

Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years

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Abstract

Declines in populations of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrrix*) have been reported from both Central Europe and the continuous boreal forests of Fennoscandia. While intensified land-use is assumed to be the underlying cause of these declines, the mechanisms are not yet understood. Predation is the proximate cause of mortality of eggs, chicks and adults throughout capercaillie and black grouse ranges, but the link between predation and habitat and/or climate change remains unclear. To investigate temporal trends in reproductive output of woodland grouse, we collated previously published and unpublished data of reproduction in capercaillie and black grouse throughout their ranges from 1930 to 2012. We show that, overall, reproductive success has decreased and stabilized at low levels in most regions whilst capercaillie reproductive output in Scotland is still declining. With today's net reproduction, capercaillie and black grouse adult survival is too low to compensate for reproduction declines. Consequently, populations are expected to further decline unless reproductive performances improve. We put our findings in the context of changes in land use, climate and generalist predator numbers. By critically reviewing how these factors limit reproductive success in capercaillie and black grouse, we hope to shed light on the underlying mechanisms causing the decline. Our results imply that measures should be undertaken to reduce mortality of capercaillie and black grouse chicks and eggs. We suggest that future studies should aim to better understand which predators limit capercaillie and black grouse populations and how predation rates are mediated by continuously changing habitat and climate.

Keywords

Capercaillie; climate; decline; grouse; land use; predation; reproduction success; survival

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Introduction

Long-term declines in population densities of capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have been documented from continental Europe, the British Isles and throughout the continuous boreal forests of Fennoscandia (Wegge, 1979; Lindén & Rajala, 1981; Helle & Helle, 1991; Baines & Hudson, 1995; Moss et al., 2000; Lindén & Helle, 2003; Storch, 2007; Ludwig et al., 2008; Sirkiä et al., 2010). These declines began earlier in the southern than in the northern range (Lovel, 1979, and references therein). In addition, previously characteristic fluctuations in population size have diminished over the past 50 years (Ludwig et al., 2006).

Intensified land-use is considered to be the underlying cause of the declines in tetraonid populations but the mechanisms are not clearly understood. In the Fennoscandian context, intensified land-use refers primarily to the expansion of modern forestry which has been the focus of several studies (i.e. Lindén & Helle, 2003; Storch, 2007; Sirkiä et al., 2010). In continental Europe and Britain, land-use change also refers to the intensification of agriculture and changes in grazing pressure by livestock, as well as increased browsing by ungulates. Nonetheless, within the suite of processes accompanying the population decline and reduction in cyclic amplitude, climate change (Moss et al., 2001; Ludwig et al., 2006; Selås et al., 2011) and an increase in generalist predators (Baines, 1991; Vos, 1995; Kurki et al., 1998) are factors that may also contribute to the negative trends in European woodland grouse. To date, these factors have received comparatively little attention.

Since the 1930s, no studies in Fennoscandia have identified malnutrition or disease as major mortality factors in capercaillie or black grouse. However, chicks of both species may be vulnerable to low insect abundance because invertebrates are an important source of protein during the first couple of weeks after hatching (Rajala, 1959; Atlegrim & Sjöberg, 2008; Wegge & Kastdalen, 2008) and food limitation may predispose chicks to predation. Predation is the dominant proximate cause of losses of woodland grouse eggs, chicks and adults (Hagen, 1952; Hörnfeldt, 1978; Angelstam, 1984; Storaas & Wegge, 1987; Kurki et al., 1997; Borchtchevski et al., 2003; Wegge & Kastdalen, 2007; Ludwig et al., 2010; Wegge & Rolstad, 2011; Åhlen et al., 2013). Mammalian predation has also been shown, in both experimental and correlative studies, to play an important role in short-term grouse population dynamics in the sense that predators predominantly limit reproduction and thus population growth rates (Marcström et al., 1988; Lindström et al., 1994; Kurki et al., 1997; Kauhala et al., 2000; Summers et al., 2004).

Capercaillie and black grouse are sympatric forest dwelling species, but traditionally, they are perceived to have contrasting habitat preferences along the forest succession continuum. Capercaillie prefer older and climax conifer forest whilst black grouse prefer open forest of younger successional stages that also include peat-bogs, heaths, sub-alpine pastures, marshes and grasslands (Seiskari, 1962; Swenson & Angelstam, 1993; Ludwig et al., 2009). Given the wide distribution of capercaillie and black grouse, they can also be considered habitat generalists

within their respective niches, at least in the boreal forest of Fennoscandia (Lande & Herfindal, 2010; Sirkiä et al., 2011a, b; Lande et al., 2014). In that sense, habitat alteration induced by forestry does not necessarily result in a shared response between capercaillie and black grouse. In the central European lowlands and Britain however, capercaillie and black grouse habitat-ranges are comparably disjointed and less overlapping. This results in a more segregated pattern of local distributions of the two species.

Forestry has dramatically altered the coniferous forest throughout the past 80 years by clear-cutting practices, increased fragmentation and a shortening of the rotation of forest stands (Storch, 2007). Whilst the proximate cause of grouse mortality is predation, the underlying (i.e. ultimate) mechanisms that relate habitat quality to survival are less obvious. Habitat fragmentation and distortion of forest stand structure affect capercaillie and black grouse reproduction negatively (Kurki & Lindén, 1995; Kurki et al., 2000). In Scotland, forest maturation is suggested to accelerate black grouse declines by reducing brood-rearing and nesting habitat following canopy closure (Pearce-Higgins et al., 2007). These man-made habitat changes may also affect mortality indirectly by altering the distribution and composition of predators in the landscape (Borchtchevski et al., 2003). Likewise, changes in habitat can affect predator-prey relationships by making predators more efficient in locating and killing grouse through edge-related effects (Andren & Angelstam, 1988).

Capercaillie and black grouse broods select for certain habitat types (Wegge & Kastdalen, 2008), and a reduction in availability of these habitats may create ecological traps by increasing the search efficiency of predators (Storaas et al., 1999). In continental Europe and Britain, more than in the Fennoscandian countries, habitat fragmentation has isolated and separated populations from one another by non-habitat and woodland grouse habitats have continuously contracted over the past century. Consequently, the phenomenon of ecological traps may be present in these areas, not only in terms of brood-rearing but also during other phases of the grouse life cycle. Conversely, in Fennoscandia, fragmentation has divided and separated optimal forest habitat with less optimal forest habitat of a different successional stage but the overall extent of the Fennoscandian boreal forest has not changed in this time period (Östlund, 1997).

In Scandinavia, and probably the rest of Fennoscandia, there has been a 0.75 to 1.5°C increase in temperature since 1900, which has primarily arisen during two periods between 1900 and 1940 and since 1980. This is in line with the pattern of temperature increase in continental Europe and Britain (IPCC, 2013). Climate change can affect grouse reproduction indirectly because increasing variability in weather conditions may predispose chicks to increased predation, particularly during wet and cold weather (Wegge & Kastdalen, 2007). Climate change may also create a mismatch between the onset of seasons and important biological events like egg production or hatching of chicks (Moss et al., 2001; Ludwig et al., 2006). Furthermore, it is suggested that increasingly warm summers can negatively affect

reproduction in capercaillie indirectly by increasing herbivory deterrents in bilberry foliage (*Vaccinium myrtillus*) (Selås et al., 2011).

Corvids, certain raptors, especially goshawk (*Accipiter gentilis*) and common buzzard (*Buteo buteo*), and generalist mammalian predators are common throughout the distribution range of capercaillie and black grouse. The raccoon dog (*Nyctereutes procyonoides*) has fairly recently become common throughout central Europe and in Finland but is absent from parts of the woodland grouse range and has not yet established noteworthy populations in Sweden or Norway (Kauhala & Kowalczyk, 2011). In Sweden, a dramatic increase in the goshawk population was shown between the early 1940s and late 1990s whilst the common buzzard decreased in the same period (Kjellén & Roos, 2000). Grouse, and especially black grouse, are important prey for goshawks, but grouse chicks might be an alternative to small mammal prey for buzzards (Valkama et al., 2005).

Both red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) are regarded as important mammalian predators of forest dwelling grouse and their populations have increased since the early 1900s (Grakov, 1978; Krott & Lampio, 1983; Vos, 1995; Helldin, 2000; Selås & Vik, 2006) due to land-use changes, legal protection, an increase in prey-base and declines in fur prices. Predation caused by high densities of generalist predators can limit reproductive output of prey, reduce amplitude in prey population peaks, and reduce prey populations to a low and stable level (Erlinge et al., 1983; Hanski et al., 1991). This was evident in tetraonids during an outbreak of sarcoptic mange (*Sarcoptes scabiei*) in the Scandinavian red fox population during the late 1970s and 1980s, when capercaillie and black grouse densities increased and declined in synchrony with the appearance and disappearance of the mange (Lindström et al., 1994; Smedshaug et al., 1999).

In this study, we attempt to describe the long-term changes in reproductive output of capercaillie and black grouse throughout large parts of their range using data with varying temporality from the past 80 years. We also infer the consequences of today's net reproduction for the future status of their populations. We place our findings in the context of changes in land-use, climate and generalist predators and critically review how these factors limit reproductive success in capercaillie and black grouse in the hope of shedding light on the underlying mechanisms causing their decline. With the ever-present population declines in mind and the fact that grouse population dynamics are largely dependent on reproduction, we expect to find negative trends in nest success, proportion of hens with a brood and number of chicks per hen.

