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Large areas of the British uplands consist of heather moorland, a habitat of global conservation importance that supports communities of threatened animal and plant species. Red grouse *Lagopus lagopus scotica* are dependent on heather and benefit from management of habitat, predators and parasites by gamekeepers employed to create a surplus of grouse for sport shooting. We compared numbers of red grouse shot across nine British regions over four discrete time periods (1890–1920, 1920–1950, 1950–1980, 1980–2010) using annual records of shooting bags from 272 estates. We examined whether trends in numbers of grouse shot may be explained by changes in keeper density, heather moor extent or replacement of moorland by afforestation. Grouse bags were consistently higher in regions of northern England than in Scotland and Wales, and declined in all nine regions except southern Pennines from 1920 to 1950. Bags in northern England increased significantly from 1950, coinciding with increases in keeper density. In north-east Scotland and Wales, numbers of grouse shot declined over the same period, coinciding with declines in keeper density and increased afforestation of moors. Regional variation in red grouse bag counts over time may be explained by changes in land use and management intensity affecting extent of suitable habitat and predator prevalence.

Upland ecosystems have undergone significant changes globally in response to changes in land use (Maltby and Immirzi 1993, Dias et al. 2010). Upland areas, especially in Britain and Ireland, have been degraded or reduced in extent by drainage, overgrazing and afforestation, which has adversely affected upland plant and animal communities (Sykes et al. 1989, Vasander et al. 2003, Holden et al. 2007). The British uplands support internationally important habitats designated as Special Areas of Conservation (SACs) and Special Protection Areas (SPAs), the latter being designated for the protection of both heath and blanket bog habitats (European Commission 2015a, b). Upland areas support internationally important animal communities (both economically and in terms of conservation; Thompson et al. 1995) and provide valuable ecosystem services for lowland areas, such as clean drinking water and flood protection (Thompson et al. 1995, Orr et al. 2008). Uplands also support land uses such as commercial forestry, sheep farming, deer stalking, and sport shooting of red grouse *Lagopus lagopus scotica*.

Red grouse are highly dependent on heather moorland (Watson and Moss 2008), a semi-natural habitat prioritised under the EU Habitats Directive (European Commission 2015a). The red grouse has been designated as an amber-listed Bird of Conservation Concern following declines in range and abundance (Eaton et al. 2009), which are thought to be facilitated by loss of heather habitat since the 1940s (Robertson et al. 2001). Loss of heather has been slower on areas managed for grouse shooting where heather habitat is maintained to benefit red grouse and increase bird numbers for sport shooting (Robertson et al. 2001), hence changes in grouse abundance are likely to vary among regions of Britain depending on land use. Red grouse populations naturally exhibit quasi-cyclical fluctuations approximating 4–8 years in relation to *Trichostrongylus tenuis* parasite abundance (Hudson et al. 1998).

Grouse shooting has been practised in Britain for around 150 years and provides an important source of revenue for upland rural communities (McGilvary 1995, PACEC 2014). Shooting estates carry out two methods of grouse shooting: driven shooting, where birds are flushed towards stationary hunters, and walked-up shooting, where hunters walk across the moor and shoot grouse they encounter. Driven shooting typically requires higher grouse densities than walked-up shooting, which are achieved by employing private gamekeepers responsible for intensive management of generalist

predators, heather habitat and grouse parasites, especially *T. tenuis* (Sotherton et al. 2009). Gamekeepers legally kill predators of grouse, such as the red fox *Vulpes vulpes*, stoat *Mustela erminea* and carrion crow *Corvus corone*. Raptors have been legally protected in the UK since 1954, but are still killed illegally on some grouse moors (Amar et al. 2011a). In northern England, gamekeepers on moorland focus on grouse management and do not deliberately manage habitat for other game species. However, on some Scottish moors, estates may also carry out management for other game species such as deer, although these are unlikely to affect management of areas for grouse (Watson and Moss 2008).

Rotational strip-burning of heather is commonly practised by moorland gamekeepers to maintain a mosaic of vegetation heights favoured by grouse and to prevent natural succession towards woodland (Palmer and Bacon 2001, Buchanan et al. 2006). Whilst rotational strip-burning can be a useful conservation management tool for maintaining upland heather moorland and has been shown to increase abundance of peat-forming plants such as *Eriophorum vaginatum* and *Sphagnum* spp. (Lee et al. 2013), there is contention regarding whether burning impairs ecosystem functions, such as carbon storage (Garnett et al. 2000, Ward et al. 2007, Davies et al. 2016).

Driven grouse shooting became fashionable in the early 1800s and large areas of upland Britain were devoted to grouse moor management from the 1880s (Lovat 1911). The extent of moorland managed for grouse shooting began to decline from the 1940s (Barnes 1987, Robertson et al. 2001), owing to widespread changes in land use and management, such as agricultural intensification, and commercial forestry using non-native trees. This resulted in fewer moorland gamekeepers, increased predator abundance (Barnes 1987, Reynolds and Tapper 1996, Baker and Harris 2006), and reduced profitability of grouse moors (Barnes 1987, Cannell and Dewar 1995, Robinson and Sutherland 2002). These changes have also been linked to declines in other ground-nesting birds, such as Eurasian golden plover *Pluvialis apricaria* and Eurasian curlew *Numenius arquata* (Amar et al. 2011b, Douglas et al. 2014).

