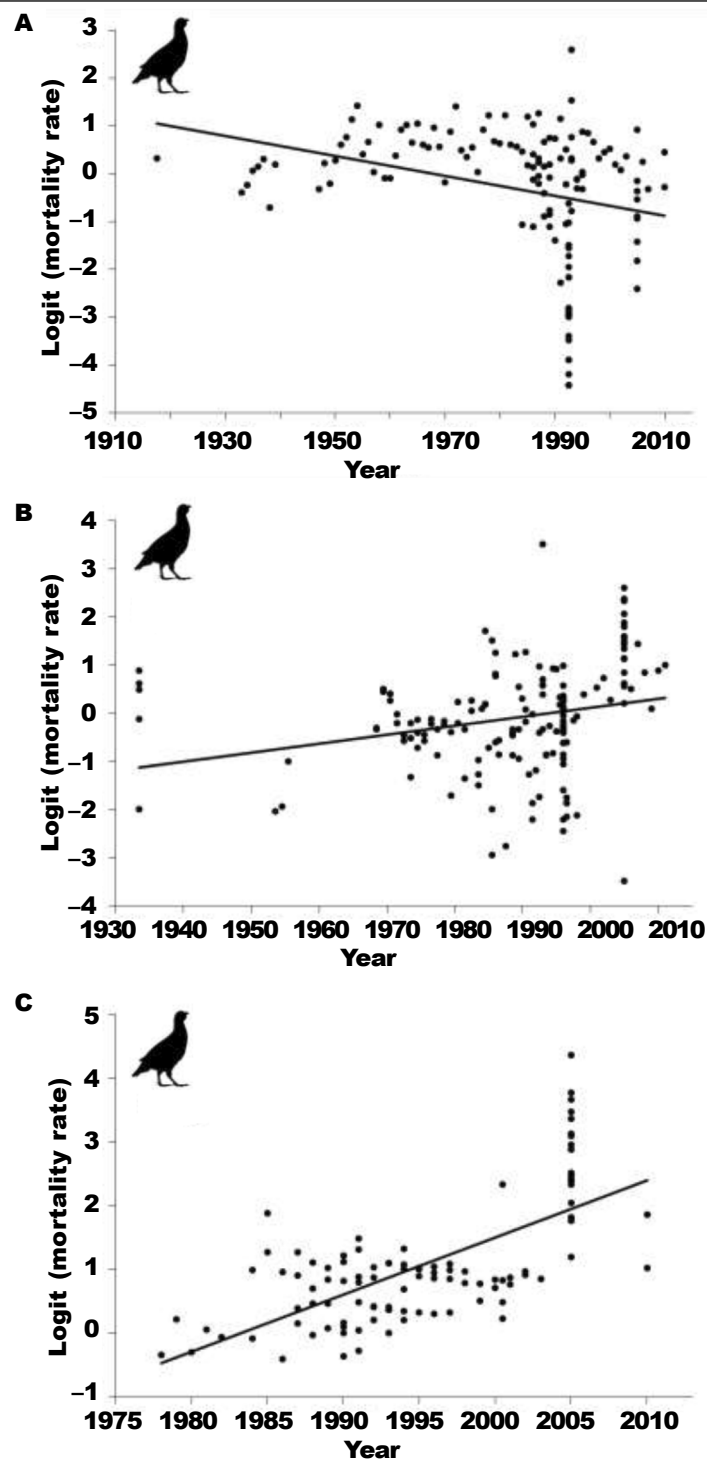


Fig. 1. Estimates of mortality rate (logit transformed) of grey partridge over time (average years) in Europe for a: A, short (one season or less); B, intermediate (from one season to less than one year); and C, long monitoring periods (greater than or equal to one year). The line indicates a significant correlation with time (see results). See figures 1s and 2s in supplementary material for the significant effects of age, methods and origin.

Fig. 1. Estimación de la tasa de mortalidad (transformada logarítmicamente) de la perdiz pardilla a lo largo del tiempo (promedio de los años) en Europa para periodos de seguimiento: A, cortos (una estación o menos); B, intermedios (más de una estación, pero menos de un año); y C, largos (un año o más). La recta indica una correlación significativa con el tiempo (véanse los resultados). En las figuras 1s y 2s del material suplementario se ilustran los efectos significativos de la edad, los métodos y el origen de los individuos.

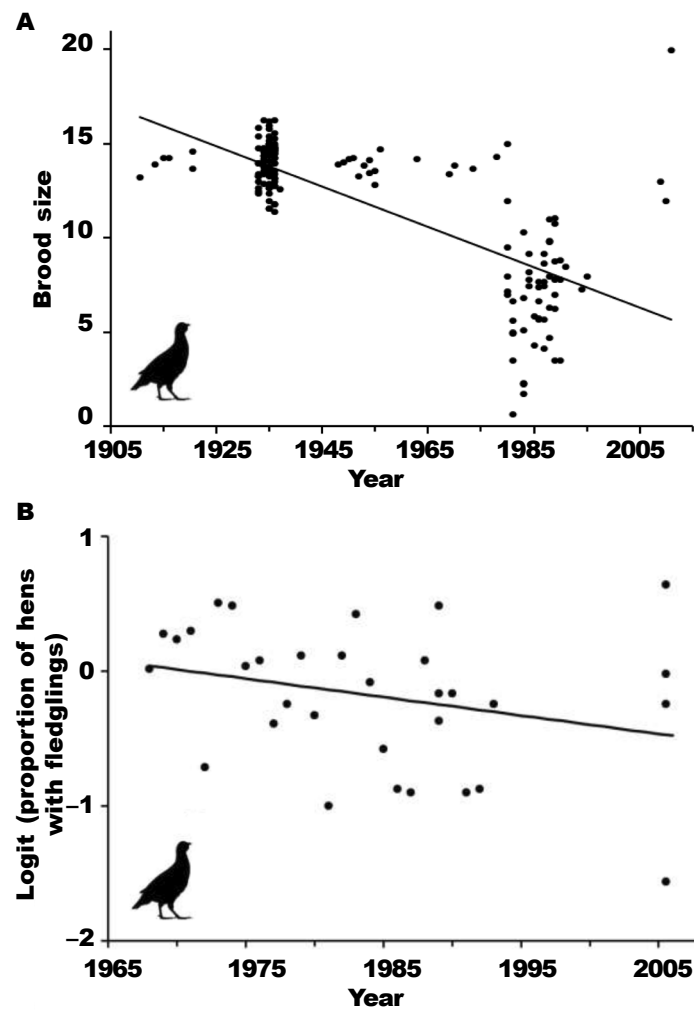


Fig. 2. Estimates in grey partridge in Europe of: A, average brood size; and B, proportion (logit transformed) of hens with fledglings over time. The line indicates a significant correlation with time (see results). See figure 3s in supplementary material for the significant effect of season of study and monitoring method

Fig. 2. Estimación, relativa a la perdiz pardilla en Europa de: A, el tamaño medio de puesta; B, la proporción (transformada logarítmicamente) de hembras con pollos a lo largo del tiempo. La recta indica una correlación significativa con el tiempo (véanse los resultados). En la figura 3s del material suplementario se ilustra el efecto significativo de la temporada de estudio y del método de seguimiento.

significant effect (table 5). Adjusted R^2 of the model on mortality rate was 0.78.