Material and methods

Data

We collated various time series of capercaillie and black grouse populations from within the period 1907–2014 from Fennoscandia and compared them with published trends from Britain and continental Europe. Population indices of capercaillie and

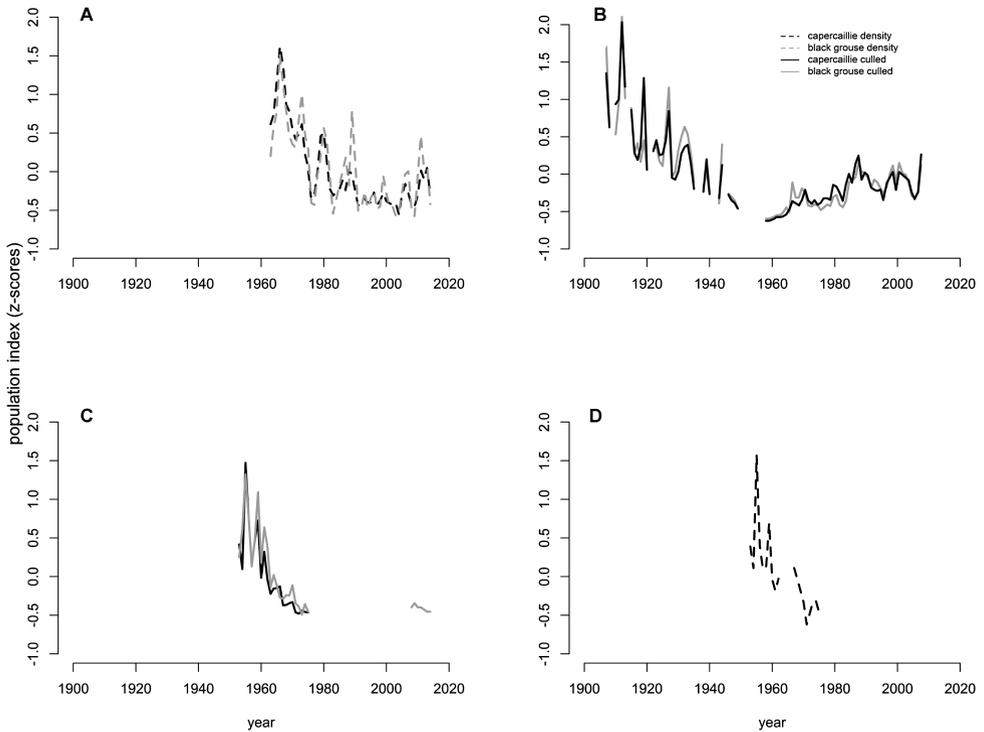


Figure 1. (A) Nationwide capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) density estimates from Finland 1964–2014. (B) Capercaillie and black grouse bagged in county of Dalarna, Sweden between 1907 and 2007. (C) Bagged capercaillie and black grouse in Hurdal municipality, Norway, in the years 1953–1975 and 2008–2014. (D) Capercaillie density in Vegårshei, Norway between 1953–1962 and 1967–1976. All values are z-scores (standardized).

black grouse from Finland were from nationwide density estimates between 1964 and 2014 (Helle & Ikonen, 2015). From Norway we had snippets of density estimates of capercaillie in Vegårshei municipality between 1953–62 and 1967–76, together with harvest data from Hurdal municipality for both species in the periods 1953–75 and 2008–14 (only black grouse was culled in the latter period) (Sørensen, 1977a, b; Wegge & Grasaas, 1977; Statistics Norway, 2016). From Sweden we collated harvest data for both species in Dalarna county between 1907 and 2007 (Mattson & Zakariasson, 2009; Danell et al., 2011) (fig. 1). Trends for black grouse in lowland Europe and Britain are presented in Ludwig et al. (2008) and Baines & Hudson (1995). Capercaillie trends in Scotland are described in Catt et al. (1998), Wilkinson & Langston (2002), Eaton et al. (2007). In fig. 2 we present a timeline of important processes occurring in Fennoscandia related to climate, forestry and predators during the investigation period.

In addition, we collated published and unpublished data from studies of nest success, proportion of hens with a brood and the number of chicks per hen (not to be confused with brood size) conducted in Fennoscandia, the British Isles and

Timeline of important events in Fennoscandia

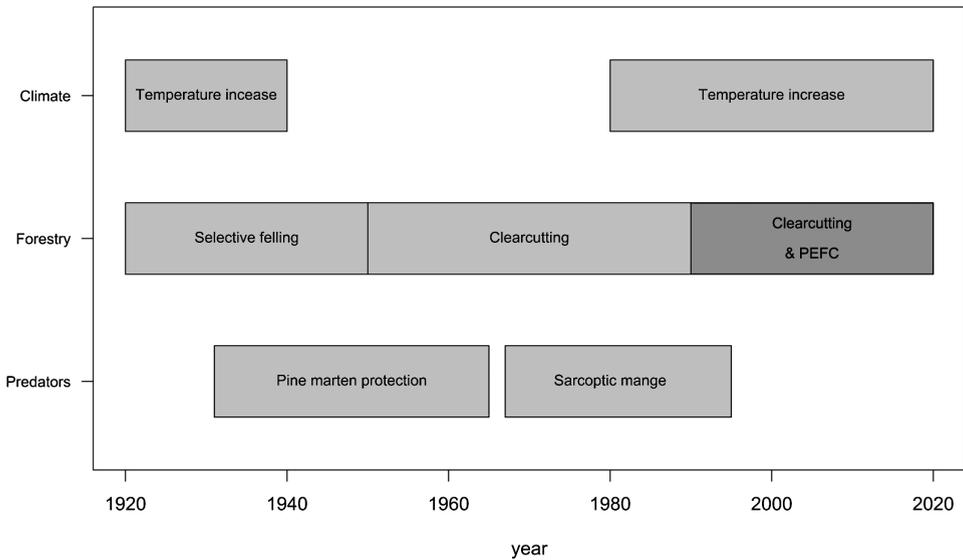


Figure 2. Overview of important processes in the boreal forests of Fennoscandia.

continental Europe between 1930 and 2012. Data were included from Finland, Karelia, Sweden, Norway, Scotland, England, Wales, Germany, Switzerland, Austria, France, Andorra, Estonia, Italy, Poland and Slovakia (tables A1-A3). Where data were presented graphically, we extracted them with GetData Graph Digitizer (2016). In total, capercaillie crude nest-success data (i.e. proportion successful to total nests found) spanned the period from 1930 to 2012 and included 17 studies from seven countries with 33 unique values of nest-success data. Black grouse nest-success data were available for 58 unique values from 18 studies in seven countries, conducted between 1932 and 2012. The proportion of hens with a brood were from 1934 for black grouse and 1946 for capercaillie to 2012 and included 16 studies with 143 unique values for capercaillie and 24 studies with 230 unique values for black grouse from seven and 10 countries, respectively. Numbers of chicks per hen were collated from 29 capercaillie and 33 black grouse studies in nine and 11 countries conducted between 1930 or 1934 and 2012 with 366 and 357 unique years, respectively. An overview of the data is shown in table 1.

Nests were primarily located in two ways across studies (see Appendix and references therein for more details of each study). Either birds were captured and fitted with radio transmitters, or nests were found by chance or actively searched for with pointing dogs. Systematic nest-searches also occurred in one study (Summers et al., 2009). Typically, nests located by radio-tracking females will give less biased estimates of nest success than nests found by chance or otherwise since nests found by chance rarely includes nests that are already predated (discussed further elsewhere). Radio transmitters, where fitted, were also used to assess the proportion of

Table 1.

Demographic variables used in the analysis, together with time span and number of unique years (N) per species and region. Apparent nest success (proportion of successful nests to total number of nests found), proportion of hens with brood (proportion of females with ≥ 1 chick in July/August) and chicks per hen ratio in July/August are shown. (See tables A1–A3 for details.)

| Region | Variable | Capercaillie | | | Black grouse | | |
|--------------------|-----------------|--------------|---------|-----|--------------|---------|-----|
| | | Time span | Studies | N | Time span | Studies | N |
| Fennoscandia | Nest success | 1930–2012 | 11 | 27 | 1932–2012 | 12 | 39 |
| | Hens with brood | 1946–2012 | 8 | 55 | 1946–2012 | 9 | 68 |
| | Chicks per hen | 1930–2012 | 17 | 197 | 1946–2012 | 15 | 166 |
| British Isles | Nest success | 1950–2007 | 3 | 3 | 1935–2004 | 3 | 12 |
| | Hens with brood | 1976–2012 | 3 | 34 | 1934–2002 | 6 | 42 |
| | Chicks per hen | 1975–2012 | 6 | 89 | 1934–2009 | 8 | 66 |
| Continental Europe | Nest success | 1971–2001 | 3 | 3 | 1977–1998 | 3 | 7 |
| | Hens with brood | 1976–2010 | 5 | 54 | 1970–2007 | 9 | 120 |
| | Chicks per hen | 1976–2010 | 6 | 80 | 1970–2007 | 10 | 125 |

hens with a brood in late summer (July/August) or this was assessed by line transects, wildlife triangle censuses and in some studies, broods detected by chance in relation to other field work. Wildlife triangle censuses are the main census method in Finland, whilst line transect counts occurred throughout most of the other studies. The number of chicks per hen was either from radio-marked birds, censuses or age determination of wing samples from harvested birds. The use of wings to assess this particular measure has been reported by several authors (Siivonen, 1954; Helminen, 1963; Semenow Tjan Shanskiy, 1979; Hörnfeldt et al., 2001). Asmyhr et al. (2012) found increased harvest risk for successful willow ptarmigan adults, meaning that adults experienced higher mortality than chicks in hunter-grouse encounters. Whether and how this differs from capercaillie and black grouse, we do not know. However, if the effect is directionally similar, it follows that our estimates of chicks per female (from harvest data) are biased low (also discussed elsewhere).

