Black grouse response to dedicated conservation management

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A b s t r a c t . Halting and reversing declines of black grouse populations in Britain represents a major conservation challenge. Programmes of dedicated management aiming to benefit black grouse have been introduced on several sites and areas across the species' British range. These initiatives generally employ various managements, most aimed at improving habitat conditions, but some at reducing direct sources of mortality. Black grouse populations appear to respond to such conservation initiatives, with increases in numbers following the introduction of management in all six cases examined. However, these increases were not always sustained, and the frequent lack of control sites and baseline data means that there is limited ability to assess the full impact of management, and to distinguish management effects from the effects of coincident environmental variation. Similarly, it is difficult to identify the specific managements critical to producing black grouse response. Evidence exists for benefits of reducing large herbivore densities and of reducing generalist predator abundance, although these may be temporary in the case of herbivore reductions. Variation in annual productivity appeared to be a major determinant of population trends at two sites where productivity estimates were available, suggesting that responses to management may often arise via effects on productivity.

Key words: *Tetrao tetrix*, conservation, habitat management, grazing reductions, predation management

Introduction

Black grouse *Tetrao tetrix* L. populations have undergone declines throughout much of their range during the last few decades, with these being particularly severe in Central and Western Europe (H a g e m e i j e r & B l a i r 1997, S t o r c h 2000). In keeping with this trend, black grouse in Britain have been in decline since the early 1900s (H o l l o w a y 1996), and the number of displaying males in spring is now estimated to be approximately 5 000, representing a 22% decline since the mid 1990s (S i m et al. 2008). Associated with this long-term decline, there has been a substantial contraction of black grouse range in Britain, with these declines and range contractions most severe in the southern parts of the British range (G i b b o n s et al. 1993, H o l l o w a y 1996). Thus, whilst the distribution remains relatively contiguous in the Scottish Highlands, populations have become fragmented and isolated in the southern parts of the range, particularly in England and Wales (H ö g l u n d et al. 2007).

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As in other parts of their European range, various wide-scale habitat and land-use changes have been the main cause of long-term declines of black grouse in Britain (Grant 2007). Such changes have directly affected both the woodland and open ground habitats on which black grouse depend, and may have resulted in increased predation pressures (Summers et al. 2004). In recent decades, the maturation and canopy closure of commercial conifer plantations, which provide suitable habitat in the early years following planting, is likely to have been a widespread cause of declines (Pearce-Higgins et al. 2007). Halting and reversing black grouse population declines in Britain represents a major conservation challenge, given the need to influence management practices across several land-use sectors, and ensure the adoption of sympathetic regimes on a wide-scale.

To date, a major conservation strategy in Britain has been to initiate programmes of dedicated management for black grouse in specific areas or sites. These range from programmes of work undertaken on single sites (often nature reserves), to those undertaken across relatively large areas, encompassing multiple sites, and effectively operating on a regional scale (e.g. North Wales – Lindley et al. 2003). A key objective of such initiatives is that they demonstrate management approaches that are effective in promoting recovery in black grouse numbers and which can be adapted for use more widely to facilitate black grouse conservation at regional or national levels. Such initiatives often employ a wide range of different management approaches, most of which aim to improve the condition of habitats for black grouse, but which can include reducing direct sources of mortality – e.g. legalised removal of predators and removal of deer fences (Table 1).

In this paper we review the findings from such conservation initiatives to determine the evidence there is for success, in terms of achieving increases in black grouse numbers. We also assess the extent to which existing data allow an understanding of the causes

Table 1. The different managements used on three sites or areas where conservation management regimes likely to benefit black grouse have been introduced.

Management	Abernethy	Corrimony	Wales 'key' sites
Reductions in numbers of deer and/or sheep	Yes	Yes	No[1]
Introduction of cattle grazing	No[2]	Yes	No
Cutting and/or burning field-layer vegetation in small blocks or strips	Yes[3]	Yes[3]	Yes
Blocking of drains to create areas of wet habitat	No	Yes	Yes
Thinning and felling in conifer plantations to reduce stand density and create open areas, particularly on edges adjacent to moorland	Yes	Yes	Yes
Tree planting to create 'native' woodland	Yes	Yes	No
Legalised control of generalist predators	Yes[4]	No	Yes[5]
Removal of deer fences	Yes	Yes	Not applicable

Notes:
1. Not incorporated as specific part of project, but some reductions in sheep numbers via implementation of agri-environment schemes.
2. A small-scale trial of effects of cattle grazing on field-layer vegetation was undertaken in one part of reserve
3. Begun in the last three to four years only, as part of trials to test the efficacy of these managements
4. Not in place for full period of management; several years without predator control as part of a test of its efficacy (Summers *et al.* 2004)
5. Not specifically incorporated as part of the conservation project, but introduced onto one of 'key' sites between 1997 and 2000, and present for whole period on parts of some other 'key' sites

behind such responses and consider the limitations in our understanding of these responses, and outline research approaches that are required to successfully develop conservation management for black grouse in Britain.