Long-term changes in red grouse bags have been described for shooting estates in Scotland (Barnes 1987), but no long-term regional comparison of red grouse abundance has been carried out for the whole of Britain. No statutory limits exist for grouse bags or for the number of shoot days. Instead, moor-specific bags are determined by each moor manager, often based on grouse counts in July, prior to shooting starting on 12 August.

We used red grouse bag records obtained from shooting estates as a proxy for grouse abundance. There are concerns that using bag data to represent changes in population abundance over- or underestimates variation in population size compared with direct counts (Lambin et al. 1999, Ranta et al. 2008). However, data from bags and counts are strongly correlated (Hudson et al. 1999 in response to Lambin et al. 1999), hence bag sizes act as an index for post-breeding density and can be used to examine long-term changes in grouse abundance (Cattadori et al. 2003). In this study, shooting records provided information about red grouse numbers over 150 years from moors throughout Great Britain, and although no data on hunting effort were available, this dataset gives rise to time-series whose lengths are unrivalled by any other monitoring scheme.

Indices of annual number of grouse shot per unit area were compared among nine regions of Britain and over four time periods to identify when and where changes in bags occurred and how they responded to changes in keeper density, area afforested (including both commercial and non-commercial woodland) and extent of heather moorland.

Material and methods

Shooting records

We used bag records obtained by the Game and Wildlife Conservation Trust (GWCT) under its National Gamebag Census (NGC) to examine long-term trends in red grouse bags. This voluntary scheme collates gamebag statistics from over 800 estates each year (on average 272 estates provide red grouse bag records annually) using postal questionnaires (Tapper 1992). Questionnaires recorded number of red grouse shot, number of gamekeepers employed, total area of heather moorland (moor extent km^2) and total area of forest (forest cover km^2). Bag records and moor extent data were available annually from >60 estates managed for red grouse (hereafter 'grouse moors') from 1860, so we considered data from 1860 onwards. NGC records on keeper density (gamekeepers km^{-2} of moor), forest cover (proportion of estate comprising woodland, but not differentiated into recent commercial afforestation or native woodland) and moor extent (proportion of estate with heather moorland) were available from 1860 to 2010 and were analysed alongside grouse bag data using the same statistical methods. No data were available detailing the number of shooters or shoot days (hunter effort) associated with the bag data. Nevertheless, bag data have been shown to be strongly correlated with grouse abundance (Cattadori et al. 2003), so we believe that the use of these data is a valid method for examining temporal and regional variation in grouse abundance.

Defining time periods and regions

Indices of annual change in number of grouse shot, keeper density, forest cover and moor extent were calculated for 1860–2010 and percentage change was considered during four discrete periods 1890–1920, 1920–1950, 1950–1980 and 1980–2010, each representing a 30-year interval. Examining intervals of this length was deemed to be a balance between representing periods of change with potential to affect grouse abundance, avoiding false trends caused by quasicycles in grouse populations and taking into account the timing of the World Wars. Many estates did not return bag records during and shortly after the First and Second World Wars owing to the suspension of shooting. Hence, we avoided war years (1914–1918 and 1939–1945) when selecting start and end years within time periods.

Grouse moors were assigned to nine regions, using definitions within the NGC (Tapper 1992) and previous analyses (Barnes 1987) (Table 1, Fig. 1), but modified for Scotland from two to four regions: northeast (NE), northwest (NW), southeast (SE) and southwest (SW). Northwest England

Table 1. Counties included within each specified region of Britain.

Region	Counties
NW Scotland	Argyll, Caithness, Dunbartonshire, Invernesshire, Ross and Cromarty, Strathclyde, Sutherland
NE Scotland	Aberdeenshire, Angus, Banffshire, Fife, Grampian, Kincardineshire, Perth and Kinross, Stirlingshire, Tayside
SW Scotland	Ayrshire, Dumfriesshire, Kirkcudbrightshire, Lanarkshire, Renfrewshire, Wigtonshire
SE Scotland	Berwickshire, East Lothian, Midlothian, Peeblesshire, Roxburghshire, Selkirkshire
NW England	Cumbia, Lancashire, Greater Manchester
N Pennines	County Durham, Northumberland, North Yorkshire (excluding North York Moors)
North York Moors	North-east Yorkshire
S Pennines	Derbyshire, East Cheshire
Wales	All counties of Wales with the addition of Shropshire (England)

Figure 1. Nine regions of Britain used in analyses of red grouse harvested in 1860–2010. Regions are based on UK administrative boundaries detailed in Table 1.