Reproduction

Controlling for the effect of country, we observed that the proportion of hens that raised fledglings increased with time in a nonlinear way from 1976 to 2000 (time²: $\beta \pm SE = 0.003 \pm 0.004$; time: $\beta \pm SE = -12.26 \pm 16.42$; fig. 6A; table 5).

Controlling for the effects of country, method and season, we found that the overall decrease in the number of fledglings per female with time from 1975

to 2009 (time: $\beta \pm SE = -0.06 \pm 0.01$; fig. 6B; table 5) was affected by country (fig. 5s in supplementary material). The number of fledglings per female increased with time in Norway ($\beta \pm SE = 0.19 \pm 0.09$), but decreased in France, Scotland and Slovakia (fig. 5s in supplementary material). Adjusted R^2 of the two models was 0.47 and 0.63, respectively.

Brown hare

Mortality rates for brown hare were collected from seven papers that referred to intermediate and long

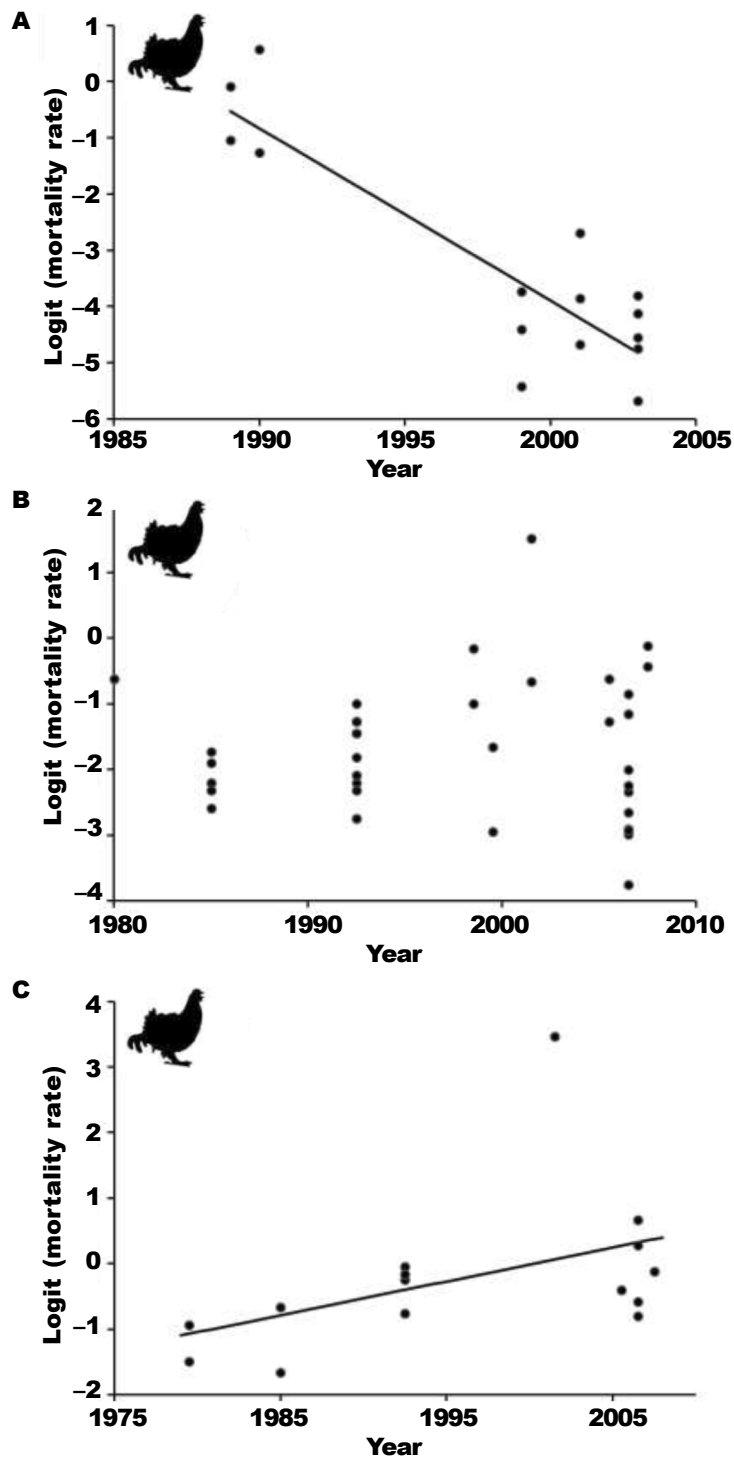


Fig. 3. Estimates of mortality rate (logit transformed) of black grouse over time (average years) in Europe for: A, short (one season or less); B, intermediate (from one season to less than one year); and C, long monitoring periods (greater than or equal to one year). The line indicates a significant correlation with time (see results).

Fig. 3. Estimación de la tasa de mortalidad (transformada logarítmicamente) del gallo lira a lo largo del tiempo (promedio de los años) en Europa para periodos de seguimiento: A, cortos (una estación o menos); B, intermedios (más de una estación, pero menos de un año); y C, largos (un año o más). La recta indica una correlación significativa con el tiempo (véanse los resultados).

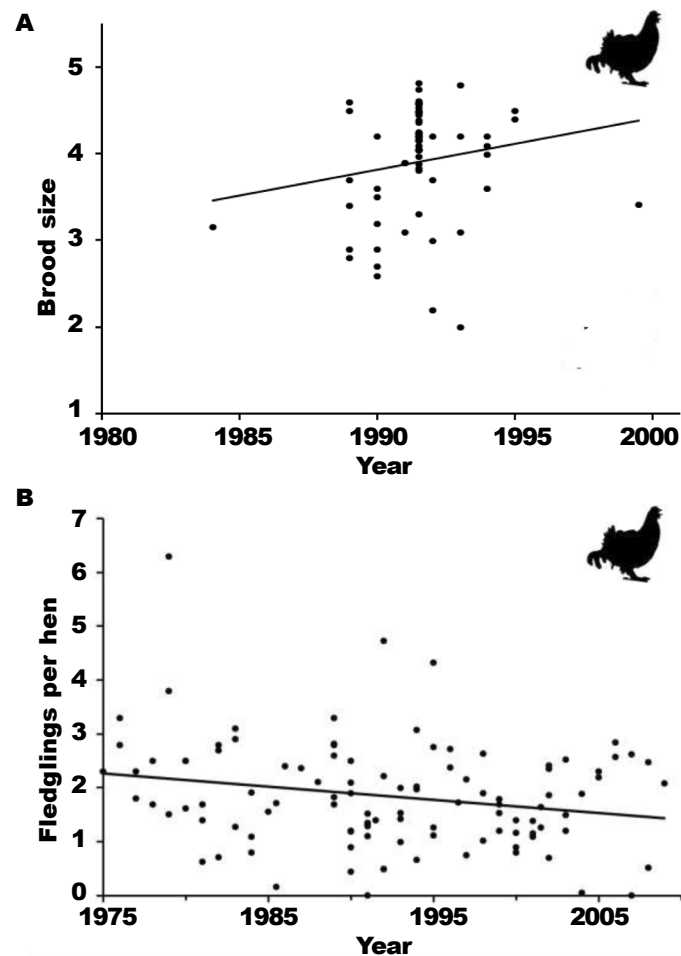


Fig. 4. Estimates, in black grouse in Europe of: A, average brood size; and B, average number of fledglings per hen over time. The line indicates a significant correlation with time (see results).