Methods

Effects of conservation management on black grouse abundance

Data on trends in black grouse abundance were available from two RSPB nature reserves in the Scottish Highlands (Abernethy Forest and Corrimony) where management regimes considered likely to benefit black grouse have been in place for 10 years or more, and from a project begun in Wales in 1997, where management for black grouse was focussed on six 'key' sites, estimated to hold 80 % of the Welsh population at the start of the project (Lindley et al. 2003, Table 2). The period of most intensive management was from 1998 to 2004 in Wales, although management still continues within the 'key' sites. Abernethy includes the largest remnant of native pinewood remaining in Scotland and covers c.137 km^2, of which c.33 km^2 are wooded, whilst Corrimony extends over an area of c.15 km^2, incorporating open moorland, birch (*Betula* spp) wood and Scots pine (*Pinus sylvestris* L.) plantation. Each of the 'key' sites in Wales was subdivided into 3 'focal lek' areas, with each 'focal lek' area centred on the location of a main lek and covering an area of 1.5 km radius around that lek. These areas remained constant, even if the lek position changed over time. Open moorland and conifer plantation were the main habitats on these 'key' sites.

In each of these cases black grouse abundance was measured using dawn counts of displaying males at spring lek sites (Cayford & Walker 1991). Searches of potentially suitable black grouse habitat were made in early morning to locate lek sites, and leks were visited at dawn to conduct counts in April and May (Gilbert et al. 1998). At Abernethy and Corrimony, two such counts (one in April, one in May) were made across all known leks on each site in each year of monitoring, with the maximum of these two counts being taken as the site total for that year. Counts in Wales were undertaken annually within the six 'key' sites from 1997 (except in 2001 due to the foot and mouth outbreak), where there was comprehensive coverage of all potentially suitable habitat (Lindley et al. 2003). In addition, data were available from earlier systematic surveys in Wales (Grove et al. 1988, Williams et al. 1992, 1995, 1997), with wider counts also being made in 1997, 2002, and 2005 – 2007 (based upon searches of all areas holding black grouse records from the earlier surveys, plus stratified random sampling from within the known black grouse range in Wales in both 2002 and 2005 – Lindley et al. 2003, Sim et al. 2008). Counts of displaying males were made between 15 April and 15 May in Wales.

Data on changes in the abundance of black grouse were obtained for a further three sites and areas where similar management initiatives were known to be underway, and where appropriate information could be sourced either from the published literature or via contacts with relevant land managers. These were Creag Meagaidh National Nature Reserve and Mar Lodge Estate, both in the Scottish Highlands, and a series of trial sites in the North Pennines (Table 2). Reductions in grazing pressure by large herbivores (red deer *Cervus elaphus* and/or sheep) were a main management in each of these cases, but the management regime at Mar Lodge has also included thinning and clearing in conifer plantations, native woodland planting and removal and marking of deer fences (Calladine et al. 2002, Scottish Natural Heritage (SNH), unpubl. data, National Trust for Scotland (NTS), unpubl. data). Dawn counts of displaying males at spring lek sites were used as the main measure of abundance in all of these cases, with data being obtained by similar methods to those described above. Such counts are used widely as an index of abundance and population size (Angelstam 1983, Hancock et al. 1999).

Table 2. The years in which management regimes likely to be sympathetic to black grouse have been introduced at six different sites and areas. The number of years over which data on changes in black grouse abundance are available is also given. Start years at some sites (e.g. Abernethy) are essentially approximate because the full suite of managements was phased in over several years.

Site/area	Year management initiated	Period over which black grouse abundance measured	Source
Abernethy, Scottish Highlands	1990–91	1991–2007	this study
Corrimony, Scottish Highlands	1997	1997–2007	this study
Wales 'key' sites	1997	1997–2007	this study
Creag Meagaidh, Scottish Highlands	1988–90	1995–2003	SNH, unpubl. data
Mar Lodge Estate, Scottish Highlands	1992	1997–2007	NTS, unpubl. data
North Pennines trial sites	early to mid 1990s (variable between sites)	≤ 9 years since grazing reduction on site	Calladine et al. 2002, Warren et al. 2003