Statistical analysis

We evaluated regional changes in nest success, broods per hen and chicks per hen over time for Fennoscandia, continental Europe and The British Isles, fitting year as the only co-variate. Due to violations of linear model assumptions, we fitted generalized additive mixed models (GAMM) via the *mgcv* library (Wood, 2006) in R (R Development Core Team, 2012) with “study” and “method” as random effects, thereby accounting for non-independence within studies. We used the median year for studies where results were presented as an average across more than one year.

Nest success and proportion of hens with brood models were fitted with quasi-binomial error structures and chicks per hen models were fitted with quasi-Poisson error structures to allow for overdispersion. Number of knots were automatically se-

lected via the implemented generalized cross-validation which balances simplicity with explanatory power (Wood, 2006). Each model was fitted with a cubic regression spline. The number of nests per study-year was used to weight nest success models whilst chick and brood models were weighted by study duration since sample sizes were often missing from these studies.

To make interpretation of the temporal trends easier, we identified periods along the trend line where the slope was different from zero. For this, we extracted first order derivatives and their respective confidence intervals according to Curtis & Simpson (2014), but see also Simpson (2014). Periods of significant change were considered to occur when zero was outside the 95% confidence interval. These are highlighted in red (decrease phase) or green (increase phase) (figs. 3-5).

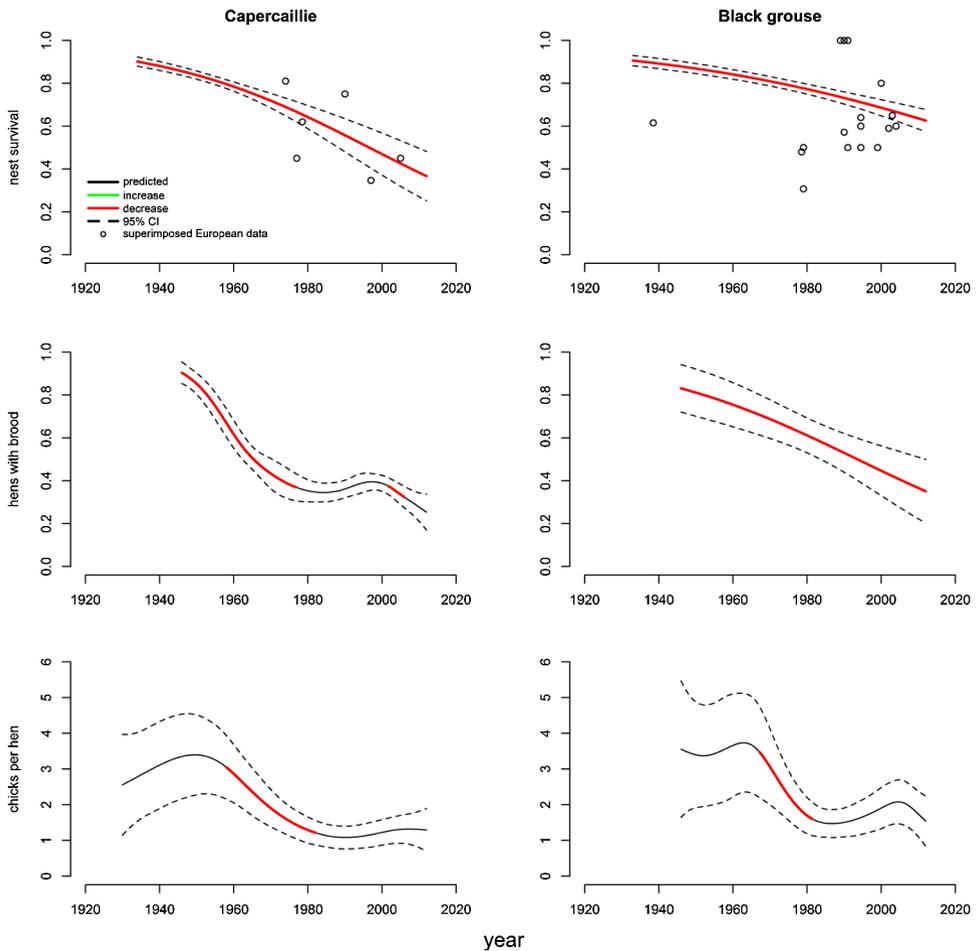


Figure 3. Predicted values from additive mixed models of reproduction in Fennoscandian capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; nest success, proportion of hens with brood and chicks per hen. British and continental European nest data are superimposed.

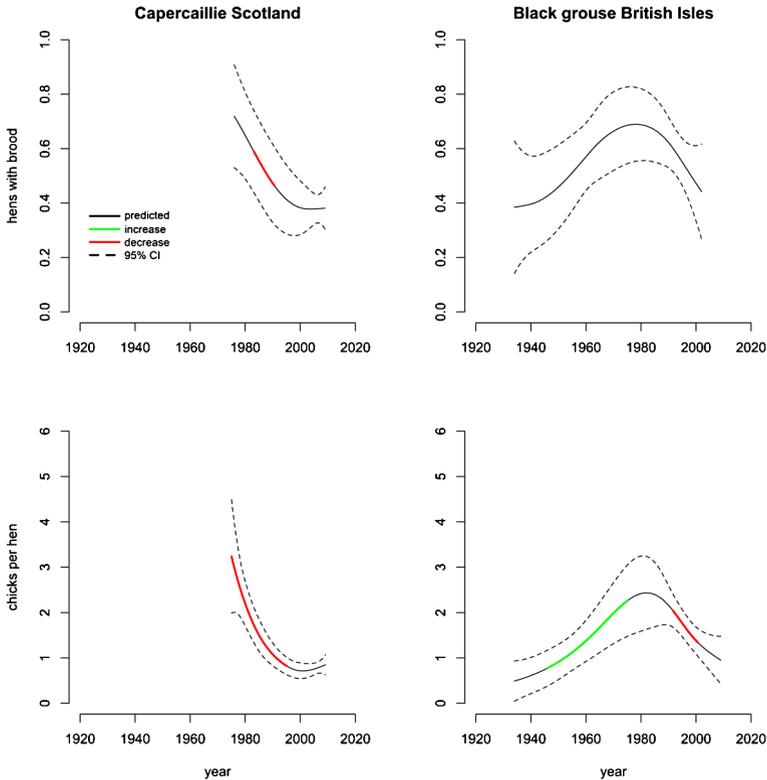


Figure 4. Predicted values from additive mixed models of reproduction in British capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; proportion of hens with brood and chicks per hen.

Numerical fluctuations are the hallmark of woodland grouse population dynamics. To assess trends in variation of net reproductive output we extracted residuals (absolute values) from the fitted chicks per hen models and fitted a locally weighted regression to the residuals (LOESS). Limited data on nest success and proportion of hens with brood prevented us from repeating this for these models.

Finally, based on the fitted trends from the chicks per hen models, we estimated the adult survival needed to offset modelled reproduction (i.e. to bring about zero population change). We used per capita chick production in July/August as an estimate of recruitment. Then we estimated the survival needed to keep the numbers of adults constant from one year to another, assuming equal survival of adults and juveniles. This assumption is not fulfilled as chicks have lower survival than adults and henceforth our estimates of required adult survival are conservative. We used female survival rates where available, otherwise we used survival rates for both sexes combined. We then compared estimates of required adult survival to the fitted trends from additive models (same procedure as reproduction models but no random effects) of actual adult survival reported from several Fennoscandian studies. From

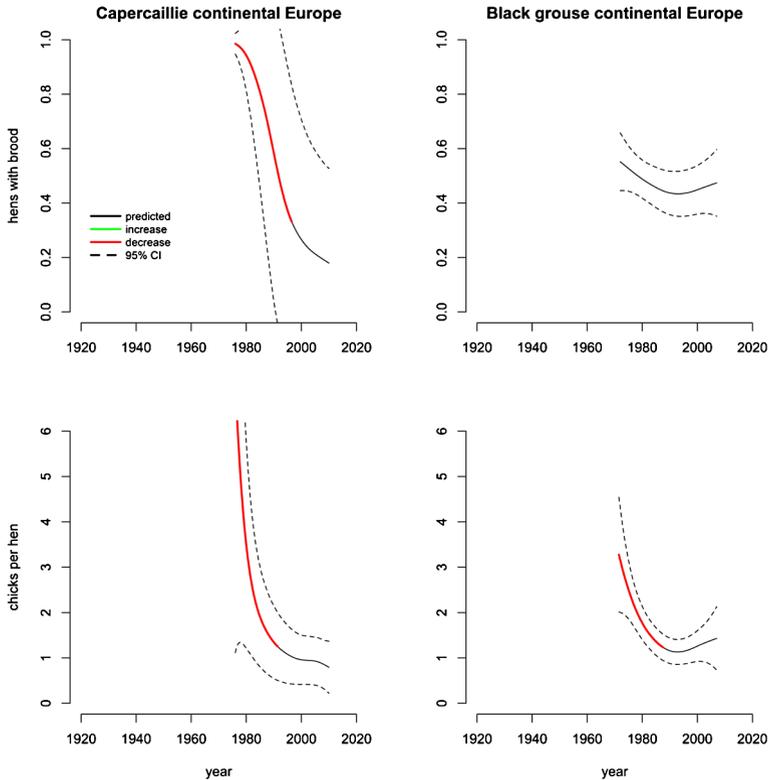


Figure 5. Predicted values from additive mixed models of reproduction in continental European capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Periods of significant change are highlighted red (decrease) and green (increase). From top to bottom; proportion of hens with brood and chicks per hen.

continental Europe and Britain, the number of estimates of adult survival was not sufficient for additive modelling. In these cases, the reported values are visualized in the figures (see table A4).