(NW England) included counties from Cumbria in the north to Lancashire in the south. Westerly regions encompassed moors situated in the wetter west of the UK, exposed to prevailing westerly weather systems. Northeast England was separated into Northern Pennines (hereafter 'N Pennines'), stretching from North Yorkshire to the Scottish borders, Southern Pennines (hereafter 'S Pennines') and North York Moor regions. The North York Moors are geographically isolated from moors of the North and South Pennines, hence this area was defined as a single region. Wales and Shropshire were combined into a single region. Examining population changes at greater spatial resolution was not possible owing to the limited number of moors in some areas. Numbers of grouse moors in each region and time period are shown in Table 2.

Statistical analyses

Using annual bag data as a dependent variable and $\log_e$-transformed moor area (km^2) as an offset (thereby effectively analysing red grouse shot per km^2 of moor), we fitted a generalised linear model (GLM) using Poisson error and $\log_e$ link function with moor and year as explanatory factors to estimate site and year effects on the $\log_e$ scale (Ter Braak et al. 1994). Annual density indices were obtained by back-transforming the year coefficients. All index values were relative to the start year in the time-series, which took a value of 1. Ninety-five percent confidence intervals around index values were obtained by bootstrapping at the moor level: for each of 199 bootstrap runs, moors equal in number to the original sample were selected at random with replacement and a new set of indices obtained as described above (Efron and Tibshirani 1986). For each year, the 95% confidence limits were taken as the lower and upper 95th percentiles of the distribution of all 200 index values. Only moors that contributed fewer than two years of data (6% of total number of moors) were omitted from analyses. It was not always clear whether blank records given in questionnaires represented zero grouse shot or missing data. To avoid potential problems caused by misinterpreting the meaning of zero and blank records, both were excluded from our analyses. Hence, bag records used in analyses were strictly positive values.

To determine whether including moors with as few as two years of data affected the results, we repeated our analysis for regions with the most moors (NE Scotland and NW Scotland), including only moors with at least 20 years of continuous data (81 and 75 moors for NE and NW Scotland respectively). A Mann–Whitney U-test showed there to be no significant difference in percentage change in grouse bags as calculated using different selection criteria ($U = 34$, $p = 0.88$, $n = 16$). Percentage change in number of grouse shot km^{-2} calculated using moors with at least two years of data or ones with at least 20 years of data showed similar statistical significance among time periods in both regions (with exception of NW Scotland in 1890–1920, Supplementary material Appendix 1 Table A1), so we carried out analyses for all regions including moors with >2 years of data, as 84% and 91% more records were available using these specifications (based on records from NE and NW Scotland respectively).

To determine the underlying long-term trend in number of grouse shot km^{-2}, we fitted a generalised additive model (GAM, Hastie and Tibshirani 1990) with one degree of freedom per decade or part-decade for the full 1860–2010-year time-series of annual indices obtained from Poisson GLMs. Doing so removed short-term cyclical fluctuations in annual indices while emphasizing the underlying long-term trend. Percentage change in the underlying trend of bag indices over each 30-year interval was estimated by calculating the percentage difference in GAM fitted values between each interval's beginning and end years. Ninety-five percent confidence intervals around percentage change values were estimated by fitting a GAM to each bootstrap sample , calculating percentage change from the underlying long-term trend and selecting the lower and upper 95% percentiles from the resultant 200 values. If the 95% confidence interval did not include zero, then the percentage change in grouse numbers within the corresponding time period was declared significant at $p < 0.05$. Similarly, we estimated percentage change in keeper density, and in proportion of estate covered by forest or heather moorland over time for each region using a similar analysis applied to number of keepers and proportions of forest cover and moor extent data (transformed using the angular transformation $\arcsin(\sqrt{p})$). Initially, GLMs with normal error distributions were carried out for transformed proportions of forest cover and moor extent and year coefficients and their confidence intervals retained as described above. These coefficients were then smoothed using GAMs to estimate trends in forest cover and moor extent.

For forest cover and moor extent, estimated changes are likely to be underestimates because moors that were converted completely to forestry, and therefore ceased grouse shooting, would no longer submit bag records to the NGC and would therefore drop out of our sample of moors. However, we found that the number of moors used to calculate change in forest cover and moor extent among periods

Table 2. Mean ± se number of red grouse shot km^{-2} and number of moors (n) included in analyses for each region and time period.

	Wales	S Pennines	North York Moors	N Pennines	NW England	SW Scotland	SE Scotland	NW Scotland	NE Scotland
1890–1920	30.0 ± 2.1 n=25	96.5 ± 4.3 n=10	89.7 ± 7.5 n=6	96.8 ± 2.9 n=28	95.6 ± 6.0 n=8	32.4 ± 1.4 n=17	33.9 ± 2.1 n=22	28.9 ± 1.0 n=61	55.6 ± 1.5 n=67
1920–1950	20.8 ± 1.1 n=23	156.5 ± 9.7 n=16	43.9 ± 3.2 n=9	67.2 ± 2.3 n=47	64.8 ± 5.3 n=16	29.2 ± 1.5 n=24	58.7 ± 5.6 n=29	23.0 ± 0.7 n=93	49.5 ± 1.2 n=89
1950–1980	10.3 ± 0.5 n=33	81.1 ± 2.9 n=14	59.1 ± 2.3 n=14	76.8 ± 2.0 n=63	51.8 ± 2.5 n=23	19.2 ± 1.1 n=27	39.6 ± 1.5 n=27	9.6 ± 0.3 n=104	32.8 ± 0.7 n=118
1980–2010	3.5 ± 0.3 n=26	47.0 ± 2.4 n=17	71.2 ± 2.7 n=15	77.3 ± 2.1 n=68	44.1 ± 2.5 n=26	11.1 ± 1.5 n=24	40.1 ± 3.5 n=35	6.7 ± 0.3 n=112	10.9 ± 0.3 n=129