Productivity and trends

Relationships between productivity of black grouse and changes in their abundance were examined for both Abernethy and Corrimony. Productivity was expressed in terms of chicks per hen, based upon counts made with trained dogs in late July or early August when chicks are well grown (Baines 1996, Calladine et al. 2002, Summers et al. 2004), and when little additional mortality is expected prior to broods breaking up (Baines 1993). Counts at Abernethy were made through sections of the forest totaling c.5 – 6 km^2 in each year, using a team of people walking line abreast with trained dogs to flush and count hens and associated chicks (Summers et al. 2004). At Corrimony counts were conducted using a single observer with a trained dog, walking a series of transects across the suitable habitat in each year. Sample sizes of hens in each year of monitoring ranged from 7 – 27 at Abernethy (mean = 15.4 ±;1.3; SE) and 5 – 11 at Corrimony (mean = 6.6 ± 0.6; SE).

At both of these sites, black grouse numbers were modelled in relation to the estimated productivity, using the productivity in a given year to predict numbers in the following year. A step-wise approach was used, with the predicted numbers modelled from the observed number in the previous year on each occasion (Rothery et al. 2002). For the purposes of this exercise it was assumed that; (i) the annual adult survival rate was 0.60 (and that this did not vary seasonally); (ii) juvenile survival rate up to 1 March was 0.45; and (iii) there was an equal sex ratio. The assumed adult survival rate represents the approximate mean value for adults from eight other study areas (Lindèn 1981, Angelstam 1984, Picozzi & Hepburn 1984, Niewold 1990, Caizergues & Ellison 1997, Baines et al. 2007), whilst for juveniles the assumed value is lower than the average of 0.58 from three study areas (a lower value is used because adult survival rates were relatively high on each of these three areas – Caizergues & Ellison 1997, Baines et al. 2007).

Black grouse chicks in the Scottish Highlands hatch in the second half of June, and are known to be vulnerable to the effects of inclement weather in the first one to two weeks after hatching. Such relationships have already been established for black grouse at Abernethy, where productivity is negatively correlated with June rainfall (Summers et al. 2004). Therefore, relationships between productivity and June rainfall were investigated for both Abernethy and Corrimony, to allow some assessment of whether apparent responses to conservation management initiatives could instead be attributable to variation in June rainfall. These relationships were investigated from 1997 onwards (no Corrimony data being available before then), using rainfall during the second half of June. Rainfall data were obtained from nearby weather stations with appropriate data series (i.e. Dorback and Corrimony Grange, for Abernethy and Corrimony, respectively) via the British Atmospheric Data Centre.

Analyses

Statistical analyses were undertaken using the GENMOD procedure in SAS 8.02 (SAS Institute 2001). Trends in counts of spring displaying males in Wales were analysed in relation to whether or not they were on 'key' sites (i.e. where conservation management was introduced) and in relation to whether they occurred in the period before or after the introduction of conservation management, with year included as a covariate. Thus, the count of males was made the dependent variable, using a Poisson error distribution and log link function. Analyses of productivity in relation to June rainfall also used a Poisson error distribution and log link function, with the number of chicks as the dependent variable and the number of hens declared as an offset. The statistical significance of variables in these analyses were assessed by treating the change in residual deviance associated with each term as χ^2 with the appropriate degrees of freedom, unless data were over-dispersed, in which case F-tests were used following rescaling (Crawley 1993, SAS Institute 2001). Step-down procedures were used in multivariate analyses. Two-tailed significance levels are used throughout, accepting significance at the level $P \leq 0.05$.

Results

Trends in black grouse abundance under conservation management

Following the introduction of conservation management, black grouse numbers increased on all three of the areas considered in most detail in this study (Fig. 1). These increases began rapidly, within one to five years of management being introduced, and in each of these areas numbers are now higher than at the start of the management programme, 11 – 18 years previously. Thus, over the full period of management to date, the numbers of spring displaying males increased from 43 to 90 at Abernethy, 16 to 57 at Corrimony and 108 to 185 on the six 'key' sites in Wales. However, these increases have not been continuous in all cases and at Abernethy, where the increase was initially greatest and most rapid, and where management has been in place longest, numbers have shown a marked fluctuation, peaking at 165 displaying males after seven years of management.