Results

Fennoscandia

Population indices for capercaillie and black grouse in Finland decreased from the early 1960s until they stabilized around 1980. A similar decrease was observed in the Norwegian data, although since 1975 bag data only existed between 2008 and 2014 at this resolution and no capercaillie were culled in this time-period. The Swedish data showed steep negative trends from 1907, reaching a minimum 20 years earlier than in Finland and Norway (around 1960), before increasing slightly towards the 1990s and then leveling off (fig. 1).

First order derivatives from cross-population model predictions in Fennoscandia suggested significant declines in crude nest success from 0.89 to 0.35 for capercaillie, and from 0.90 to 0.55 for black grouse, between 1934 and today. Similarly, broods per capercaillie hen decreased from 0.9 to 0.37 between 1946 and 1977 and then stabilized before decreasing again from 0.37 to 0.32 between 2001 and 2006. The proportion of black grouse hens with a brood decreased continually from 0.83 to 0.35 throughout the whole period between 1946 and 2012. The number of chicks per capercaillie hen decreased from 3.1 to 1.2 chicks per hen between 1958 and 1982. The chicks per black grouse hen showed a similar trend between 1967 and 1987 from 3.5 to 1.6 chicks per hen (fig. 3, highlighted red).

Residuals from chicks per hen models complemented the observed declines with decreasing year-to-year variation in net reproductive success for both species. They fluctuated considerably early in the period and the variation diminished throughout the time series, however with some slightly increasing trends the past 20 years. The variation decreased four-fold for capercaillie and two and a half-fold for black grouse from the beginning until today (fig. 6A, B).

The estimated adult survival required to counterbalance the observed decline in chicks per hen and so stabilize population growth has increased in line with decreasing reproductive output for both capercaillie and black grouse. Although reported adult survival has been increasing in Fennoscandian capercaillie and black grouse, rates have not been sufficient to offset the diminishing reproductive output and allow populations to grow since before the 1970s (fig. 7A, B).

British Isles

Broods per capercaillie hen in Scotland decreased from 0.59 to 0.46 between 1983 and 1991. For the British Isles as a whole, we did not detect any significant changes in black grouse brood frequencies between 1934 and 2002. The capercaillie chicks per hen in Scotland declined from 3.2 to 0.8 chicks over the 20 years between 1975 and 1995. Chicks per black grouse hen on the British Isles increased from 0.8 to 2.3 between 1946 and 1975 before decreasing from 2.0 to 1.3 chicks between 1992 and 2001 (fig. 4).

Variation in net reproductive success for capercaillie in Scotland increased from 1975 to a peak in the mid-1980s and has steadily decreased since then. Variation in black grouse reproductive output had a similar curve as capercaillie, but variation increased from 1934 until it peaked in the early 1990s. Since then, variation in reproductive output for black grouse on the British Isles has decreased (fig. 6C, D).

There are few reports of adult survival of capercaillie and black grouse in Scotland or the rest of the British Isles, so the assessment of population growth should be treated cautiously. In capercaillie, the survival required to maintain population size overshoot reported values in the 1990s. Reported values for adult black grouse survival vary (range 0.39 to 0.72). The higher survival rate reported is more in line with those reported for capercaillie, which typically have higher adult survival than

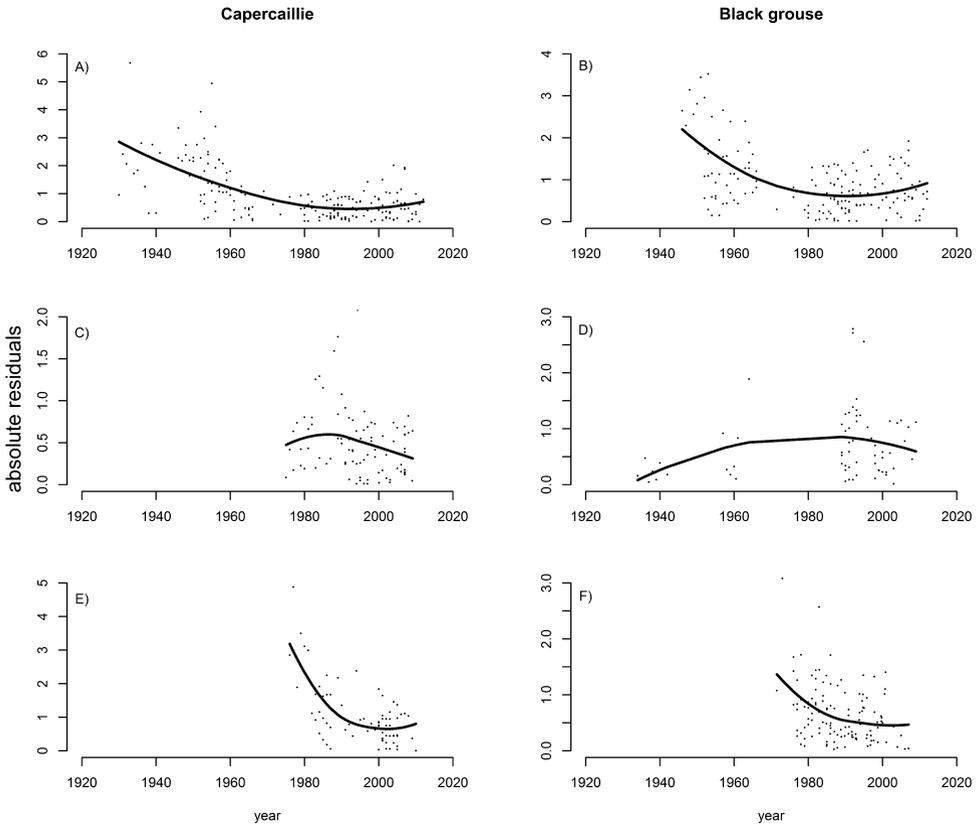


Figure 6. (A) Absolute residuals (dots) from Fennoscandian chicks per capercaillie (*Tetrao urogallus*). (B) Black grouse (*Lyrurus tetrix*) hen models with fitted locally-weighted regression function (lines). (C, D) depict variation in capercaillie reproduction in Scotland and black grouse reproduction on the British Isles. (E, F) show variation in reproduction for capercaillie and black grouse in continental Europe.

black grouse. Disregarding the lower value, last reports indicate that adult British black grouse counterbalance reproduction (fig. 7C, D).

Continental Europe

No temporal changes were detected in the proportion of black grouse hens with a brood. A decrease in the proportion of capercaillie hens with a brood from 0.98 to 0.33 was estimated between 1976 and 1997. Chicks per hen declined for both species. In 1976, capercaillie hens averaged an estimated 7.1 chicks which decreased to 1.3 chicks by 1991. Black grouse hens had 3.3 chicks in 1971 decreasing to 1.2 chicks in 1988 (fig. 5).

Residuals from capercaillie chick models exhibit a similar pattern to that of Fennoscandia. The overall trend is decreasing variation with a slight increase to-

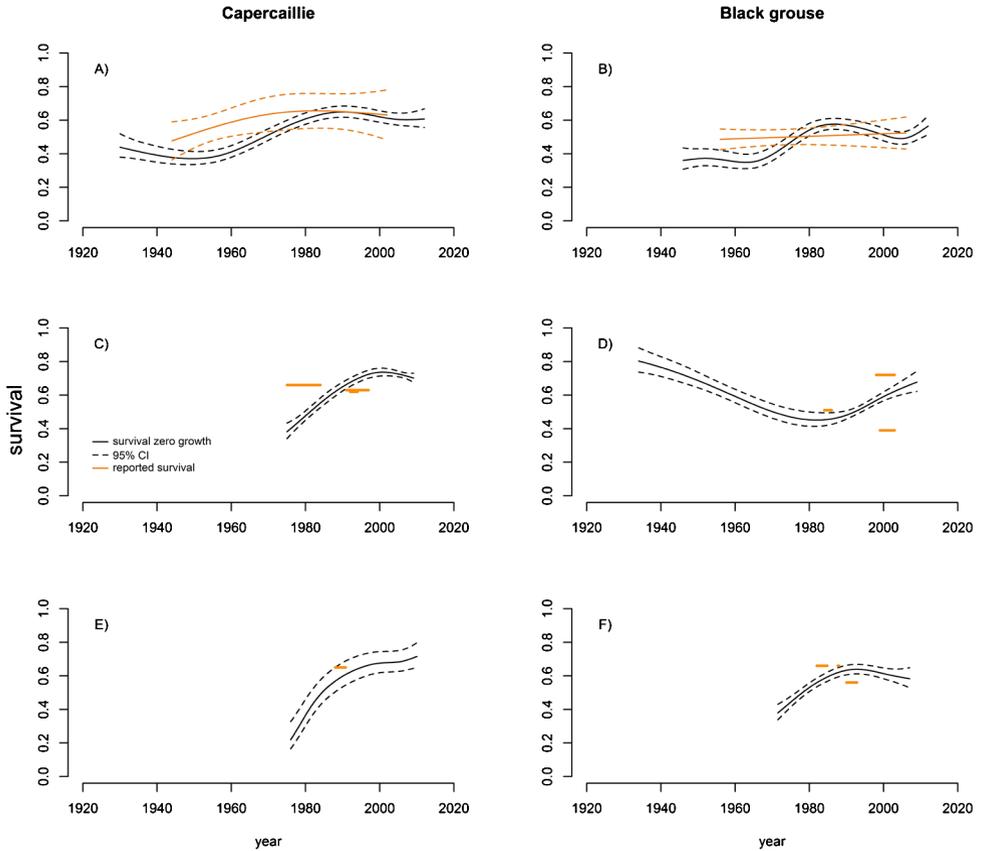


Figure 7. (A, B) Estimated adult survival required in Fennoscandia to counterbalance number of chicks per hen in a zero population-growth scenario with 95% CI for capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). Orange lines are most parsimonious models of observed adult survival estimates reported from different Fennoscandian studies (see table A4). (C, D) depict estimated adult survival required to counterbalance reproduction for Scottish capercaillie and British black grouse. Reported adult survival is superimposed orange line segments. (E, F) show estimated adult survival required to counterbalance reproduction for continental European capercaillie and black grouse. Reported adult survival rates are highlighted in orange.

wards the end of the time series. This trend was similar for black grouse, but the decrease alleviates in the last 10 years (fig. 6E, F).