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increased over time and that 81% of moors available in the first time period (1890–1920) were still submitting records in the last period (1980–2010) (Supplementary material Appendix 1 Table A2).

To evaluate whether trends in grouse bags, keeper density, forest cover and moor extent varied among time periods and regions, we used overlap in confidence intervals to check for significant differences in percentage change. If confidence intervals for different time periods and regions did not overlap, differences in percentage change between periods and regions were regarded as significant at p < 0.05.

To determine which explanatory variables were most important in explaining variation in percentage change in grouse bags, we used a GLM with percentage change in bags for each region (n = 9) and time period (n = 4) as the response variable and percentage change in keeper density, forest cover and moor extent as explanatory variables. Region and time period were also included as categorical variables. To reduce heteroscedasticity and normalise the response variable, percentage change in grouse bags was log_e-transformed (x + 100) prior to analysis. Each main effect was tested for significance using Wald statistics (distributed approximately as χ^2). We analysed change at the level of the 30-year interval because keeper density, forest cover and moor extent varied little at shorter time-scales.

Statistical analyses were implemented in R ver. 3.2.2 (< www.r-project.org >) and Genstat v 17.1 (VSN Int. Ltd).

Results

Number of moors selected per time period and region

The number of moors available for each time period in nine regions of Britain ranged from 6 to 129 (Table 2). During the periods 1920–1950, 1950–1980 and 1980–2010, 42%, 73% and 85% more moors were available respectively than during 1890–1920 across all regions. Numbers of moors included in analyses were consistently highest in NW Scotland and NE Scotland and lowest in the North York Moors and S Pennines across all four time periods (Table 2).

Variation in bag trends among time periods and regions

Mean number of grouse shot varied among time periods and regions. Bags were highest in almost all regions from 1890 to 1920 and were highest in the S Pennines for most time periods. In the most recent time period (1980–2010), mean number of grouse shot was highest in the N Pennines and lowest in Wales (Table 2). Figure 2 shows that grouse bag indices fluctuated in a cyclical manner over time with cycles approximating 4–8 years depending on region. It also shows how GAM smoothing removed the effect of cycles, leaving the underlying long-term trend. Trends in bag indices varied among regions of Britain. Figure 2 shows a post-1940 decline in bag indices in eight regions, including NW England, S Pennines, northern Scotland and Wales.

For each region, the percentage changes over the 30-year interval between the first and last years of each period are shown in Fig. 3. From 1890 to 1920, numbers of grouse shot km^{-2} declined by –48%, –20% and –35% in the North York Moors, NW Scotland and SW Scotland respectively, whilst numbers shot increased by almost 200% in SE Scotland over the same period. No increase in number of grouse shot km^{-2} was observed in any region from 1920 to 1950. In northern English regions, declines of –36%, –64% and –69% occurred in the N Pennines, North York Moors and NW England respectively from 1920 to 1950. In Scottish regions, declines of –72%, –42%, –45% and –58% in number of grouse shot km^{-2} were apparent in NW, NE, SW and SE Scotland and a decline of –63% occurred in Wales from 1920 to 1950. Post-1950 regional variation in bag trends became apparent, with differences in percentage change between northern English regions and those in Scotland and Wales. From 1950 to 1980, bags increased by 106%, 202% and 127% in the N Pennines, North York Moors and NW England and declined by 16% in the S Pennines, while only SE Scotland showed an increase in number of grouse shot during the same period (82%). Other regions in Scotland or Wales showed no significant trend in number of grouse shot from 1950 to 1980. During 1980–2010, bags increased by 42% in the N Pennines, but declined by 54% in NE Scotland and 83% in Wales.

Variation in keeper density, forest cover and moor extent among time periods and regions

Keeper density varied among time periods in each region (Table 3). During 1890–1920, keeper density declined by 12% in the North York Moors, increased by 17% in NE Scotland and showed no significant change elsewhere (Fig. 4). During 1920–1950, keeper density declined by 21% in NW Scotland. Keeper density in N Pennines increased by 14% and 25% during 1950–1980 and 1980–2010, respectively. Declines of 25% and 11% occurred in the S Pennines and NE Scotland from 1950 to 1980, followed by a 43% increase in NE Scotland from 1980–2010. Percentage increases in keeper density of 49% and 74% also occurred in the North York Moors and in SE Scotland during 1980–2010 (Fig. 4). Although changes were apparent in some other time periods and regions, only significant differences are reported here.