Black grouse also appeared to respond to management on the three other areas for which data were obtained, although at both Creag Meagaidh and Mar Lodge abundance data were not available for the first few years after the start of management (Table 2). Thus, at Creag Meagaidh numbers of spring displaying males increased from c.30 to 67 between 1995 and 1998 (SNH, unpubl. data), and at Mar Lodge from 105 to 192 between 1997 and 2007 (NTS, unpubl. data). On the North Pennines trial sites, the average numbers had increased by c.50 % within four or five years after the reductions in sheep densities (W a r r e n et al. 2003). However, the trends on both Creag Meagaidh and the North Pennines sites mirrored those at Abernethy; numbers at Creag Meagaidh subsequently declined to 23 males by 2003 and after nine years of reduced sheep densities, numbers on the North Pennines sites had returned to levels similar to those when sheep densities were first reduced. Despite these trends on the North Pennines trial sites, the overall population in this region has increased in recent years, with the increase being coincident with the wider adoption of sheep reductions, combined with other habitat managements (e.g. planting of native woodland in hillside 'ghylls') and increases in existing levels of predator control in some areas (W a r r e n & B a i n e s 2004, 2008).

Of the six management initiatives reviewed here, only the Wales 'key' sites and the North Pennines trial sites had either pre-management baseline data or data from some form of control sites available, against which to compare the trends occurring under the management regimes (C a l l a d i n e et al. 2002, L i n d l e y et al. 2003). These comparisons showed that on the 'key' sites in Wales, prior to the introduction of conservation management, numbers of displaying males had been declining steadily since at least 1986, whilst no equivalent reversal of the decline occurred outside of the 'key' sites. The difference in trends associated with the occurrence of management was significant (Fig. 2). In the North Pennines, the trends

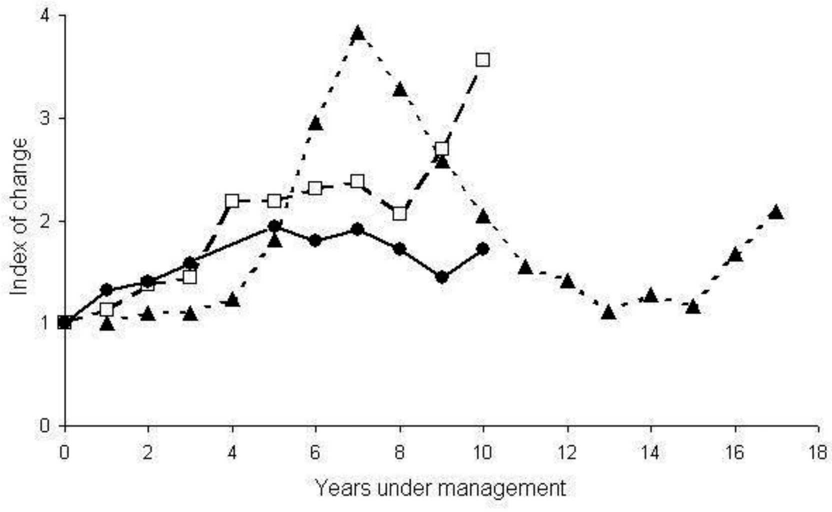

Fig. 1. Changes in the abundance of black grouse in relation to the time since the introduction of conservation management at three sites or areas. The index is calculated as the number of spring displaying males in that year divided by the number in the year when management began (so that values > 1 represent increases, values < 1 decreases). Trends are shown for Abernethy (filled triangles, short dashed line), Corrimony (open squares, long dashed line) and Wales 'key' sites (solid circles, solid line).

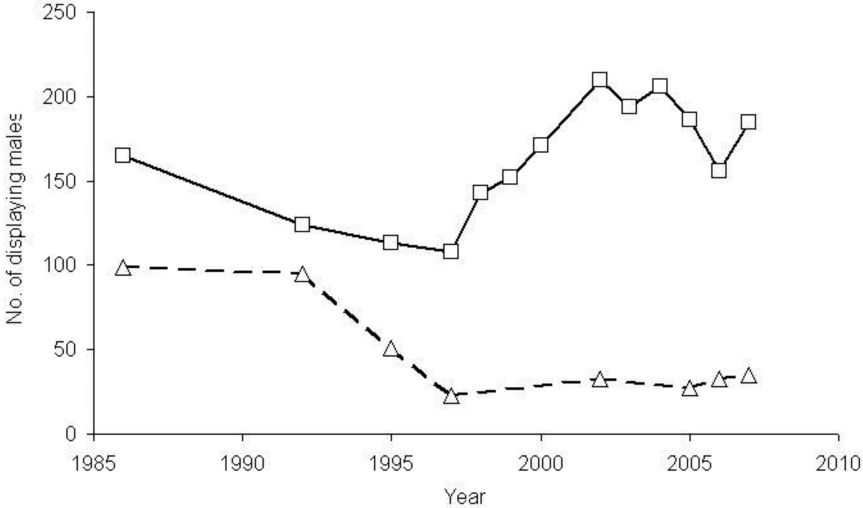

Fig. 2. Trends in the number of spring displaying male black grouse on 'key' sites in Wales (square, solid line) in relation to the introduction of conservation management, and at other black grouse sites in Wales (triangle, dashed line). Management was introduced onto 'key' sites in 1997. The effect of the interaction between year and management occurrence was significant ($F_{1, 16}$ = 15.82, P = 0.001) as were effects of 'key' site ($F_{1, 16}$ = 23.6, P < 0.001) and management occurrence ($F_{1,16}$ = 15.68, P = 0.001), whilst year had a close to significant effect ($F_{1,16}$ = 3.77, P = 0.07). There was no significant effect of the interaction between year and 'key' site ($F_{1,15}$ = 1.12, P = 0.31).