As for the British Isles, there were few reports of adult survival rates for continental European capercaillie and black grouse. For both species however, reported adult survival has been within the range of what is needed to counterbalance current reproductive output (fig. 7E, F).

Discussion

Reproductive success of Fennoscandian capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) has declined throughout the past 80 years and year-to-year

variation in net reproductive output has decreased by a factor of four for capercaillie and two and a half for black grouse. The decrease in reproductive success has brought about large-scale population declines. Although adult survival trends are positive for both species, the decline in net reproductive output has not been compensated for. Assuming that adult survival has not increased since the last reports, then there has been no large-scale population growth in Fennoscandian capercaillie or black grouse since the 1970s. When investigating the discrepancy between required and actual adult survival, the consequences of declining reproduction appear more severe for black grouse. The parallel decline in reproduction of both species supports the view that they are affected by the same extrinsic forces in the boreal forests (Wegge & Rolstad, 2011).

Our results suggest that black grouse populations were performing better in Britain for a period than contemporary populations elsewhere. Although a decrease in the net reproduction occurred during the 1990s, British black grouse produced an increasing number of chicks until then. Furthermore, we did not detect any change in number of broods per hen in Britain or in continental Europe. For grouse in general, in which the vast majority of females attempt to reproduce each year (Bergerud *et al.*, 1988), the proportion of hens with brood maxima is a direct consequence of nest success. Any variation in proportion of hens with brood beyond what may be ascribed to nesting success is due to variation in chick survival. Hence, the observed pattern in chicks per hen in British and continental European black grouse may well be caused by varying chick survival rather than overall changes in black grouse nest success. This is somewhat supported by the apparent lack of trends (albeit few data points) in the combined nest success data for the British Isles and continental Europe (fig. 3, top). In which case, black grouse chick survival to late summer has decreased by 77% in Britain and 83% in the continental European countries since 1992 and 1971 respectively. Reported values of annual black grouse adult survival were quite high in northern England (Warren & Baines, 2002) whereas in Wales, Bowker *et al.* (2006) reported an estimated annual adult survival of 0.39 which is very low. It is therefore unclear to what extent population declines of black grouse in Britain are related to adult survival failing sufficiently offset poor reproduction. Less variation was reported in adult survival of continental European black grouse. When data of adult survival and offset-rates were overlapping, reproduction levelled off. Today however, black grouse females in continental Europe must have annual survival rates in the range of 0.7–0.8 to allow populations to grow, which is high, but similar to 0.72 reported by Warren & Baines (2002).

Our analysis of capercaillie reproduction in both Scotland and countries of continental Europe showed steep declines over a relatively short time period (ca. 40 years). However, the situation pre-1970s remains speculative for both areas. For continental Europe, the negative slope has probably been less steep than what we present here as it seems unlikely that almost all hens had a brood and that there were seven chicks per hen in late summer in the mid-1970s, considering the long term declines described in several studies.

Within Fennoscandia, nest success was probably over-estimated because some nests were predated before detection and most studies detected nests by chance (Mayfield, 1975). Similarly the loss of chicks could be under-estimated because it is easier to detect a brood than a single individual female (Buckland et al., 2005) or because in harvest data, number of chicks might be biased low (Asmyhr et al., 2012). At any rate, studies that collected data from harvest occurred before or in the early part of the decline phase (Siivonen, 1954; Helminen, 1963; Semenov Tjan Shanskiy, 1979). We suspect that continental European capercaillie data suffer partly from detection differences between single birds and broods, especially due to low sample sizes early in the series. Below we discuss our findings in the context of historical changes of three major environmental factors and their possible interactions that could contribute to the observed declines; 1) Intensified land-use, 2) Climate change, and 3) Increased generalist predator densities.

Intensified land-use

In the Fennoscandian context, intensified land use refers mainly to the expansion of modern forestry. Forestry practices have changed from manual single-tree cutting via mechanical stand-level clear-cutting to ecological sustainable forestry. Ecological sustainable forestry, whereby key biotopes are preserved and deciduous species are not targeted as before, is today implemented at various extents across Fennoscandia (see also Wegge & Rolstad, 2011). These changes have probably not affected nest predation directly (Wegge, 1985) as predation of cryptic eggs laid by cryptic birds can be regarded as incidental (Vickery et al., 1992). In general, it occurs when predators searching for their main prey come close enough to detect or flush the incubating female, thus exposing the nest. Capercaillie and black grouse nest in all the habitat types that they commonly use (Storaas & Wegge, 1987) and considering the high population turnover rates, a stronger preference for certain nesting habitat types could be expected if there was selection brought about by predation. Forestry practices might however, make nest predators more efficient by limiting or confining optimal nesting or brooding habitats, or by making these habitats more accessible to predators. In artificial nest experiments, proximity to forest edges, roads or agricultural land have all been found to increase egg predation (Andren, 1992; Paton, 1994). Nonetheless, this probably relates to the distribution of predators in the landscape (Kurki et al., 1998) rather than the innate ability of edges, roads or agricultural fields to improve predator searching efficiency and nest predation.

Nest survival of species that nest in open landscapes where nest predators are identified (e.g. greater sage grouse (*Centrocercus urophasianus*) in the presence of raven (*Corvus corax*)) has been found to depend strongly on vegetation structure and the availability of nest cover (Coates & Delehanty, 2010). However, corvids have not been identified as important nest predators of capercaillie and black grouse eggs, effects of habitat are ambiguous and no single effect of habitat on nest predation has been identified and agreed upon in forest dwelling woodland grouse

(Storaas & Wegge, 1987; Brittas & Willebrand, 1991; Storch, 1994; Ludwig et al., 2010). This could partly be because visually hunting predators (e.g. corvids) are less important in the boreal forests of Fennoscandia than in the sagebrush grassland of North America. In a recent study, Jähren et al. (2015) showed that red fox and pine marten together accounted for nearly all identified predation incidents of capercaillie and black grouse nests in Norway while corvids, even though present, were not important. In Abernethy, Scotland, where foxes are controlled and pine martens are protected, pine martens were the only predators recorded preying on capercaillie nests (Summers et al., 2009).

Sirkiä et al. (2010) proposed that capercaillie persistence at a landscape scale relates to conifer forest cover in general, and is independent of configuration of stand age-classes. A similar hypothesis has also been put forward for black grouse in relation to abundance of birch (*Betula pubescens*) (Lindén & Helle, 2003). In this context, population declines related to habitat deterioration or loss may be true for the Fennoscandian black grouse, but the extent of conifer forest cover (i.e. capercaillie habitat) has not changed in the time period at hand (Östlund, 1997). Moreover, reduced carrying capacity induced by habitat loss will not necessarily reduce per capita reproductive output directly, so much that it forces adults to vacate poorer areas in favor of more suitable habitat. Something similar has been observed in willow ptarmigan (*Lagopus lagopus*), in which reproduction seems to be spatially independent (Hörnell-Willebrand et al., 2006; Kvasnes et al., 2014).

Hens with broods are more constrained in their habitat selection than brood-less hens (Wegge & Kastdalen, 2008). Storaas et al. (1999) hypothesized that during the development of clear-cut stands into thickets, good quality brood habitat becomes scarce and its limited availability could be regarded as an ecological trap. However, this probably has a finite temporal effect in the boreal forests as broods have recently been reported to forage in re-developing stands as they transition into older forest (Wegge & Kastdalen, 2008; Wegge & Rolstad, 2011). A similar mechanism was reported from Finland and Scotland, where broods survived better with increasing bilberry (*Vaccinium myrtillus*) cover (Baines et al., 2004; Lakka & Kouki, 2009). After clear-cutting, bilberry is usually replaced by forbs and graminoids but, after a short-term reduction in bilberry cover coinciding with increasing forest density and younger-aged forest, it later reappears in post sapling-stands (Lakka & Kouki, 2009; Hedwall & Brunet, 2013).

Forest management in Fennoscandia is undergoing rapid development and previous habitat conditions suspected of having negative effects on grouse vital rates may no longer be present. Over the past few decades, the forestry industry has been attempting to accommodate both timber management and biodiversity considerations (Spence, 2001; Vanha-Majamaa & Jalonen, 2001; Indufor Oy, 2005) and the importance of habitat diversity for chick production in both capercaillie and black grouse is now recognized (Lande et al., 2014). As such, there should be ongoing improvements in habitat for both capercaillie and black grouse in Fennoscandia that should in turn be reflected by a recovery in reproductive rates. However, today's habitat

structure in Fennoscandia has not been shown to limit chick production under contemporary densities (i.e. Sirkiä et al., 2010) and the suggested habitat requirements for both capercaillie and black grouse are not as rigid as previously suspected (e.g. Sirkiä et al., 2011a, b; Lande et al., 2014).