Extent of heather moorland was similar in most regions pre-1950, but declined thereafter in the North York Moors, first by 7% during 1950-80 and then by 22% (1980–2010) and by 3% in NE Scotland and 9% in SE Scotland from 1950 to 1980 (Fig. 4). Declines in moor extent were linked to increases in forest cover, which rose in the North York Moors by 6% from 1950 to 1980 and by 10% from 1980 to 2010, and in SE Scotland by 8% during 1980–2010. Significant increases in forest cover were also apparent in the N Pennines (3%), NW Scotland (6%) and Wales (14%), but no corresponding declines in heather moorland extent occurred in these regions (Fig. 4).

As percentage change in forest cover and moor extent were negatively correlated (Pearson's product-moment correlation: r = 0.72, p < 0.001, n = 36), we included only moor extent in a GLM examining variation in percentage change in grouse bags. No significant correlation between keeper density and moor extent was found (r = –0.11, p = 0.52,
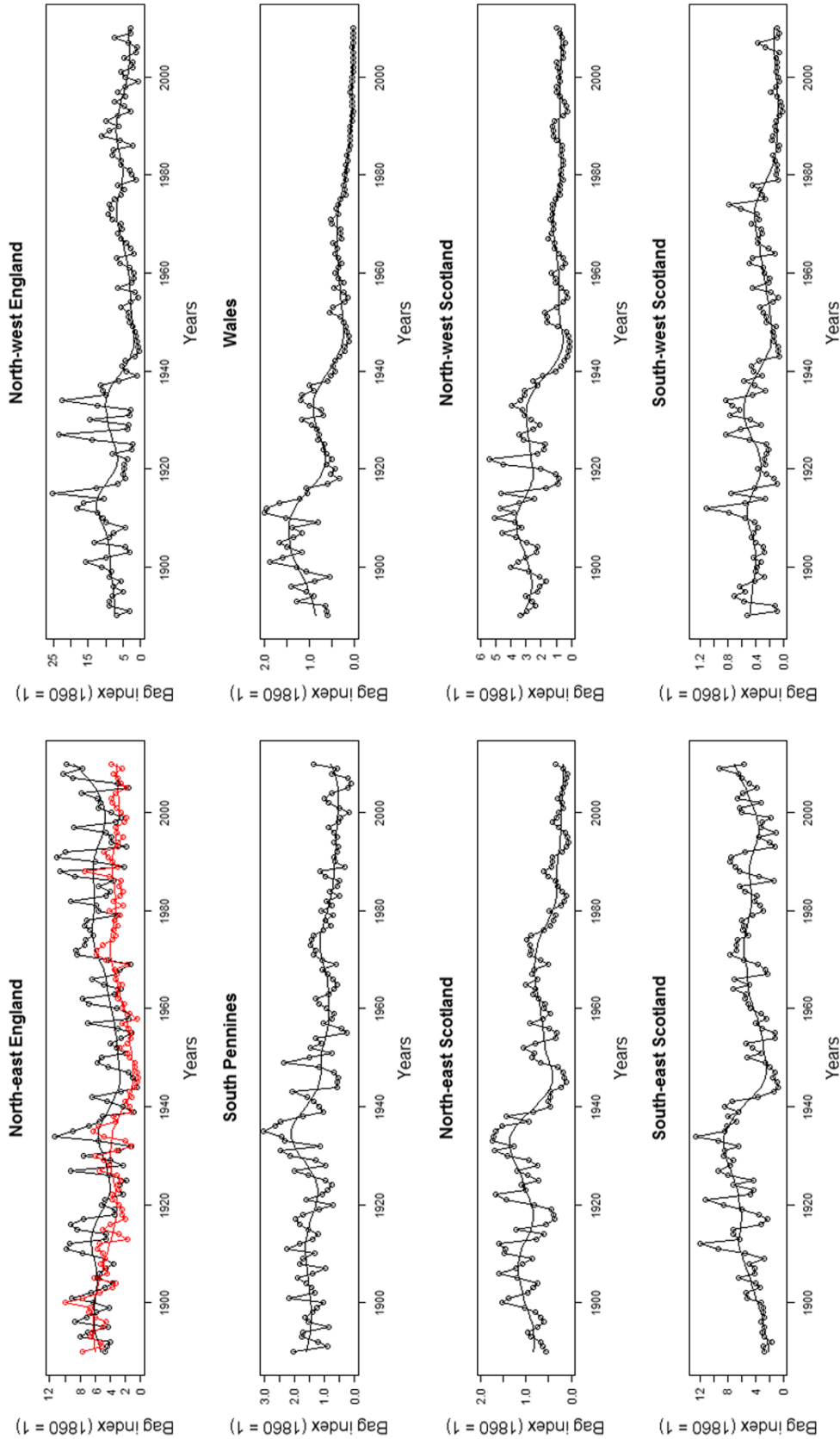
Figure 2. Annual red grouse index of bag density (number of birds shot km⁻²) with underlying long-term trends from GAMs for nine regions of Britain from 1890–2010 where 1860 = 1. For North-east England, N Pennines = black line and North York Moors = red line. Note differences in scale.
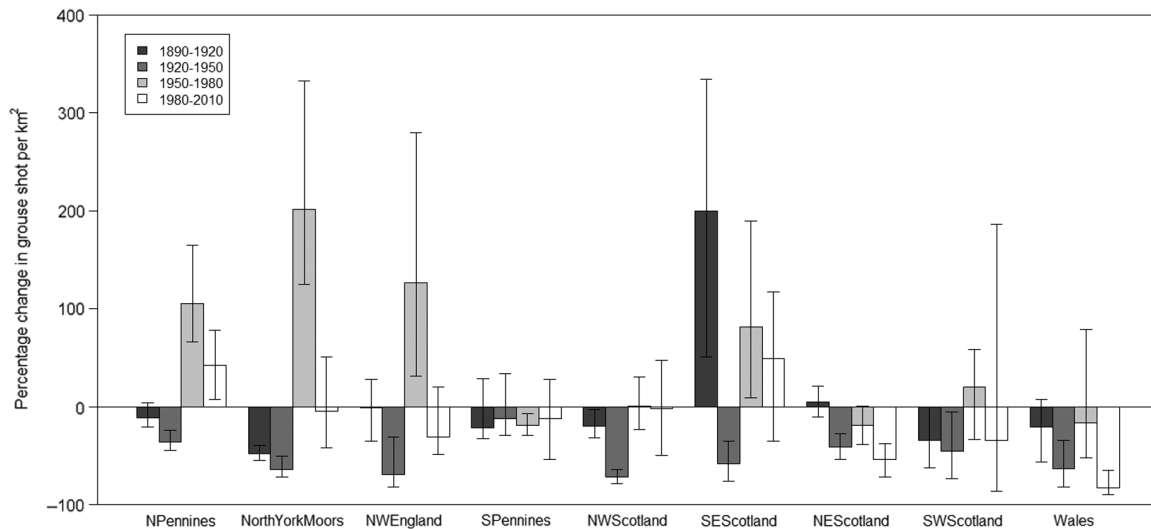
Figure 3. Percentage change in red grouse bag indices from 1890–2010 in each region. Upper and lower 95% confidence limits are displayed.