on the trial sites were not mirrored on 'paired' reference sites with no stock reductions, so providing stronger evidence that the changes in black grouse abundance on the trial sites were indeed a consequence of the stock reductions (C a l l a d i n e et al. 2002).

Productivity and trends

The annual percentage change in the number of spring displaying males at Abernethy was positively correlated with estimated productivity (i.e. chicks per hen) in the previous year (r = 0.57, P < 0.05). However, at Corrimony the relationship between the annual change in numbers and the estimated productivity in the previous year was negative, although it was not significant (r = -0.59, P = 0.07). The modelling of spring numbers on the basis of annual productivity demonstrated close agreement between predicted and observed numbers at Abernethy, indicating that variation in the productivity of birds at Abernethy has been the main driver of population change on this site (Fig. 3). Analogous modelling of the Corrimony data suggested reasonable agreement between observed and predicted abundance, despite the lack of positive correlation between annual changes in numbers and the previous year's productivity. The main discrepancy between the predicted and observed numbers at Corrimony occurs in the last two years of the data series, with observed and predicted trends differing (Fig. 3). Possible causes for discrepancies may include the relatively small size of the Corrimony site (e.g. causing productivity on neighbouring land to sometimes have a large influence on the numbers of displaying males on this site), and small sample sizes leading to unreliable productivity estimates in some years. Alternatively, there may have been real changes during the monitoring period in either the survival rate of adults on the site, or of immigration and emigration of adults to and from the site.

As expected from previous analyses (Summers et al. 2004), productivity at Abernethy was negatively correlated with June rainfall, but there was no significant relationship between rainfall and productivity at Corrimony (Fig. 4). Rainfall during the second half of June at the two sites was not significantly correlated across years (r = 0.56, $P = 0.09$).

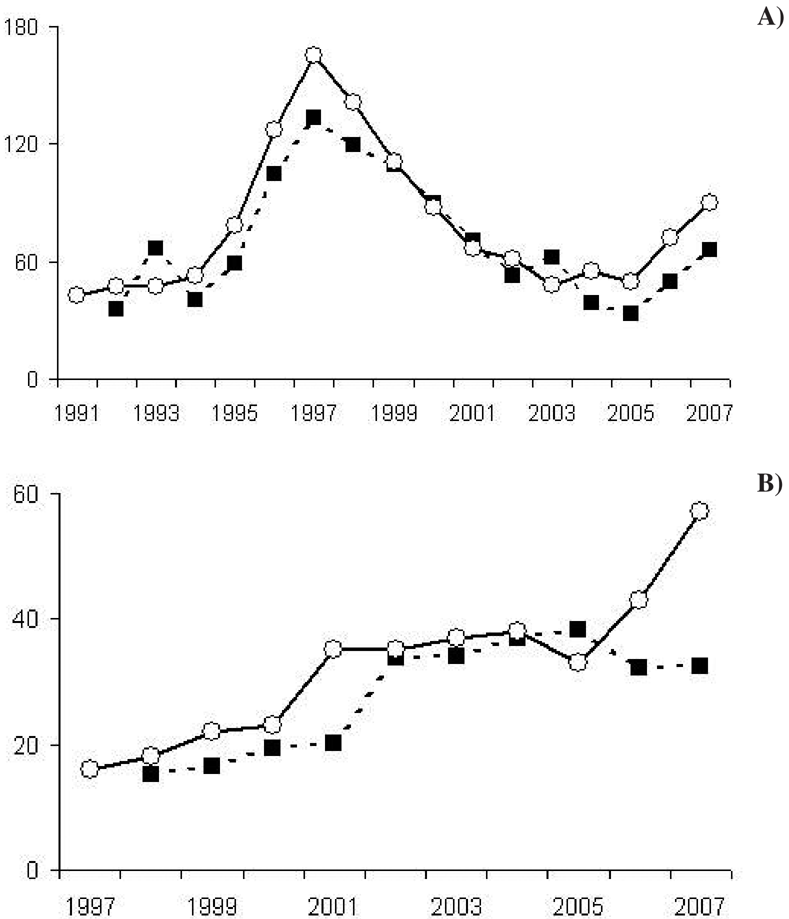

Fig. 3. Observed (open circle, solid line) and predicted (filled square, dashed line) black grouse abundance at Abernethy (A) and Corrimony (B). Predictions of abundance are produced from the estimated annual productivity, using assumed adult and juvenile survival rates (see text). For Abernethy; predicted = 0.79*observed + 6.68 ($r^2 = 0.85$, $P < 0.0001$). For Corrimony; predicted = 0.54*observed + 9.56 ($r^2 = 0.46$, $P = 0.03$).