Fig. 4. Estimación, relativa al gallo lira en Europa, de: A, el tamaño medio de puesta; y B, la media de pollos por hembra a lo largo del tiempo. La recta indica una correlación significativa con el tiempo (véanse los resultados).

monitoring periods. The lowest and highest mortality rates were 0.12 (Frylestam, 1979) and 0.94 (Wasilewski, 1991) (both in intermediate monitoring periods).

Controlling for age, season and country, we found that mortality rates of brown hare in intermediate monitoring periods seemed stable between 1966 and 1989 (fig. 7A, table 5) although this link was affected by age. The mortality of young hare increased over time ($\beta \pm SE = 0.13 \pm 0.03$) while the mortality of adults decreased ($\beta \pm SE = -0.05 \pm 0.03$) (fig. 6s in supplementary material).

Mortality rates in long monitoring periods appeared stable between 1959 and 2007 (fig. 7B) while none of the control factors appeared significant (age, sex, country, method; table 5). Adjusted R^2 of the model on mortality rates was 0.71.

Discussion

Variation of demographic traits over time

Grey partridge and black grouse were the species for which data most consistently indicated an alteration in their demographic traits over time. In grey partridge, the decrease in reproductive traits (fig. 2) and the increase in annual mortality over time from long monitoring studies (fig. 1) supports the observed European decrease in population reported in the literature (e.g. Kuijper et al., 2009). The results showed that post-hatching brood size appeared stable between 1910 and 1980 but that reproductive success seemed to collapse from the 1980s (be discussed below). In black grouse, annual mortality rates from long monitoring studies increased between 1980 and 2008

Table 4. Results regarding the links between demographic traits and time in Black grouse *Tetrao tetrix*: factors, F -values and p -values.

Tabla 4. Resultados relativos a la relación entre los parámetros demográficos y el tiempo para el gallo lira *Tetrao tetrix*: factores y valores F y p .

Mortality rates		Reproduction	
Short monitoring periods		Brood size	
Time	$F_{1,7} = 46.84, p < 0.01$	Time	$F_{1,53} = 12.63, p < 0.001$
Age	$F_{2,7} = 3.16, p = 0.09$	Method	$F_{1,53} = 4.92, p = 0.03$
Method	$F_{1,7} = 1.55, p = 0.24$	Country	$F_{4,53} = 19.43, p < 0.001$
Country	$F_{2,7} = 2.43, p = 0.14$	Season	$F_{2,53} = 27.84, p < 0.001$
Season	$F_{2,7} = 0.87, p = 0.37$	Number of fledglings per female	
Intermediate monitoring periods		Time	$F_{1,91} = 5.22, p = 0.02$
Time	$F_{1,33} = 0.30, p = 0.59$	Method	$F_{1,91} = 2.32, p = 0.13$
Age	$F_{2,33} = 5.56, p < 0.01$	Country	$F_{6,91} = 1.83, p = 0.10$
Sex	$F_{2,33} = 2.45, p = 0.10$	Season	$F_{3,91} = 1.71, p = 0.17$
Method	$F_{1,33} = 11.00, p < 0.01$	Age	$F_{2,91} = 1.52, p = 0.23$
Country	$F_{5,33} = 1.26, p < 0.001$		
Long monitoring periods			
Time	$F_{1,3} = 11.46, p = 0.01$		
Age	$F_{2,3} = 2.81, p = 0.11$		
Sex	$F_{2,3} = 23.65, p < 0.001$		
Method	$F_{2,3} = 0.79, p = 0.48$		
Country	$F_{4,3} = 21.21, p < 0.001$		

(fig. 3). Moreover, post-hatching brood size seemed to increase between 1989 and 1995, contrasting with a decrease in the average number of fledglings per female (fig. 4), suggesting a reduction in chick survival. Overall, these results agree with the past population decreases reported for this species (Storch 2007; Ludwig et al., 2008; Sim et al., 2008).

The other species, capercaillie and brown hare, gave fewer clues about population decreases. Capercaillie annual mortality seemed stable between 1985 and 2002 (fig. 5), although the small amount indicated the observed pattern should be interpreted with caution. The proportion of females with fledglings may have increased between 1977 and 1999, while this pattern was balanced by a decrease in the number of fledglings per female from 1975 to 2009 (fig. 6). With such contrasting results, it is hard to highlight an overall European pattern in capercaillie populations. Previous studies highlighted predictions that depended on the structural assumptions of the models in this species in Finland (Kangas and Kurki, 2000). Nevertheless, some authors have claimed from population modelling that populations might decline when the mortality rates does not compensate for low reproductive success or recruitment (Fernández-

Olalla et al., 2012). This hypothesis is supported by recent studies in a population of capercaillie affected by marten species (*Martes martes* and *M. foina*) (Moreno-Opo et al. 2015).

In brown hare, we were unable to analyse the importance of changes in reproductive traits. Some studies have reported that adult survival is relatively constant (in non-hunted areas in the absence of disease outbreaks) and that breeding success can vary between sites and years (Marboutin and Peroux, 1995; Marboutin and Hansen, 1998; Marboutin et al., 2003). However, the low amount of data, the apparent stability of mortality, and the age-dependent pattern suggested by the results (fig. 6s in supplementary material) prevent clear conclusions on the strength of the decline reported since the 1960s (Edwards et al., 2000). In addition, studies reporting an overall population decline in brown hare rely on hunting bags as a proxy of population abundance, which may be rather hazardous. Indeed, hunting bag dynamics do not necessarily match abundance dynamics in game species because of, for instance, voluntary hunting restraint, saturation effects or hunting legislation changes (Sarasa and Sarasa, 2013; Kahlert et al., 2015).

Table 5. Results of the links between demographic traits and time in capercaillie *Tetrao urogallus* and in Brown hare *Lepus europaeus*: factors, F -values and p -values.

Tabla 5. Resultados relativos a la relación entre los parámetros demográficos y el tiempo para el urogallo *Tetrao urogallus* y la liebre europea *Lepus europaeus*: factores y valores F y p .