n = 36). There was a significant positive relationship between percentage change in grouse bags and keeper density (Wald test: $\chi^2_1 = 5.90$, p < 0.01; slope $\pm$ SE = 0.008 $\pm$ 0.003), while no effect of moor extent was found ($\chi^2_1 = 0.27$, p = 0.25).

Discussion

Red grouse are dependent upon heather habitat and benefit from predator control (Stillman and Brown 1994, Fletcher et al. 2010), and long-term changes in numbers may be explained by spatiotemporal changes in upland land use and management. Although cycles in grouse populations were apparent in all nine regions, we found that the underlying long-term trends in red grouse abundance calculated using bag records varied among regions of Britain, and coincided with changes in intensity of moor management, as represented by keeper density on grouse moors.

Change in land use has been shown to be a factor driving declines in upland bird populations, including red grouse, black grouse *Tetrao tetrix*, curlew and golden plover, by contributing to declines in extent of suitable habitat or by creating habitat, such as forestry, preferred by generalist predators (Baines 1996, Robertson et al. 2001, Calladine et al. 2002, Amar et al. 2011b, Douglas et al. 2014). Loss of heather moorland to afforestation reduces habitat availability for moorland birds and may also increase vulnerability to predation by predators that use forests (Stroud et al. 1990, Paton 1994, Baker and Harris 2006). However, natural regeneration of woodland in upland areas can have positive effects

on woodland birds, such as black grouse (Watson and Moss 2008), noting that mature closed-canopy forestry plantations are unlikely to benefit this species (Grant and Dawson 2005). Some ground-nesting moorland birds benefit from predator control conducted by gamekeepers (Fletcher et al. 2010) and declines in gamekeeper density and associated predator control and heather burning since the 1940s (Barnes 1987, Heydon et al. 2000) may be linked to national declines in grouse bags from 1920 to 1950 and with regional declines in post-1950 grouse bags.

Changes in red grouse bags over time varied among regions after 1950. During 1950–1980, most English regions (with the exception of the S Pennines) exhibited increases in number of grouse shot km^{-2}, and further increases occurred in the N Pennines from 1980 to 2010. In comparison, most Scottish regions exhibited no significant changes in grouse bags from 1950 and declines occurred in NE Scotland and Wales from 1980 to 2010.