Discussion

Evidence of response to conservation management

The findings from the initiatives examined and reviewed here suggest that black grouse do respond to conservation management, and this appears to be a consistent occurrence. However, we have been able to assess findings from a small number of such initiatives only, and of those considered, in just two cases were data available from pre-management periods

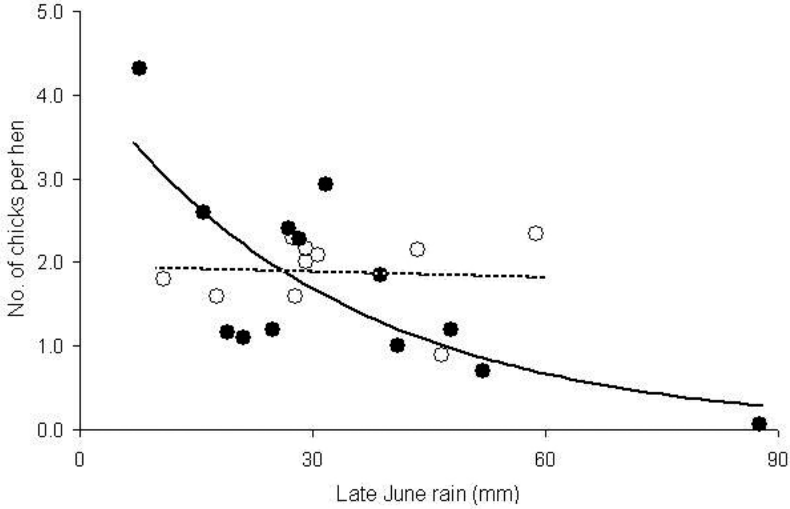

Fig. 4. The relationship between black grouse productivity and rainfall during the second half of June, at Abernethy (filled circles, solid line) and Corrimony (open circles, dashed line). For Abernethy; chicks per hen = exp(-0.031*rain + 1.44), $F_{1,11} = 15.01$, $P < 0.01$. For Corrimony; chicks per hen = exp(-0.0012*rain + 0.67), $\chi^2_1 = 0.03$, $P = 0.86$.

and/or from some form of control sites. Thus, in some cases at least, the apparent response of black grouse may simply have been coincident with the occurrence of management, as opposed to having been caused by it. The findings from Abernethy may appear to reflect such a situation. At this site variation in productivity appears to be the major determinant of population trends, with June rainfall having a significant effect upon productivity. Therefore, June rainfall has been an important factor in determining population trends at Abernethy, but despite the potentially strong influence of this effect, there have still been demonstrable effects of management, with trials demonstrating that the removal of crows (*Corvus corone*) is associated with higher productivity in years of low June rainfall (Summers et al. 2004). At Corrimony, productivity appears to be largely unaffected by June rainfall, so that the increase in numbers on this site appears to be unrelated to this particular environmental determinant of black grouse productivity (although the small samples from which productivity estimates are derived at Corrimony needs to be borne in mind in making such a conclusion – see above).

The consistency of the apparent responses to management, combined with the findings from those situations in which more detailed assessments have been possible (i.e. Abernethy, Wales 'key' sites and North Pennines trial sites), indicate that these management initiatives generally do have a real effect on black grouse populations. However, further rigorously designed management trials, incorporating control sites, are required to fully assess the extent of the management effects and disentangle them from other potentially confounding effects. Furthermore, although evidence of black grouse response was consistently found, in some situations the initial increases in black grouse abundance following the introduction of management were not sustained, with declines occurring subsequently. To date, such a response has occurred at Abernethy, Creag Meagaidh and on the North Pennines trial sites, indicating some limitations in the ability of such management initiatives to deliver recovery of black grouse populations over the longer term.