Mortality rates of capercaillie		Reproduction of capercaillie	
Intermediate monitoring periods		Proportion of hens that raised fledglings	
Time	$F_{1,18} = 8.06, p < 0.01$	Time	$F_{1,49} = 1.96, p = 0.17$
Time x age	$F_{1,18} = 9.98, p < 0.01$	Time ²	$F_{1,49} = 12.41, p < 0.001$
Age	$F_{1,18} = 21.38, p < 0.001$	Country	$F_{3,49} = 11.69, p < 0.001$
Sex	$F_{1,18} = 0.44, p = 0.52$	Number of fledglings per female	
Country	$F_{1,18} = 18.83, p < 0.001$	Time	$F_{1,122} = 12.33, p < 0.001$
Season	$F_{1,18} = 7.98, p = 0.08$	Time x country	$F_{3,122} = 6.12, p < 0.001$
Long monitoring periods		Method	$F_{1,122} = 0.45, p = 0.51$
Time	$F_{1,9} = 0.29, p = 0.60$	Country	$F_{3,122} = 39.34, p < 0.001$
Age	$F_{1,9} = 0.00, p = 0.97$	Season	$F_{3,122} = 13.19, p < 0.001$
Sex	$F_{1,9} = 0.03, p = 0.87$		
Country	$F_{1,9} = 1.51, p = 0.26$		
Mortality rates of brown hare		Mortality rates of brown hare	
Intermediate monitoring periods		Long monitoring periods	
Time	$F_{1,31} = 0.01, p = 0.91$	Time	$F_{1,1} = 3.09, p = 0.11;$
Time x age	$F_{2,31} = 9.86, p < 0.001$	Age	$F_{1,1} = 1.64, p = 0.23;$
Age	$F_{2,31} = 28.11, p < 0.001$	Sex	$F_{2,1} = 1.99, p = 0.19$
Season	$F_{1,31} = 8.06, p < 0.01$	Country	$F_{3,1} = 1.72, p = 0.24$
Country	$F_{2,31} = 0.73, p = 0.49$	Method	$v_{3,1} = 1.72, p = 0.24$

Explanatory factors

The decrease in annual survival rates in grey partridge and black grouse might be triggered by habitat changes (Berg 1997; Stoate et al., 2001; Panek 2002; Benton et al., 2003). The observed patterns with time are consistent with the homogenisation reported in farmland systems during agriculture intensification (Benton et al., 2002; Wretenberg et al., 2006). Reduction or removal of hedges that formerly fragmented the fields has been reported as an important factor in grey partridge population decline, by increasing predation rates of nests, chicks and adults, and reducing arthropod density and thus chick food availability (Potts, 1980, 1986; Rands, 1985, 1987; Kaiser, 1998; Šálek et al., 2004; Holland et al., 2006). In addition, direct and indirect effects of pesticides (e.g. neonicotinoids) on wildlife (Goulson, 2013; Gibbons et al., 2015; Pisa et al., 2015; Van der Sluijs et al., 2015) including farmland birds (Boatman et al., 2004; Lopez-Antia et al.,

2013; Hallmann et al., 2014; Lopez-Antia et al., 2015) have been reported particularly regarding to the massive use of neonicotinoids after 1990 (Simon-Delso et al., 2015). The drastic drop in post-hatching brood size in grey partridge in the 1980s (fig. 2A) points out the sudden appearance of a major destabilising factor rather than to progressive changes in the ecological interactions. This might be a consequence of an abrupt intensification of agriculture (wide re-parcelling, scrapping of edges and scattered trees, rise of oilseed rape, use of pesticides and inorganic fertilizers) occurring in the 1980s in Europe (Chamberlain, 2000; Plieninger, 2012). This illustrative example should be considered in further agri-environmental schemes. For instance, with adaptive measures (restriction or banning of problematic pesticides, increase in edge abundance, artificial feeding and predator control), the density of grey partridge in August can even be quadrupled (Fragó, 2001). On the contrary, studies have pointed out that too small cover trips or an

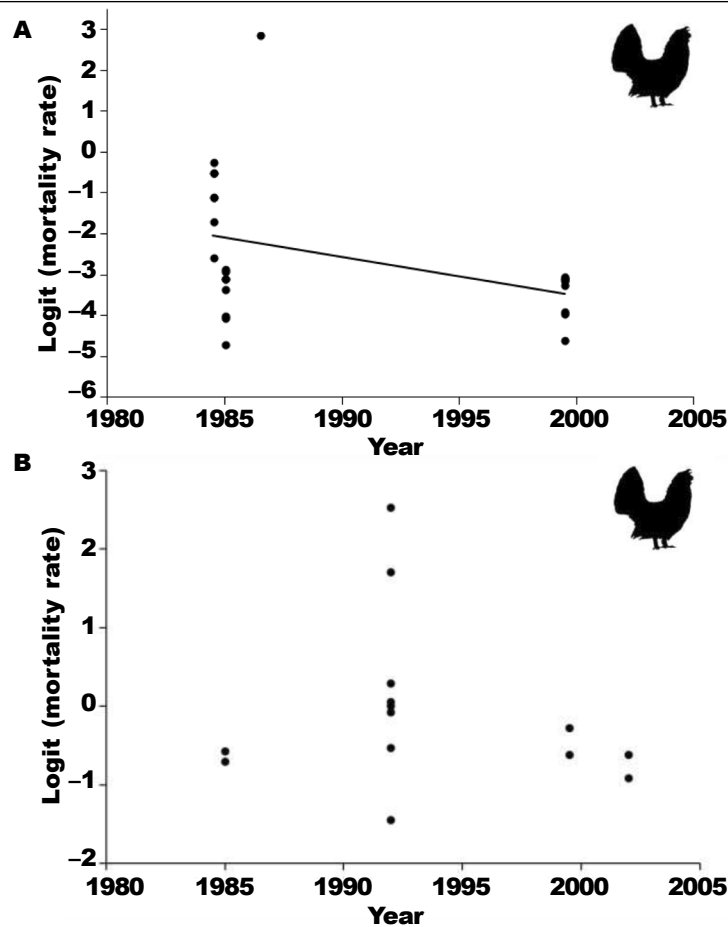


Fig. 5. Estimates of mortality rate (logit transformed) of capercaillie over time (average years) in Europe for: A, intermediate (from one season to less than one year); and B, long monitoring periods (greater than or equal to one year). The line indicates a significant correlation with time (but see figure 4s in supplementary material for the age effect).

Fig. 5. Estimación de la tasa de mortalidad (transformada logarítmicamente) del urogallo a lo largo del tiempo (promedio de los años) en Europa para periodos de seguimiento: A, intermedios (más de una estación, pero menos de un año); y B, largos (un año o más). La recta indica una correlación significativa con el tiempo (en la figura 4s del material suplementario se ilustra el efecto de la edad).

inadequate amount of cover trips at the landscape scale might be associated with an increase of predation rates (Bro et al., 2004). These contrasted results in several countries (Faragó, 2001; Bro et al., 2004; Ewald et al., 2010) suggest that further studies are needed to understand ecological and landscape drivers of populations dynamics in grey partridge.