In continental Europe and Britain, intensified land-use refers to a number of processes. These are primarily intensified agriculture, changes in grazing pressure, afforestation, forest maturation and increased disturbance from leisure activities such as ski-resorts (Storch, 2007). In Swiss alpine populations of black grouse, there are concerns that reduced grazing pressure by domestic livestock along the timberline brought about by the abandonment of traditional farming techniques will lead to shrub encroachment of alpine pastures (Patthey et al., 2012). This may also affect the capercaillie in Switzerland, which selects for open and grazed forests during winter (Sachot et al., 2003). Lower biodiversity might be a consequence of reduced grazing pressure as well as negative impacts on the trade-offs between cover and food-searching that brood-rearing hens exhibit (Signorell et al., 2010). By contrast, in Britain, over-grazing by both red deer (*Cervus elaphus*) and domestic sheep (*Ovis aries*) is associated with lower densities of black grouse, lower insect abundance and reduce black grouse reproduction (Baines, 1996; Calladine et al., 2002).

Climate change

Production of eggs and incubation are costly activities (Storaas et al., 2000). A change in onset of spring due to climate change could be leading to a mismatch between production of eggs and nutritional development of forage plants which may have adverse effects on female body condition and subsequent endurance during incubation and the production of good quality offspring (Moss et al., 2001). Additionally, it might lead to lower re-nesting rates as this is weight-related (Storaas et al., 2000). Effects of climate change on female vitality have, however, scarcely been studied and we found no data of body weights or declining egg numbers consistent with lowered female spring body condition. Furthermore, we could not separate between first nests and re-nests in our analysis so any potential decline in re-nesting rates could not be evaluated. We have no data indicating that a large proportion of the increasingly unsuccessful nests were due to female desertion or adverse weather events.

Climate is probably a more important driver of chick survival than nest success as chicks are reliant on insectivorous foods for the first couple of weeks post-hatching (Rajala, 1959; Atlegrim & Sjöberg, 2008; Wegge & Kastdalen, 2008). Furthermore, chick survival is positively related to temperature during the first two weeks post hatching and chick mortality directly related to adverse weather is rare, but cold and wet weather can predispose chicks to higher predation (Wegge & Kastdalen, 2007).

In vast areas of Fennoscandia, the start of the growing season is not only increasingly early but also increasingly irregular (Karlsen et al., 2009). The south to north

distribution of capercaillie and black grouse covers a wide range of mean temperatures and season start dates. Black grouse have exhibited plasticity as they adapt to earlier spring by advancing egg laying, but a mismatch can occur when the chicks hatch in unseasonably warm summer temperatures or in advance of insect phenology (Ludwig et al., 2006). Although some aspects of climate change obviously have adverse effects on reproduction, the irregular nature of today's climate is not manifested in a variable reproductive output that is detectible in our data. Moreover, the discrepancy in results from the bulk of studies investigating relationships between weather and different reproduction parameters indicate that climatic factors might be overridden or masked by other forces (i.e. Tornberg et al., 2012), at least in short-term capercaillie and black grouse population dynamics.

Our results suggest that there are considerable differences in reproductive success between capercaillie and black grouse in Britain. For capercaillie, links between climate change and reproduction have been established (Moss et al., 2001), but not so for black grouse (Moss, 1986). In Britain and central Europe, the two species are not sympatric to the same extent as in the boreal forests. Where they coexist in Scotland, capercaillie inhabit mature forest plantations which are considered unsuitable for black grouse (Pearce-Higgins et al., 2007). The range of black grouse habitat is also larger and possibly provides more variation in, e.g., precipitation and thus climate refuges. Similarly, climate trends also failed to explain variation in black grouse reproduction in the French Alps (Barnagaud et al., 2010). Consequences of climate change are predicted to increase in severity with increasing latitude (Houghton et al., 2001) and species may not simply have latitudinal or altitudinal range-shifts to compensate for e.g. warmer climate. The lack of negative effects of climate on black grouse reproduction in the Alps and Britain but not Finland might be related to seasonality. Boreal forest grouse might have comparatively restricted seasonal ranges to match timing of hatching of chicks, for example.

Increased predator densities

Both red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) are potentially important predators of forest grouse chicks and eggs. Whilst reliable long-term population indices of these carnivores are lacking in general, a few studies suggest long-term increases in both pine marten and red fox populations (Krott & Lampio, 1983; Helldin, 2000; Selås & Vik, 2006). The evidence of an increase in pine marten populations is stronger than that of the red fox. Pine marten populations were decimated by over-harvesting and so were totally protected in Scandinavia from the early 1930s. The period of legal protection varied in length between countries but by the 1960s and 1970s, the harvest re-opened across all Scandinavia (Helldin, 2000). By contrast, the red fox has never been protected from harvest, but the economic incentives for hunting them have declined since the era when furs could be

worth more than a month's wage (Statistics Norway, 1934, 1936, 1946). Furthermore, there are indications that foxes remained regionally scarce in Finland because of persecution until the early 1960s (Vuorisalo et al., 2014).

In large parts of Britain, black grouse share habitat with red grouse (*Lagopus lagopus scoticus*) which is managed for shooting. It follows that British black grouse may benefit from management actions undertaken on grouse moors (e.g. killing of predators and habitat improvement). It is therefore unexpected that the presence of gamekeepers has been found to have little or no effect on black grouse reproduction (Baines, 1996). Whilst gamekeepers can legally kill red foxes and crows, pine martens and raptors are protected and both goshawk and pine marten populations in Britain have increased since legal protection (Strachan et al., 1996; Lensink, 1997) and numbers of gamekeepers have declined (Summers et al., 2009). Hooded crows have been shown to be important predators of willow ptarmigan nests on an island where mammals were absent (Erikstad et al., 1982) but knowledge of their importance to nest survival in capercaillie and black grouse nests is derived from artificial nest experiments. If they have little impact on reproduction in capercaillie and black grouse, their removal may not have any effect. Moreover, our results might indicate that a recent change in chick survival is more likely to have occurred than changes in nest success for British and continental European black grouse, particularly because we do not see changes in broods per hen which is closely related to nest success. The relative importance of corvids to chick survival remains unclear, while the importance of raptors (Park et al., 2008; Tornberg et al., 2012) and mammalian predators (Marcström et al., 1988) is more certain.

We argue that the decrease in Fennoscandian capercaillie (61%) and black grouse (39%) nest success that we report here cannot be explained by increased predator efficiency alone. Irrespective of predation, grouse eggs occur at low densities and are difficult to find. Hence, they are not a reliable source of food for either red foxes or pine martens (Angelstam, 1983; Storaas & Wegge, 1984). It is therefore likely that nest predation occurs opportunistically when generalist predators find them while searching for other prey. Under such a scenario, predation could be expected to increase in relation to predator abundance. During the time span of our study, the proximate causes of nest failure have changed. In early studies, nest failure was often not related to predation and, in some cases, direct and indirect anthropogenic causes were more prominent (Siivonen, 1953) whereas in later studies, the proximate causes have been nest- and chick predation (Storaas & Wegge, 1987; Brittas & Willebrand, 1991; Wegge & Kastdalen, 2007). In a recent Finish study, nest loss among 210 black grouse nests was solely due to predation (Ludwig et al., 2010).

Chicks per hen in autumn is the product of nest success and chick survival. The varying pattern we present for chicks per hen in the first half of our Fennoscandian time series coincides well with that of the alternative prey hypothesis (Angelstam et al., 1984) or other density dependent regulators like parasites, as shown in willow ptarmigan and red grouse (*Lagopus lagopus scoticus*) (Hudson et al., 1998; Holmstad et al., 2005). In fact, preceding the start of the time series presented here,

frequent observations of dead forest grouse initiated extensive work on grouse parasites and disease in Fennoscandia (Brinkmann, 1926). Since then, parasites have not been suspected to play an important role in capercaillie and black grouse population dynamics.

The subsequent dampening of variation in Fennoscandian chicks per hen coincides with the simultaneous dampening in vole cycles and increases in pine marten and red fox populations. Vole cycles, the main driver of small game fluctuations in Fennoscandia, shifted from regular 4 to 6 year amplitude intervals, to diminished or irregular patterns (Ims et al., 2008; Kausrud et al., 2008; Cornulier et al., 2013). The collapse of vole cycles is a phenomenon to be considered together with the increase in generalist predators. Until the early 1970s, voles were highly cyclic and constituted an unpredictable food source for vole-eating predators (Hörnfeldt et al., 2005). Since then, the large-scale dampening of the vole cycles (Ims et al., 2008; Cornulier et al., 2013) may have resulted in voles constituting a new type of stable and predictable food source allowing vole-eaters to reproduce regularly as opposed to only in years with vole peaks.

Furthermore, across the whole region, large herbivore populations have undergone an exponential increase throughout the same period (Milner et al., 2006; Elmhagen et al., 2015), and today there is an unprecedented availability of offal and carcasses for small and medium-sized carnivores. As such, seasonal bottlenecks like winter, are not necessarily regulating small and medium-sized carnivores as they might have done earlier (Selås & Vik, 2006). In combination with the ready availability of food resources before and during the winter period, a reduction in seasonality and winter severity brought about by climate change may have facilitated mesopredators such as the red fox (Hersteinsson & MacDonald, 1992; Bartoń & Zalewski, 2007; Elmhagen et al., 2015). Reduced snow cover may also remove protection from predators for black grouse (Spidsø, Hjeljord & Dokk, 1997).

Population change and conclusion

In such long-term and spatially comprehensive trends, it is hard to separate between causal and correlative relationships. Throughout the time-period, capercaillie and black grouse habitats have undergone substantial biotic and abiotic changes. It is likely that there is not one single factor causing declines in woodland grouse reproduction but several acting in unison. Interregional comparisons of population status in continental Europe and the British Isles with Fennoscandia illuminates key differences in which limiting factors are important. Limiting factors expected to interact with habitat deterioration, habitat retraction and small population size, are important in continental Europe and Britain and should not be underestimated. By contrast, Fennoscandia comprises about 1.2 million km² of land of which large parts are continuous capercaillie and black grouse habitat (74, 37 and >50% of Finland, Norway and Sweden respectively). Currently, there are few cues to any single effect of habitat, direct or indirect, that could change the demographic rates of capercaillie and black grouse in the northern boreal forests.