Understanding responses and identifying the important managements

The wide range of different management treatments used in most of the initiatives considered here, together with the lack of control sites in most cases, means that it is generally impossible to determine the relative contributions of the different managements in causing black grouse response. However, on the North Pennines trial sites the response was a consequence of sheep reductions (this being the sole treatment applied – Calladine et al. 2002), whilst reductions of deer and sheep numbers also appear to have been the main management associated with the apparent (similar) response at Creag Meagaidh (SNH, unpubl. data). Reductions in large herbivore densities may therefore provide initial benefits that are not sustained without further management intervention. This could arise if release from heavy grazing or browsing led to short-term increases in plant productivity, causing increases in the abundance of invertebrate foods for chicks and/or the nutritional status of plant foods for adults – e.g. allowing improved body condition in hens prior to nesting. Alternatively, such effects could occur via changes in the structure of field-layer vegetation; initial benefits of increased height and density (e.g. via improved cover) being lost as vegetation becomes so tall as to impede chick mobility and possibly prevent chicks from drying out in wet weather, so increasing mortality from chilling. Thus, situations in which initial increases in black grouse abundance are followed by declines may be associated with reductions in large herbivore densities and could be explained by the types of processes described above.

Predation may limit black grouse density (Marcström et al. 1988), and the findings from Abernethy (demonstrating the benefits of crow removal to black grouse productivity – Summers et al. 2004), suggest that management to reduce predation is likely to contribute to black grouse response, in some instances at least. However, the importance of predator removal relative to other managements, and the potential interaction between predator densities and habitat managements, including the role that predator densities play in influencing black grouse response to habitat management, remain to be determined. Levels of predator control varied between the six 'key' sites in Wales, providing the opportunity to investigate such effects, and ongoing analyses are attempting to elucidate these issues further.

The close links between black grouse productivity and changes in population size at Abernethy, and to a lesser extent at Corrimony, suggest that much of the response to management at these sites may have arisen via effects on productivity. Annual changes in numbers of displaying males on the Wales 'key' sites are also positively correlated with productivity in the previous year (unpubl. data), whilst productivity on the North Pennines trial sites tended to be higher than on the associated reference sites (Calladine et al. 2002). Therefore, data suggest that much of the benefit to black grouse from these conservation management initiatives often arise via effects on productivity, although the mechanisms for such effects are largely unknown and overall there is a poor understanding of the links between management and demographic processes.

Developing conservation management for black grouse

The findings from the management initiatives considered here provide cause for optimism, in terms of the ability of conservation management to produce increases in black grouse abundance, even if the increased abundance levels are not always sustained. However, it is clear that in most cases a wide range of different managements have been applied in these initiatives, and our understanding of which have been key to producing (and in some cases sustaining) increased black grouse abundance is incomplete. Furthermore, the findings from the existing management initiatives provide us with limited ability only to disentangle real management impacts from other potentially confounding effects. These issues need to be addressed if the efficacy of such conservation management initiatives is to be improved and, perhaps more importantly, if the critical elements of management are to be identified and transferred into wider land management practices (e.g. via forestry policies and agri-environment schemes).

Further research is urgently required to achieve this, particularly in relation to determining the effects of different managements on black grouse productivity and abundance, as well as on the availability of key resources. Management trials that aim to determine the effects of patch burning and cutting of field-layer vegetation on potentially important resources (i.e. vegetation composition and structure, and invertebrate abundance during the early chick-rearing period), and on the usage of the managed patches by black grouse, are now underway at both Abernethy and Corrimony. Trials of this type should aid our understanding of how specific managements affect key resources and, if linked to larger-scale trials that examine management effects on productivity and abundance, may substantially advance existing knowledge and enable more effective conservation.

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LITERATURE

Angelstam P. 1983: Population dynamics of tetraonids, especially the black grouse *Tetrao tetrix* L., in boreal forests. *Abstracts of Uppsala Dissertations from the Faculty of Science 675.*

Angelstam P. 1984: Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scand. 15: 123–134.*

Baines D. 1993: The black grouse report: first approaches towards the restoration of black grouse numbers in Britain. *Unpublished report to English Nature and Scottish Natural Heritage.*

Baines D. 1996: The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. *J. Appl. Ecol. 33: 54–62.*

Baines D., Warren P. & Richardson M. 2007: Variations in the vital rates of black grouse *Tetrao tetrix* in the United Kingdom. *Wildl. Biol. 13 (Suppl. 1): 109–116.*

Caizergues A. & Ellison L.N. 1997: Survival of black grouse *Tetrao tetrix* in the French Alps. *Wildl. Biol. 3: 177–188.*

Calladine J., Baines D. & Warren P. 2002: Effects of reduced grazing on population density and breeding success of black grouse *Tetrao tetrix* in northern England. *J. Appl. Ecol. 39: 772–780.*

Cayford J.T. & Walker F. 1991: Counts of male black grouse (*Tetrao tetrix*) in North Wales. *Bird Study 38: 80–86.*