Black grouse and capercaillie seem to be highly influenced by land cover (Storaas and Wegge, 1987; Wegge and Rolstad, 2011; Seibold et al., 2013; White et al., 2013) (including via resource availability), especially chick survival which is particularly dependent on the abundance of insects (Picozzi et al., 1999; Ludwig et al., 2010). Nevertheless, their populations appear to respond differently to habitat changes, which could

explain the difference in observed patterns between the two species in our results. The clear-cutting of forest and its replacement by young plantations may have contrasted and un-expected effects on abundance and sex-ratio of black grouse and capercaillie in August, whereas similar positive effects on the number of young per hen were observed in Sweden in the two species (Wegge and Rolstad, 2011). Habitat homogenisation might also have a strong impact on populations. For instance, black grouse selects transitional habitats (moors, heaths, meadows, young and open forests), which have been massively converted into farmland and mature forest during recent decades (Pearce-Higgins et al., 2007; Ludwig et al., 2009a, 2009b). Black grouse may benefit from habitat

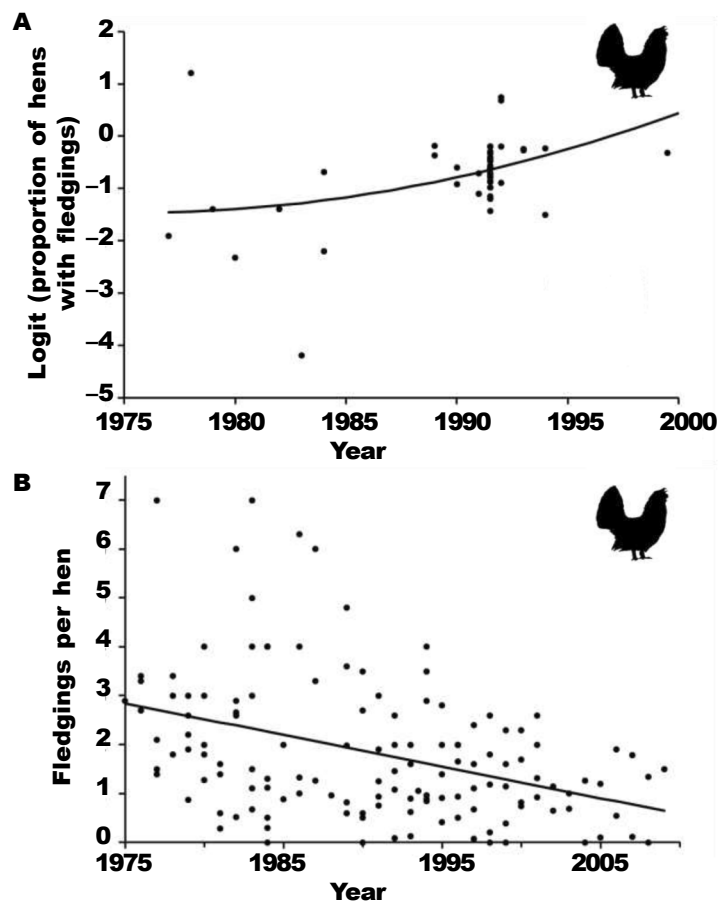


Fig. 6. Estimates related to capercaillie in Europe regarding: A, proportion of hens with fledglings (logit transformed); and B, average number of fledglings per hen over time. (See figure 5s in supplementary material for the significant effect of country).

Fig. 6. Estimación, relativa al urogallo en Europa, de: A, la proporción (transformada logarítmicamente) de hembras con pollos; y B, la media de pollos por hembra a lo largo del tiempo. (En la figura 5s del material suplementario se ilustra el efecto significativo del país).

changes as early stages of trees provide food and nest sites (Scridel et al., 2017). In contrast, capercaillie selects for mature forest although the importance of habitat matrix including key resources should not be neglected (Quevedo et al., 2006a, 2006b; Teuscher et al., 2011). The reported agricultural abandonment and reforestation in mountain areas during the last century, such as in the Alps and the Pyrenees (MacDonald et al., 2000; Lasanta-Martínez et al., 2005; Caplat et al., 2006; Agnoletti, 2007; Kulakowski et al., 2011), have probably disadvantaged populations of black grouse while favouring capercaillie. Incidentally, we did not find any clear support of an overall decline in this latter species. Thus, demographic traits and abundance estimates need to be updated for the reappraisal of the dynamics of forest grouse, particularly capercaillie, in European countries.

The opposing patterns in mortality rates for different lengths of monitoring period in grey partridge and black grouse might appear contradictory at first sight. However, the three monitoring periods underline different information. Mortality data from short monitoring periods corresponded mostly to the breeding season and thus chick mortality. Chick survival seemed unable to explain the observed decline between 1968 and 1993 in England (Potts and Aebischer, 1995), while other studies reported that it was crucial in the understanding of the population dynamics in grey partridge (Potts, 1980, 1986; Topping et al., 2010). This could agree with the decrease in mortality rates in shorter monitoring periods (fig. 1A) while populations declined. However, this finding may also suggest that the main studied season (spring–summer) does not have a major effect on the decline and that processes

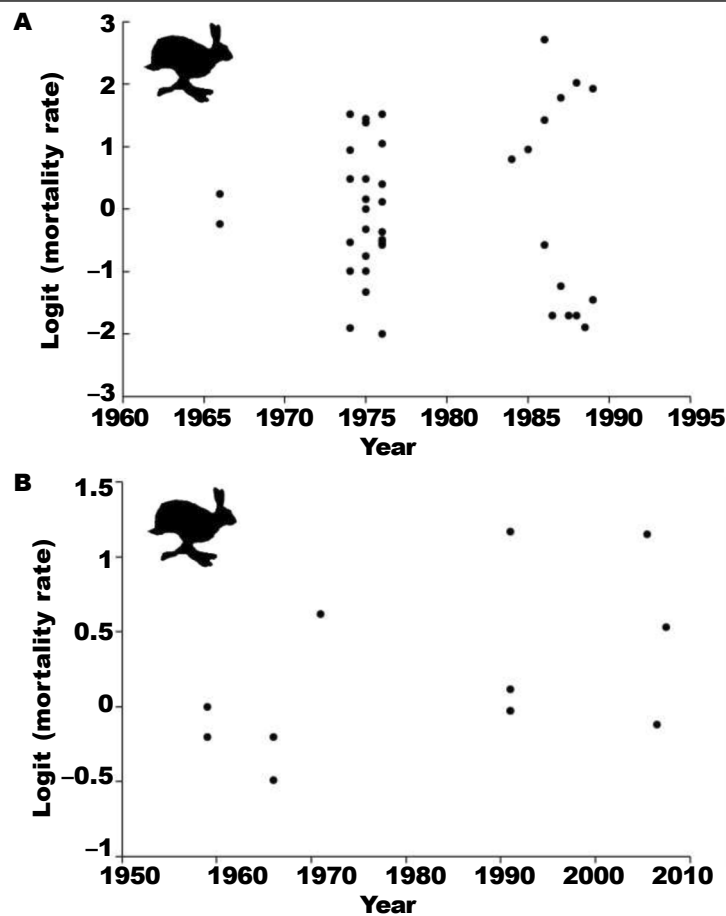


Fig. 7. Estimates of mortality rate (logit transformed) of brown hare over time (average years) in Europe for: A, intermediate (from one season to less than one year); and B, long monitoring periods (greater than or equal to one year). (See figure 6s in supplementary material for the significant effect of the interaction time \times age).