It has been shown that predation can override effects of, for example, intensified land-use on small herbivores (Schmidt et al., 2004) and potential effects of habitat change might be obscured further when grouse densities are low. Most habitat-related studies on capercaillie and black grouse in the Fennoscandian boreal forests have been conducted during low grouse densities. Despite the different challenges facing Fennoscandian compared with British and continental European populations, a common limiting factor is predation. It is unlikely that declines in reproduction of this spatiotemporal magnitude can be explained without an increase in small and medium-sized mammalian carnivores.

Despite their sympatry, capercaillie and black grouse diverge in their habits and life histories. Their winter diet is essentially different and whilst capercaillie lek in closed canopy forest, black grouse lek in open habitat types. Forces mediated through habitat change that suppress one of the two species will not necessarily suppress the other. Their joint decline is therefore somewhat contrary to the idea of one common habitat-linked causal mechanism. In addition, a strikingly similar development in the dynamics of the Norwegian willow ptarmigan (*Lagopus lagopus*) population has been reported (Hjeljord, 2015), despite not being directly related to forestry.

In the Fennoscandian countries, bag limits are common and hunting is seasonally and regionally restricted. Censuses are also carried out (apart from Sweden) before the onset of harvest. Hence, in large parts of Fennoscandia, stakeholders are attempting to reduce the impact of harvest on capercaillie and black grouse populations but with unknown effects. In Finland, harvest was found to strongly affect black grouse populations in the subsequent year (i.e. additive mortality), but to a lesser extent in capercaillie, although harvest did not induce negative population trends (Lampila et al., 2011). In Finland at the time, harvest recommendations for the upcoming season were not based on August censuses. This may partly explain the need for a lag-term when describing harvest mortality as a function of population size in this particular study, which caused over-harvest in the decline phase of the population cycle. From studies conducted on willow ptarmigan, bag size is more closely related to hunter effort than population density and harvest rate is relatively higher at low than high densities (Willebrand et al., 2011). More needs to be understood of harvest and its effect on grouse populations and studies on this should be welcomed. Therefore, caution should be valued in grouse management and managers need to be proactive in their restrictions. According to the last Fennoscandian reports on adult female survival, our results imply that populations of capercaillie need 1.6 and black grouse need 1.9 chicks per hen annually to remain stable. This is higher than our model predictions of contemporary values of 1.2 and 1.6 chicks per hen respectively. Reproduction-based threshold harvesting is a management strategy that may be suitable in this case.

Grouse reproduce at an early age. They invest in many offspring and have high growth rates. It follows that losses in net production can be high, but when reproductive outputs are continuously declining and fluctuating patterns diminishing, it

is a sign of mortality rates to which the populations are not adapted. The consistent absence of periods with sequential years of positive growth rates are preventing populations of capercaillie and black grouse from breaking out of the current negative trends. Attributing this to a functional and/or numerical response remains speculative but there is little doubt that reducing predator numbers would improve grouse reproduction and densities (Marcström et al., 1988; Lindström et al., 1994; Kauhala et al., 2000). It is also clear that changes in forestry practices over the last 20 years (e.g. Green Tree Retention and The Programme for the Endorsement of Forest Certification, PEFC standards) have yet to have any detectible positive effects on capercaillie and black grouse reproduction.

Our results imply that capercaillie and black grouse populations should be intensively monitored and measures should be undertaken to reduce mortality of eggs and chicks. Most of recently reported adult survival rates are in line with or higher than the earliest reports obtainable. More needs to be understood of the complex spatial and temporal mechanisms involved in generalist predator dynamics and their prey. There is a need to investigate not only the suite of predators acting on grouse but also how they limit grouse in different phases of their life history. We suggest that future studies should aim to better understand the predators limiting grouse reproduction throughout their ranges and how predation rates are mediated by continuously changing habitat and climate.

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Appendix

Table A1.

Summary of nest success data used in analysis, for capercaillie and black grouse.

| Region | Source | Year(s) of study | Resoluton | Method | Country |
|---------------------|-----------------------------|------------------|-----------|--------------|----------|
| Capercaillie | | | | | |
| Fennoscandia | Barikmo et al., 1984 | 1980-1984 | mean | telemetry | Norway |
| | Höglund, 1953 | 1953 | yearly | conventional | Sweden |
| | Lindén, 1981 | 1966-1977 | mean | conventional | Finland |
| | Myrberget & Hagen, 1974 | 1934 | yearly | conventional | Norway |
| | Semenow Tjan Shanskiy, 1979 | 1930-1957 | mean | conventional | Russia |
| | Siivonen, 1953 | 1946-1952 | mean | conventional | Finland |
| | Storaas & Wegge, 1984 | 1979-1983 | yearly | both | Norway |
| | Wegge & Grasaas, 1977 | 1953-1976 | mean | conventional | Norway |
| | Grubbström, 1979 | 1977-1978 | yearly | conventional | Sweden |
| | This study, Hedmark | 2009-2012 | yearly | conventional | Norway |
| British Isles | This study, Nord-Trøndelag | 2010-2012 | yearly | conventional | Norway |
| | Jones, 1982 | 1978-1979 | mean | conventional | Scotland |
| | Proctor & Summers, 2002 | 1950-1998 | mean | conventional | Scotland |
| Continental Europe | Summers et al., 2009 | 2003-2007 | mean | conventional | Scotland |
| | Klaus, 1985 | 1971-1983 | mean | conventional | Germany |
| | Saniga, 2002 | 1993-2001 | mean | conventional | Slovakia |
| | Storch, 1994 | 1988-1992 | mean | telemetry | Germany |
| Black grouse | | | | | |
| Fennoscandia | Angelstam, 1983 | 1977-1982 | mean | telemetry | Sweden |
| | Lindén, 1981 | 1966-1977 | mean | conventional | Finland |
| | Ludwig et al., 2010 | 2003-2006 | mean | telemetry | Finland |
| | Marjakangas & Törmälä, 1997 | 1989-1993 | yearly | telemetry | Finland |
| | Myrberget & Hagen, 1974 | 1932-1934 | yearly | conventional | Norway |
| | Siivonen, 1953 | 1946-1952 | mean | conventional | Finland |
| | Storaas & Wegge, 1984 | 1980-1983 | yearly | both | Norway |
| | Valkeajärvi & Ijäs, 1994 | 1988-1992 | mean | telemetry | Finland |
| | This study, Hedmark | 2010-2012 | yearly | conventional | Norway |

Table A1.
(Continued.)

| Region | Source | Year(s) of study | Resoluton | Method | Country |
|-----------------------|--|------------------|-----------|--------------|------------------------------|
| | This study, Nord-Trøndelag | 2010-2012 | yearly | conventional | Norway |
| | Willebrand, T. unpubl. | 1990-1992 | mean | telemetry | Sweden |
| | Willebrand, 1988 | 1984-1987 | yearly | telemetry | Sweden |
| British Isles | Baines et al., 2007 | 1999-2004 | mean | telemetry | Wales, England & Scotland |
| | Starling, 1992 | 1989-1991 | yearly | telemetry | England |
| | Watson & Nethersole- Thompson, 2006 | 1935-1942 | mean | conventional | Scotland |
| Continental Europe | Caizergues & Ellison, 2000 | 1991-1998 | mean | telemetry | France |
| | Ellison et al., 1982 | 1977-1980 | mean | conventional | France |
| | Niewold, 1981 | 1978-1980 | mean | conventional | The Netherlands |

Table A2.

Summary of data on broods per hen used in analysis, for capercaillie and black grouse.

| Region | Source | Year(s) of study | Resoluton | Method | Country |
|---------------------|--|------------------|-----------|------------|----------------|
| Capercaillie | | | | | |
| Fennoscandia | Kurki et al., 2000 | 1989-1994 | yearly | census | Finland |
| | Rajala, 1974 | 1963-1966 | yearly | census | Finland |
| | Sørensen, 1977a, b | 1976 | yearly | census | Norway |
| | Wegge & Rolstad, 2011 | 1979-2008 | yearly | census | Norway |
| | Siivonen, 1955 | 1946-1952 | yearly | calculator | Finland |
| | Census Norway | 2001-2012 | yearly | census | Norway |
| British Isles | Baines et al., 2011 | 1991-2009 | yearly | census | Scotland |
| | Kortland & Peace, 2013 | 2002-2012 | yearly | census | Scotland |
| | Moss & Oswald, 1985 | 1976-1983 | yearly | census | Scotland |
| Continental Europe | Colloque galliformes de montagne, 1987 | 1976-1986 | yearly | census | France |
| | Ménoni & Novoa, 1988 | 1984-1987 | yearly | census | France |
| | Mossol-Torres & Ménoni, 2006 | 2000-2005 | yearly | census | Andorra |
| | Saniga, 2011 | 1983-2010 | yearly | census | Slovakia |
| | Steiner et al., 2007 | 2000-2002 | yearly | census | Austria |
| Black grouse | | | | | |
| Fennoscandia | Kurki et al., 2000 | 1989-1994 | yearly | census | Finland |
| | Marjakangas & Törmälä, 1997 | 1989-1993 | yearly | telemetry | Finland |
| | Rajala, 1974 | 1963-1966 | yearly | census | Finland |
| | Sørensen, 1977a, b | 1976 | yearly | census | Norway |
| | Siivonen, 1955 | 1946-1952 | yearly | calculator | Finland |
| | Census Norway | 2002-2012 | yearly | census | Norway |
| | Willebrand, T. unpubl. | 1990-1992 | yearly | telemetry | Sweden |
| | Willebrand, 1988 | 1984-1987 | yearly | telemetry | Sweden |
| British Isles | Baines, 1996 | 1991-1993 | yearly | census | Scotland |
| | Bowker et al., 2006 | 2000-2002 | yearly | telemetry | Wales |
| | Calladine et al., 2002 | 1996-2000 | yearly | census | England |
| | Baines, 1991 | 1989-1990 | yearly | census | England |
| | Watson, 2010 | 1957-1964 | yearly | census | Scotland |
| | Watson & Nethersole-Thompson, 2006 | 1934-1942 | yearly | census | Scotland |
| Continental Europe | Barnagaud et al., 2010 | 1990-2007 | yearly | census | France |
| | Colloque galliformes de montagne, 1987 | 1985-1987 | yearly | census | France & Italy |
| | De Franceschi et al., 1991 | 1987-1991 | yearly | census | Italy |
| | Ellison, 1978 | 1977-1978 | yearly | census | France |
| | Ellison et al., 1982 | 1976-1980 | yearly | census | France |
| | Ellison et al., 1984 | 1977-1981 | yearly | census | France |
| | Miquet, 1988 | 1985-1987 | yearly | census | France |

Table A2.
(Continued.)

| Region | Source | Year(s) of study | Resoluton | Method | Country |
|--------|--------------------------|------------------|-----------|--------|-------------|
| | Zbinden & Salvioni, 2003 | 1981-2002 | yearly | census | Switzerland |
| | Vith, 1974 | 1970-1973 | mean | census | Estonia |

Table A3.