Crawley M.J. 1993: GLIM for ecologists. *Blackwell Scientific Publications, Oxford.*

Gibbons D.W., Reid J.B. & Chapman R.A. 1993: The new atlas of breeding birds in Britain & Ireland: 1988–1991. *Poyser, London.*

Gilbert G., Gibbons D.W. & Evans J. 1998: Bird monitoring methods. *RSPB, Sandy.*

Grant M.C. 2007: Black grouse. In: Forrester R.W., Andrews I.J., McInerny C.J., Murray R.D., McGowan R.Y., Zonfrillo B., Betts M.W., Jardine D.C. & Grundy D.S. (eds), The birds of Scotland. *The Scottish Ornithologists' Club, Aberlady.*

Grove S.J., Hope Jones P., Malkinson A.R., Thomas D. & Williams I. 1988: Black grouse in Wales, spring 1986. *British Birds 81: 2–9.*

Hagemeijer W.J.M. & Blair M.J. 1997: The EBCC atlas of European breeding birds. *Poyser, London.*

Hancock M., Baines D., Gibbons D., Etheridge B. & Shepherd M. 1999: Status of male black grouse *Tetrao tetrix* in Britain in 1995–96. *Bird Study 46: 1–15.*

Höglund J., Larsson K.J., Jansman H.A.H. & Segelbacher G. 2007: Genetic variability in European black grouse (*Tetrao tetrix*). *Conserv. Gen. 8: 239–243.*

Holloway S. 1996: The historical atlas of breeding birds in Britain and Ireland: 1875–1900. *Poyser, London.*

Lindèn H. 1981: Estimation of juvenile mortality in the capercaillie *Tetrao urogallus* and the black grouse *T. tetrix* from indirect evidence. *Finnish Game Res. 39: 35–51.*

Lindley P., Johnstone I. & Thorpe R. 2003: The status of black grouse in Wales in 2002 and evidence for population recovery. *Welsh Birds 3: 318–329.*

Marcström V., Kenward R.E. & Engren E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. *J. Anim. Ecol. 57: 859–872.*

Niewold F.J.J. 1990: The decline of black grouse in the Netherlands. In: Lumeij J. T. & Hoogeveen Y.R. (eds), The future of wild Galliformes in the Netherlands. *Amersfoort.*

Pearce-Higgins J.W., Grant M.C., Robinson M.C. & Haysom S.L. 2007: The role of forest maturation in causing the decline of black grouse *Tetrao tetrix*. *Ibis 149: 143–155.*

Picozzi N. & Hepburn L.V. 1984: A study of black grouse in north-east Scotland. *Proc. Int. Grouse Symp. 3: 462–480.*

Rothery P., Harris M.P., Wanless S. & Shaw D.N. 2002: Colony size, adult survival rates, productivity and population projections of Black-legged Kittiwakes *Rissa tridactyla* on Fair Isle. *Atlantic Seabirds 4: 17–28.*

SAS Institute 2001: SAS/STAT User's Guide, Version 8.02. *Cary, NC: SAS Institute,* http://v8doc.sas.com/sashtml/stat/index.htm

Sim I.M.W., Eaton M.A., Setchfield R.P., Warren P. & Lindley P. 2008: Abundance of male black grouse (*Tetrao tetrix*) in Britain in 2005, and change since 1995–96. *Bird Study 55: 304–313.*

Storch I. 2000: An overview to population status and conservation of black grouse worldwide. *Cahiers d'Ethologie 20: 153–164.*

Summers R.W., Green R.E., Proctor R., Dugan D., Lambie D., Moncrieff R., Moss R. & Baines D. 2004: An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. *J. Appl. Ecol. 41: 513–525.*

Warren P., Baines D. & Henderson C. 2003: Cutting trials to enhance brood rearing habitats for black grouse in northern England. *Sylvia 39 (Suppl.): 81–86.*

Warren P. & Baines D. 2004: Black grouse in northern England: stemming the decline. *British Birds 97: 183–189.*

Warren P. & Baines D. 2008: Current status and recent trends in numbers and distribution of black grouse (*Tetrao tetrix*) in northern England. *Bird Study 55: 94–99.*

Williams I.T., Anderson C. & Holloway D. 1992: Black grouse in Wales spring 1992. *Unpublished RSPB report, Sandy.*

Williams I.T., Owen M. & Watts C. 1995: Black grouse in Wales spring 1995. *Unpublished RSPB report, Sandy.*

Williams I.T., King A., Cowan T. & Hughes B. 1997: Black grouse in Wales spring 1997. *Unpublished report to Countryside Council for Wales, Bangor.*