Fig. 7. Estimación de la tasa de mortalidad (transformada logarítmicamente) de la liebre europea a lo largo del tiempo (promedio de los años) en Europa para periodos de seguimiento: A, intermedios (más de una estación, pero menos de un año); y B, largos (un año o más). (En la figura 6s del material suplementario se ilustra el efecto significativo de la interacción entre el tiempo y la edad).

occurring in autumn–winter should be studied further. In forest grouse, most studies attributed the population decline to a reduced recruitment of young (Kurki et al., 1997; Storch, 2007; Ludwig et al., 2009a; Summers et al., 2010), a mortality of adults (Caizergues and Ellison, 1997) or both adults and fledged young (Wegge and Rolstad, 2011). Our study suggests that reproduction is the demographic trait that is the most consistent with the demographic decline of grouse. The two proxies suggesting reproductive patterns indicated a decrease in black grouse (fig. 4), whereas they were contrasted in capercaillie (fig. 6), for which it is hazardous to infer a demographic evolution. Mortality patterns in black grouse also support the idea of a population decrease, as mortality seemed to increase

for longer monitoring periods (fig. 3C). However, this was not the case in capercaillie (fig. 5B).

During the last decades, hunting management has become increasingly restrictive (Angulo and Villafuerte, 2004; Čas, 2008; Ministère de l'Écologie du Développement durable des Transports et du Logement, 2012; Ikonen et al., 2014) and abundance of small game hunters was reported as rather decreasing (Lecocq and Meine, 1998). Thus, absolute hunting pressure on small game species is expected to have decreased during this recent period. Hunting bans have already been highlighted to limit incentives from hunters and landowners for wildlife monitoring although habitat preservation is ultimately needed for sustainability of small game species (Storch, 2007; Čas, 2008). Thus,

this overall situation and our results might emphasize the urgency of addressing further the predominant factors in these species, such as habitat (Evans, 2004; Whittingham and Evans, 2004; Scridel et al., 2017).

Limitations of the analysis

Several limitations might affect the present study. First, if articles that reported past declines (Sirkiä et al., 2010) rather than stable or recent increasing populations (Aebischer and Ewald, 2012; Scridel et al., 2017) were more likely published, a pessimistic appraisal of European dynamics in wild species might be highlighted. In addition, data from studies that use successive counts of the number of individuals are prone to the effects of confounding factors (e.g. detectability problems, migration events) (Thompson, 2002). Moreover, the use of radio-collars makes individual-based studies possible but might affect survival and reproduction (Putaala et al., 1997; Caizergues and Ellison, 1998; Mech and Barber, 2002; Barron et al., 2010; Gibson et al., 2013). Both monitoring techniques have a different bias, but radio-collars have mainly been used since the 1980s, implying a possible shift in bias over time (Barron et al., 2010; Naef-Daenzer and Gruebler 2014). Miniaturisation in biotelemetry is expected to provide more accurate estimates of demographic traits in future studies that will use lighter transmitters (< 3 % of the bird's weight) (Casas et al., 2015). Concerning reproductive traits, the number of fledglings per female is reported heterogeneously across the literature (chicks almost old enough to fly and young), which might also involve a bias. Data on mortality and reproduction in four small game species including wild rabbit, hazel grouse, pheasant and red-legged partridge are rare and thus prevent robust statistical analyses.

We attempted to control for a part of the variability in mortality and reproduction data including factors such as age, method, season, sex, origin and country in our models. Efforts to homogenise demographic traits in further studies, particularly proxies of reproductive success, could strengthen future reappraisals of the literature.

Our data sets included spatial heterogeneity. For example, in grey partridge, most of data in reproduction traits ($n = 580$) came from studies investigating populations in England (73.4%) and actually few articles existed from populations in France (11.0%), Poland (10.3%), or other countries (5.2% together). Such disparities also occurred in black grouse, capercaillie and brown hare and should alert on the challenge to address scenario on expected future decline at the scale of distribution area.

In addition, a temporal heterogeneity is present between and within species. For instance, data available on the mortality in grey partridge ranged from 1917 to 2011; however, there were few data before 1970 for intermediate and longer monitoring periods. An insufficient number of data related to reproduction was available in grey partridge after 1995. Capercaillie and black grouse seem to be rather recently studied species with no data on reproduction and mortality rates before 1975 while data are rather scarce after

2005 in these two species. This lack of information prevents an accurate, updated analysis of recent population dynamics.

Conclusion

The present study suggests that data from demographic parameters (mortality and reproductive traits) extracted from published articles might be used to investigate population trends with time. The effects of age, sex, origin of birds, season, country and method on demographic traits should encourage further studies to consider these factors in their experimental design to avoid misleading findings regarding potential patterns. For instance, methodological issues might arise from animal equipment that would affect survival and reproduction rate. Similar comments can be addressed for the effect of the monitoring period, particularly when investigating mortality rates. Although it is not the case in capercaillie and brown hare, our study seems to support the overall decrease that has been reported in grey partridge and black grouse during the last decades. Although black grouse, capercaillie, brown hare and grey partridge were relatively well-studied species, studies from the last 10–20 years on demographic traits are scarce or lacking, hampering the understanding of ongoing demographic processes and current status of species. Thus, long-term studies including recent publications in peer-reviewed journals are needed to investigate the links between mortality, reproduction and density, predation, and habitat changes.