Keeper density was positively associated with change in grouse bags. Increases in keeper density occurred from 1950 in the N Pennines (14% and 25% during 1950–1980 and 1980–2010 respectively) and from 1980 to 2010 in the North York Moors (49%). Increases in keeper density may explain why management practices that improve habitat for red grouse, such as rotational burning, have increased in northern England since 1970s (Yallop et al. 2006, Douglas et al. 2015). Whilst keeper density in NE Scotland increased by 43% during 1980–2010, no corresponding increase in grouse bags occurred. However, keeper density declined by 11% in NE Scotland from 1950–1980 and remained low during 1980–2010, which may explain

Table 3. Mean $\pm$ se number of keepers per km^2 of moorland for each region and time period.

|	Wales	S Pennines	North York Moors	N Pennines	NW England	SW Scotland	SE Scotland	NW Scotland	NE Scotland
1890–1920	0.19 ± 0.03	0.21 ± 0.01	0.11 ± 0.01	0.09 ± 0.01	0.08 ± 0.20	0.13 ± 0.01	0.22 ± 0.02	0.06 ± 0.01	0.12 ± 0.01
1920–1950	0.20 ± 0.03	0.40 ± 0.04	0.09 ± 0.01	0.24 ± 0.04	0.23 ± 0.05	0.14 ± 0.01	0.19 ± 0.01	0.08 ± 0.01	0.14 ± 0.01
1950–1980	0.07 ± 0.01	0.13 ± 0.01	0.11 ± 0.01	0.11 ± 0.01	0.15 ± 0.01	0.16 ± 0.02	0.09 ± 0.01	0.04 ± 0.01	0.11 ± 0.01
1980–2010	0.09 ± 0.01	0.12 ± 0.01	0.10 ± 0.01	0.14 ± 0.01	0.15 ± 0.01	0.29 ± 0.03	0.11 ± 0.01	0.05 ± 0.01	0.09 ± 0.01
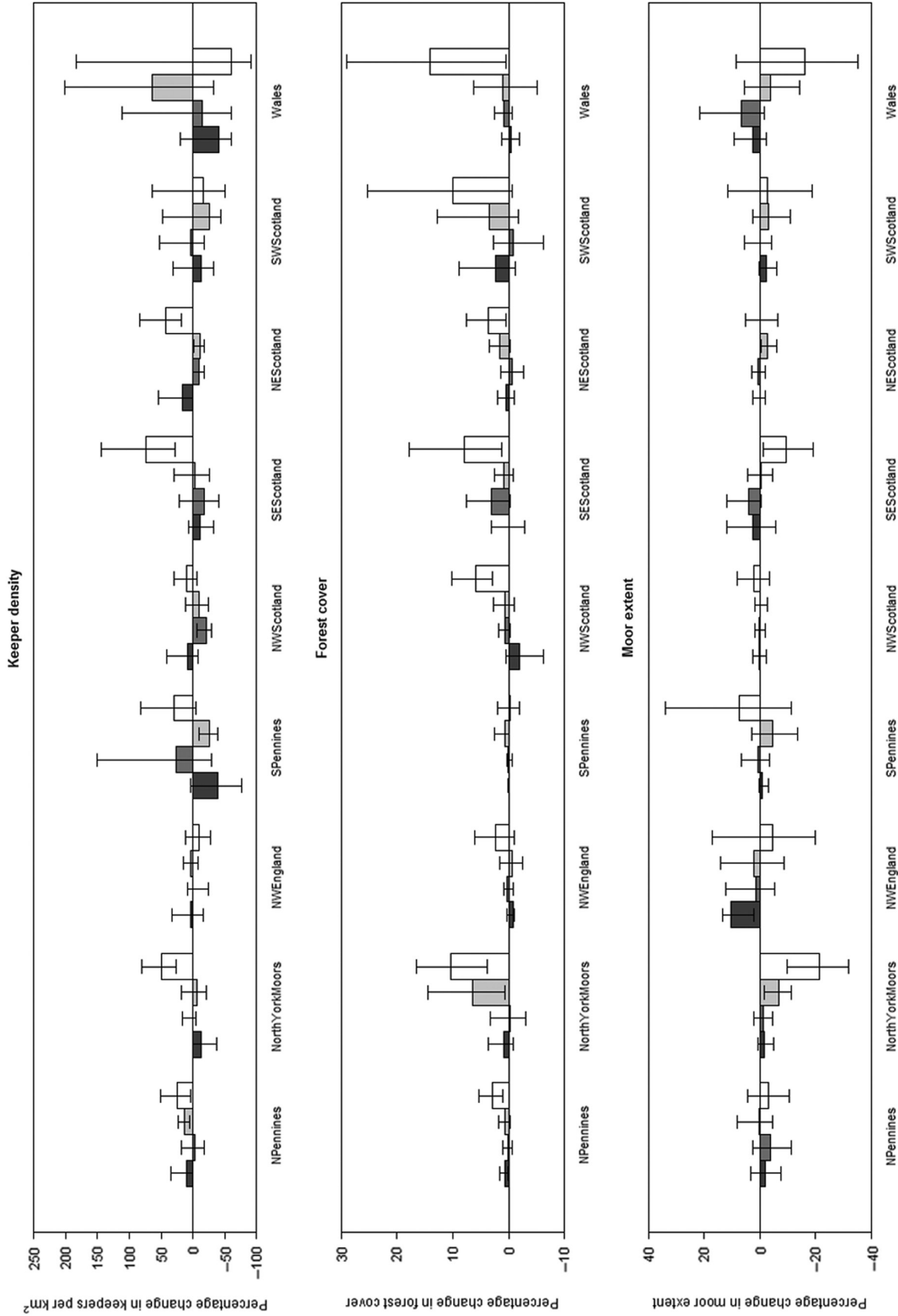
Figure 4. Percentage change in indices for keeper density, forest cover and moor extent from 1890–2010 in each region. Upper and lower 95% confidence limits are displayed. Note differences in scale.