Summary of chicks per hen data used in analysis, for capercaillie and black grouse.

| Region | Source | Year(s) of study | Resolution | Method | Country |
|---------------------|--|------------------|------------|-----------|----------|
| Capercaillie | | | | | |
| Fennoscandia | Helminen, 1963 | 1952-1961 | yearly | harvest | Finland |
| | Kurki et al., 2000 | 1989-1994 | yearly | census | Finland |
| | Lindén, 1981 | 1967-1976 | mean | census | Finland |
| | Rajala, 1974 | 1963-1966 | yearly | census | Finland |
| | Semenow Tjan Shanskiy, 1979 | 1930-1957 | yearly | harvest | Russia |
| | Siivonen, 1954 | 1946-1954 | yearly | harvest | Finland |
| | Solvang et al., 2009 | 2007-2012 | yearly | census | Norway |
| | Spidsø & Stuen, 1983 | 1979-1982 | yearly | telemetry | Norway |
| | Sørensen, 1977a, b | 1976 | yearly | census | Norway |
| | Wegge & Grasaas, 1977 | 1968-1976 | mean | census | Norway |
| | Wegge & Rolstad, 2011 | 1979-2008 | yearly | census | Norway |
| | Kastdalen, 1992 | 1987-1989 | yearly | census | Norway |
| | Ringaby, 2014 | 2000-2005 | yearly | telemetry | Sweden |
| | Census Boda, Sweden | 1980-2010 | yearly | census | Sweden |
| | Census Norway | 2001-2012 | yearly | census | Norway |
| British Isles | Baines et al., 2011 | 1991-2009 | yearly | census | Scotland |
| | Kortland & Peace, 2013 | 2002-2012 | mean | census | Scotland |
| | Moss & Weir, 1987 | 1977-1984 | yearly | census | Scotland |
| | Moss et al., 2001 | 1975-1998 | yearly | census | Scotland |
| | Summers et al., 2004 | 1989-1999 | yearly | census | Scotland |
| | Summers et al., 2010 | 1989-2009 | yearly | census | Scotland |
| Continental Europe | Colloque galliformes de montagne, 1987 | 1976-1986 | yearly | census | France |
| | Ménoni & Novoa, 1988 | 1984-1987 | yearly | census | France |
| | Ménoni et al., 2002 | 2000-2005 | yearly | census | France |
| | Mossol-Torres & Ménoni, 2006 | 2000-2005 | yearly | census | Andorra |
| | Saniga, 2011 | 1983-2010 | yearly | census | Slovakia |
| | Zawadzki & Zawadzka, 2012 | 1996-2010 | mean | census | Poland |
| Black grouse | | | | | |
| Fennoscandia | Helminen, 1963 | 1952-1961 | yearly | harvest | Finland |
| | Kurki et al., 2000 | 1989-1994 | yearly | census | Finland |
| | Lindén, 1981 | 1967-1976 | mean | census | Finland |
| | Rajala, 1974 | 1963-1966 | yearly | census | Finland |
| | Siivonen, 1954 | 1946-1954 | yearly | harvest | Finland |
| | Solvang et al., 2009 | 2007-2012 | yearly | census | Norway |
| | Sørensen, 1977a, b | 1976 | yearly | census | Norway |
| | Wegge & Rolstad, 2011 | 1979-2008 | yearly | census | Norway |
| | Willebrand, 1992 | 1984-1987 | mean | telemetry | Sweden |
| | Kastdalen, 1992 | 1987-1989 | yearly | census | Norway |
| | Census Boda, Sweden | 1980-2010 | yearly | census | Sweden |
| | Census Norway | 2002-2012 | yearly | census | Norway |

Table A3.
(Continued.)

| Region | Source | Year(s) of study | Resoluton | Method | Country |
|--------------------|--|------------------|-----------|-----------|----------------|
| British Isles | Willebrand, T. unpubl. | 1990-1992 | mean | telemetry | Sweden |
| | Willebrand, 1988 | 1984-1987 | yearly | telemetry | Sweden |
| | Baines, 1991 | 1989-1990 | yearly | census | Scotland |
| | Baines, 1996 | 1991-1993 | yearly | census | Scotland |
| | Bowker et al., 2006 | 2000-2003 | yearly | telemetry | Wales |
| | Calladine et al., 2002 | 1996-2000 | mean | census | England |
| | Summers et al., 2010 | 1991-2009 | yearly | census | Scotland |
| | Warren & Baines, 2002 | 1998-2000 | yearly | telemetry | England |
| | Watson, 2010 | 1957-1964 | mean | census | Scotland |
| Continental Europe | Watson & Nethersole-Thompson, 2006 | 1934-1942 | yearly | census | England |
| | Barnagaud et al., 2010 | 1990-2007 | yearly | census | France |
| | Caizergues & Ellison, 2000 | 1991-1998 | mean | census | France |
| | Colloque galliformes de montagne, 1987 | 1982-1987 | yearly | census | France & Italy |
| | Ellison, 1978 | 1976-1977 | yearly | census | France |
| | Ellison et al., 1982 | 1976-1980 | yearly | census | France |
| | Ellison et al., 1984 | 1977-1981 | yearly | census | France |
| | Marti & Pauli, 1983 | 1973-1983 | yearly | census | Germany |
| | Miquet, 1988 | 1985-1987 | yearly | census | France |
| | Zbinden & Salvioni, 2003 | 1981-2001 | yearly | census | Switzerland |
| Vith, 1974 | 1970-1973 | mean | census | Estonia | |

Table A4.

Survival rates of adult females/both sexes combined.

| Source | Species | Duration | Survival rate | Country |
|-----------------------------|--------------|-----------|---------------|----------|
| Semenov Tjan Shanskiy, 1979 | capercaillie | 1930-1957 | 0.52 | Karelia |
| Semenov Tjan Shanskiy, 1979 | capercaillie | 1930-1957 | 0.41 | Karelia |
| Helminen, 1963 | capercaillie | 1952-1961 | 0.53 | Finland |
| Helminen, 1963 | capercaillie | 1952-1961 | 0.51 | Finland |
| Helminen, 1963 | capercaillie | 1952-1961 | 0.48 | Finland |
| Helminen, 1963 | capercaillie | 1952-1961 | 0.45 | Finland |
| Lindén, 1981 | capercaillie | 1952-1971 | 0.71 | Finland |
| Moss, 1987 | capercaillie | 1975-1984 | 0.66 | Scotland |
| Wegge & Rolstad, 2011 | capercaillie | 1980-1990 | 0.64 | Norway |
| Storch, 1993 | capercaillie | 1988-1992 | 0.65 | Germany |
| Moss et al., 2000 | capercaillie | 1991-1997 | 0.63 | Scotland |
| Catt et al., 1994 | capercaillie | 1992-1994 | 0.62 | Scotland |
| Wegge & Rolstad, 2011 | capercaillie | 1996-2003 | 0.57 | Norway |
| Åhlen et al., 2013 | capercaillie | 2000-2004 | 0.68 | Sweden |
| Helminen, 1963 | black grouse | 1952-1961 | 0.5 | Finland |
| Helminen, 1963 | black grouse | 1952-1961 | 0.44 | Finland |
| Helminen, 1963 | black grouse | 1952-1961 | 0.42 | Finland |
| Lindén, 1981 | black grouse | 1952-1971 | 0.53 | Finland |
| Angelstam, 1984 | black grouse | 1977-1981 | 0.56 | Sweden |
| Caizergues & Ellison, 1997 | black grouse | 1982-1988 | 0.66 | France |
| Picozzi & Hepburn, 1986 | black grouse | 1984-1986 | 0.51 | England |
| Willebrand, T. unpubl. | black grouse | 1984-1987 | 0.5 | Sweden |
| Caizergues & Ellison, 1997 | black grouse | 1990-1995 | 0.56 | France |
| Wegge & Rolstad, 2011 | black grouse | 1996-2003 | 0.43 | Norway |
| Warren & Baines, 2002 | black grouse | 1998-2000 | 0.72 | England |
| Bowker et al., 2006 | black grouse | 1999-2003 | 0.39 | Wales |
| Pekkola et al., 2014 | black grouse | 2005-2007 | 0.53 | Finland |
| Pekkola et al., 2014 | black grouse | 2005-2007 | 0.69 | Finland |