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Supplementary material

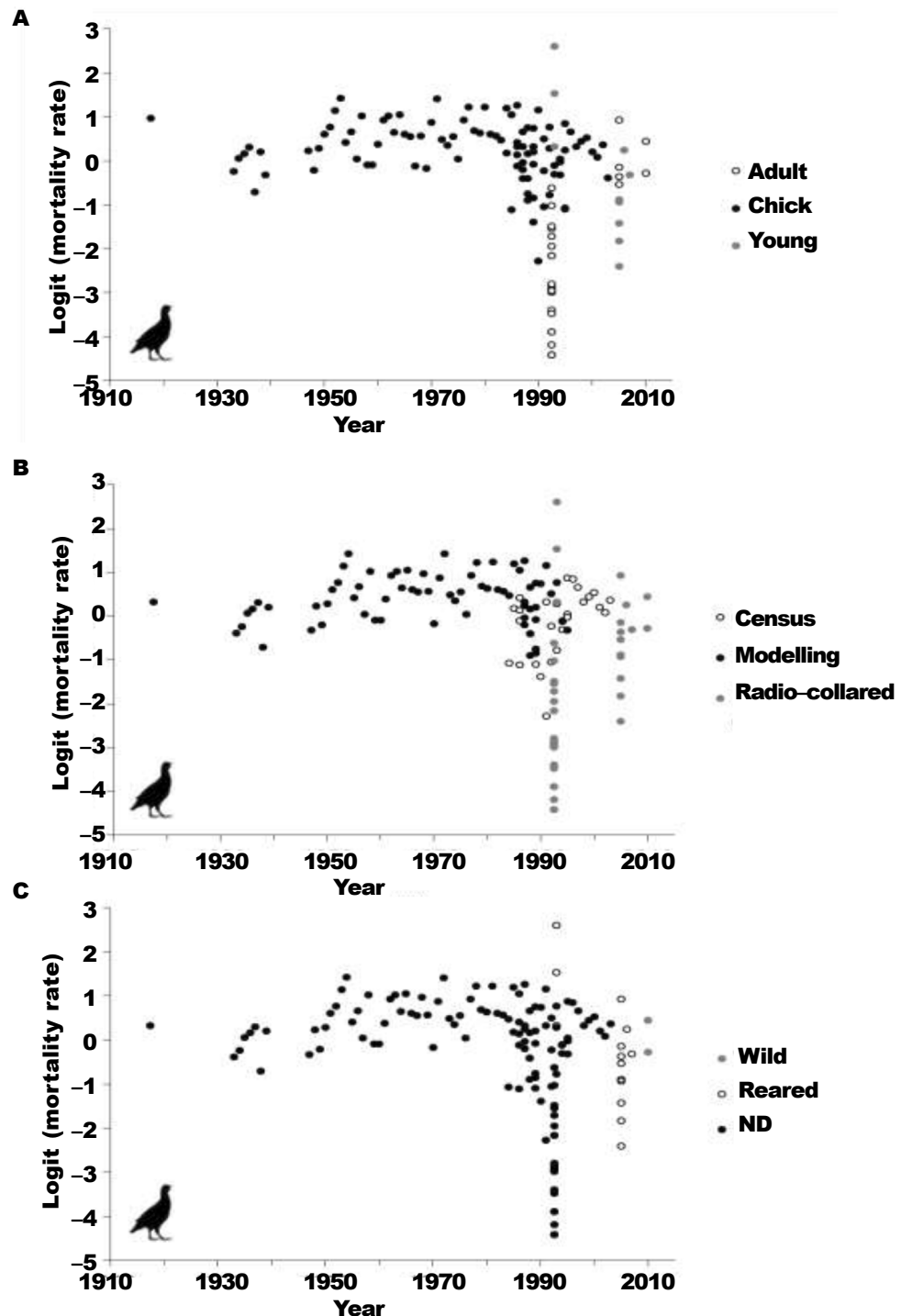


Fig. 1s. Estimates of mortality rate (logit transformed) of grey partridge over time in shorter monitoring periods in relation to: A, age; B, method; and C, origin of birds. ND, not determined.

Fig. 1s. Estimación de la tasa de mortalidad (transformada logarítmicamente) de la perdiz pardilla a lo largo del tiempo (año promedio) para periodos cortos en relación con: A, la edad; B, el método de estimación; y C, el origen de las aves. ND, no determinado.

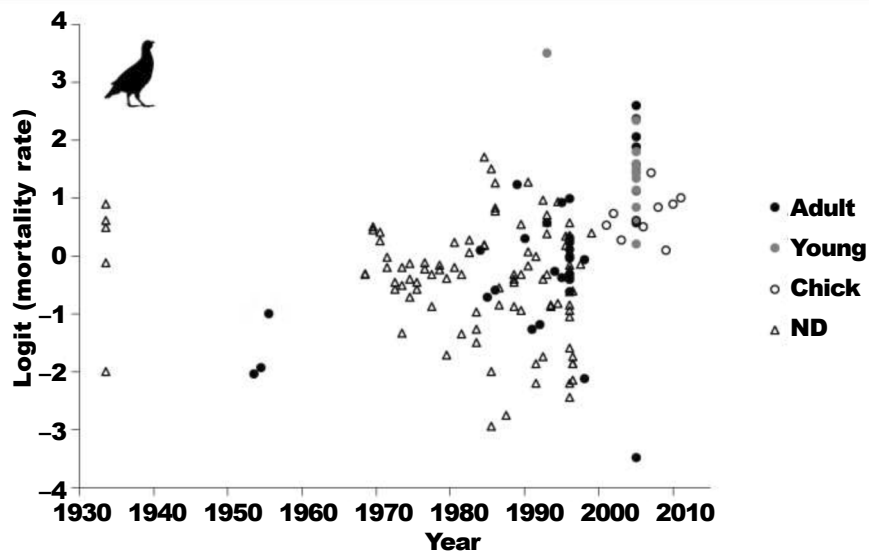


Fig. 2s. Estimates of mortality rate (logit transformed) of grey partridge over time in intermediate monitoring periods in relation to age of birds: ND, not determined.

Fig. 2s. Estimación de la tasa de mortalidad (transformada logarítmicamente) de la perdiz pardilla a lo largo del tiempo (año promedio) para periodos intermedios en relación con la edad de las aves: ND, no determinado.