why grouse bags declined in the latter period. A number of studies have shown that changes in keeper density produce changes in grouse abundance (Robertson et al. 2001, Baines et al. 2008, Fletcher et al. 2010), and that there is a direct causal relationship resulting from the management carried out by moorland gamekeepers. Employing keepers is a major investment for a grouse moor, hence moor owners may remove gamekeepers if grouse numbers decline to the point where a shoot becomes unviable. In such cases driven shooting ceases and management switches to alternative forms of land use such as intensive sheep grazing or forestry, with negative effects on grouse habitat and abundance.

Forest cover also increased in NE Scotland from 1980 to 2010. Afforestation rates, particularly of non-native species, increased across upland Britain from the 1950s, and peaked in the 1970s and 1980s, owing to the introduction of state funded incentives, encouraging public and private planting initiatives (Barton and Robertson 1997). Afforestation rates varied among British regions, but tended to be highest in northern Scotland and Wales in the 1970s and 1980s (Barton and Robertson 1997, Shrubb et al. 1997, Mackey et al. 1998). While afforestation is likely to reduce extent of suitable habitat for moorland birds, we found no relationship between moor extent and changes in grouse bags in different regions. However, this is perhaps not surprising as management intensity is likely to be more important in affecting number of grouse shot per km^2 of moorland than size of moor. Afforestation has been linked to increased abundance of predators (such as red fox and corvids), thus increasing predation risk amongst ground-nesting birds, including grouse, which may then tend to avoid forest edges (Stroud et al. 1990, Andrén 1992, Douglas et al. 2014).

While there was no significant decline in keeper density post-1950, moors in Wales showed the greatest increase in forest cover of any region during 1980–2010. With no corresponding increase in keeper density, increased forestry may increase predation of birds nesting on nearby moorland (Stroud et al. 1990, Baker and Harris 2006). Hence, increased afforestation in Wales together with declines in grouse moor management practices may explain declines in both grouse bags and the abundance of golden plover and curlew (Shrubb et al. 1997, Sim et al. 2005, Warren and Baines 2014).

Our analyses describe general changes in land use and management in different regions of Britain, but our use of questionnaire data to examine changes in land use and management over time has some limitations. Areas of private moorland, sold to and afforested by the state, may not have been included in questionnaire responses; and moors where grouse shooting had ceased, especially post-1940, may not have continued providing responses, thus underestimating declines in grouse, keeper density and moor extent in some regions (Barnes 1987, Robertson et al. 2001). Uneven distribution of bag records within time periods may have introduced bias into estimation of trends, especially in regions where grouse shooting has declined in recent years (e.g. Wales, Warren and Baines 2014). Also, as no data were available on the annual number of shooters or shoot days per moor, we cannot prove that variation in hunter effort did not affect our results. Bag size of willow ptarmigan

L. l. lagopus has been shown to be related to hunter effort (Willebrand et al. 2011), and sex- or age-related bias in bags may be apparent depending on differences in vulnerability to shooting (Hannon and Martin 2006, Bunnefeld et al. 2009). However, hunting methods and habitat management for red grouse and willow ptarmigan are very different, as red grouse habitat and predators are deliberately managed by gamekeepers to ensure a surplus that is harvested by driven shooting. Studies comparing counts and bags have shown that over extended time periods red grouse harvest data provide a good proxy for red grouse abundance (Cattadori and Hudson 1999, Cattadori et al. 2003), not least because the number of shoot days is set according to pre-shooting abundance. Over 100 years ago, it was already recognized that factors such as habitat, predators and parasites were more influential in determining bags than hunter effort (Lovat 1911). Hence if there is an effect of effort, we do not expect it to be important.

As well as driving declines in red grouse abundance in the British uplands, loss of managed heather moorland is likely to have impacted other moorland birds of national and international conservation concern, such as curlew and golden plover (Eaton et al. 2009, Amar et al. 2011b). Thus the long-term NGC data, by relating grouse bags to keeper density and land use change, may identify possible drivers of changes in other birds. Techniques that restore heather habitats and reduce generalist predators within and in proximity to them may help conserve red grouse and other upland birds such as black grouse and waders breeding on moorland (Tharme et al. 2001, Warren and Baines 2004, Fletcher et al. 2010, Douglas et al. 2014). However, changes in public perception of grouse shooting, and hunting in general could potentially influence policy and land use in the uplands with consequences for bird populations dependent upon managed grouse moors.

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Supplementary material (available online as Appendix wlb.00276 at <www.wildlifebiology.org/appendix/wlb-00276>). Appendix 1.