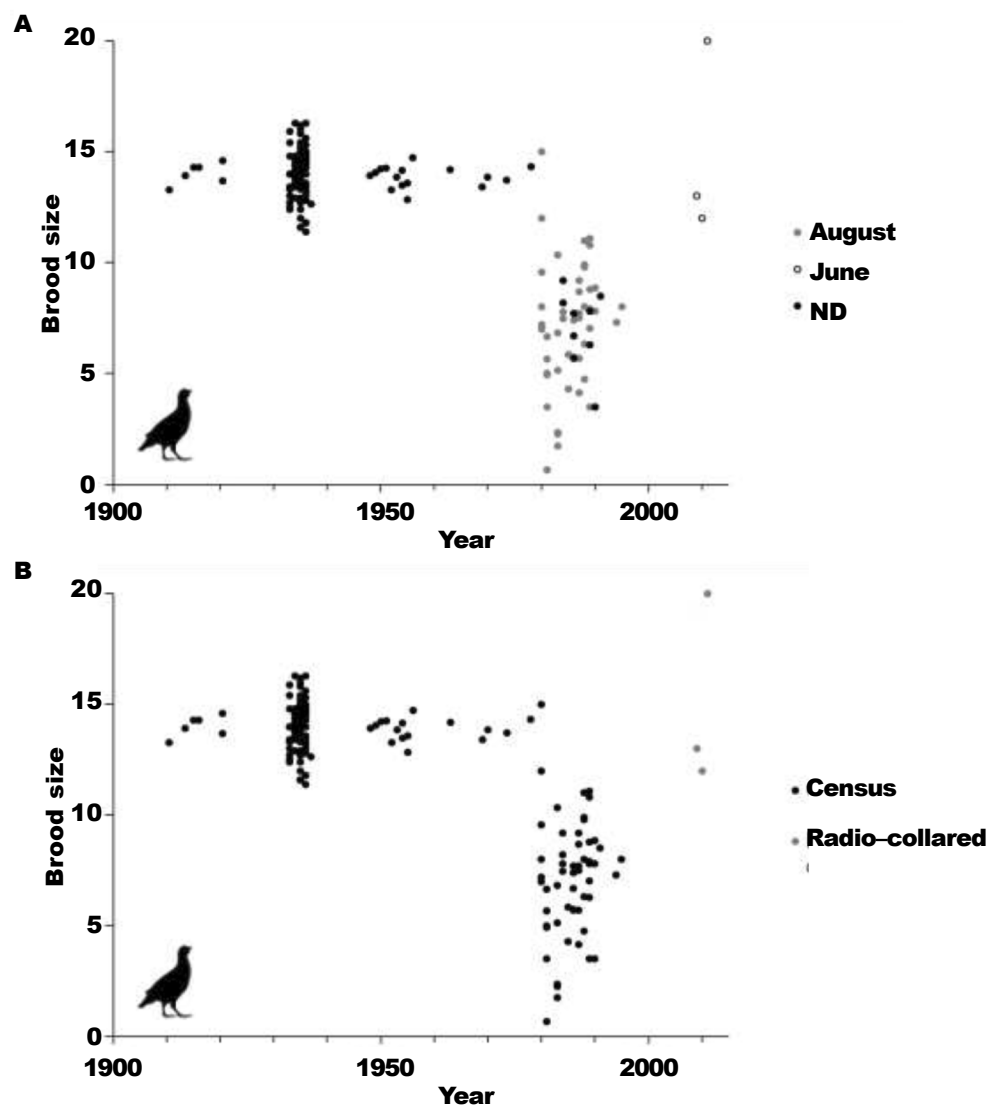


Fig. 3s. Estimates, in grey partridge of average brood size over time and in relation to: A, season of study; and B, monitoring method. ND, not determined.

Fig. 3s. Estimación, relativa a la perdiz pardilla, del tamaño medio de puesta a lo largo del tiempo y según: A, la temporada de estudio; y B, el método. ND, no determinado.

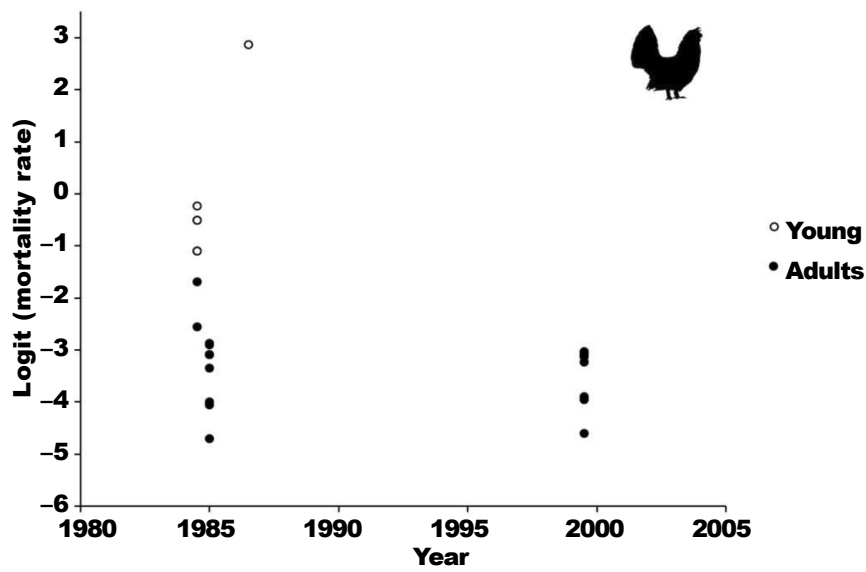


Fig. 4s. Estimates of mortality rate (logit transformed) of capercaillie over time (average years) in intermediate monitoring periods in relation to age.

Fig. 4s. Estimación de la tasa de mortalidad (transformada logarítmicamente) del urogallo a lo largo del tiempo (promedio de los años) en periodos intermedios y según la edad.

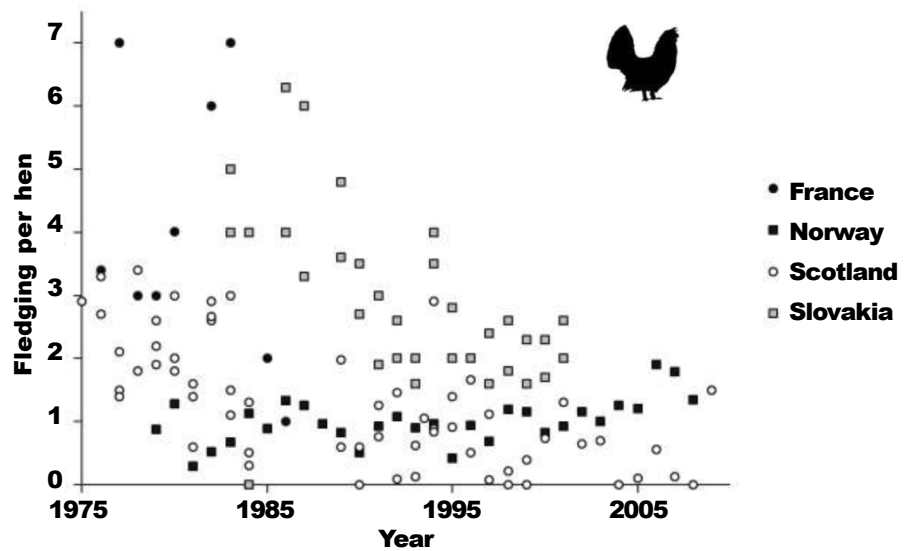


Fig. 5s. Estimates, in capercaillie, of average number of fledglings per hen over time in different countries.

Fig. 5s. Estimación, relativa al urogallo, de la media de pollos por hembra a lo largo del tiempo y según el país.

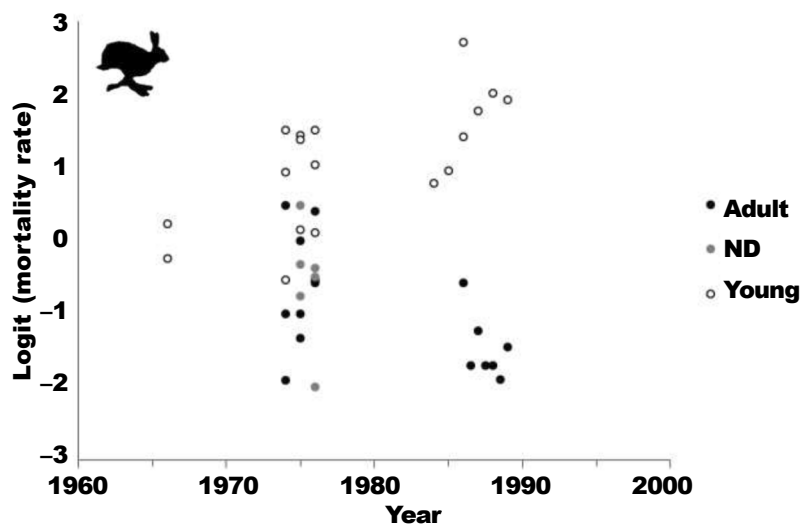


Fig. 6s. Estimates of mortality rate (logit transformed) of brown hare over time (average years) for intermediate monitoring periods in relation and according to age: ND, not determined.

Fig. 6s. Estimación de la tasa de mortalidad (transformada logarítmicamente) de la liebre europea a lo largo del tiempo (promedio de los años) para periodos intermedios y según la edad: ND, no determinado.