BioOne COMPLETE

Impacts of predator abundance on red grouse Lagopus lagopus scotica during a period of experimental predator control

Authors: Fletcher, Kathy, Hoodless, Andrew N., and Baines, David

Source: Wildlife Biology, 19(3) : 248-256

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-009

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 19: 248-256 (2013)
DOI: 10.2981/12-009
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Impacts of predator abundance on red grouse *Lagopus lagopus scotica* during a period of experimental predator control

Kathy Fletcher, Andrew N. Hoodless & David Baines

During a nine-year study manipulating predator abundances, post-breeding numbers of red grouse *Lagopus lagopus scotica* increased initially in response to experimentally reduced levels of key predator species (i.e. red fox *Vulpes vulpes*, carrion crow *Corvus corone*, stoat *Mustela erminea* and least weasel *M. nivalis*), but subsequently declined whilst predator control continued. Raptors, which were not controlled, were also present and may have influenced grouse demography. Our study examines the relative importance of controlled predators and raptors on grouse breeding success and survival. Raptor abundance did not differ between periods of predator control and periods of no predator control. However, during the breeding season, the survival of adult grouse was negatively correlated with the abundance of both raptors and controlled predators. Within the group of controlled predators, the strongest effects on red grouse adult survival were attributed to small mustelid abundance. Grouse breeding success was negatively correlated with the abundance of controlled predators, particularly carrion crows; however, no significant effect of raptor abundance was detected.

Key words: crow, Lagopus lagopus scotica, moorland management, predation, raptors, red fox, red grouse, Vulpes vulpes

Kathy Fletcher & David Baines, Game & Wildlife Conservation Trust, The Coach House, Eggleston Hall, Co. Durham, DL12 0AG, UK - e-mail addresses: kfletcher@gwct.org.uk (Kathy Fletcher); dbaines@gwct.org.uk (David Baines)
Andrew N. Hoodless, The Game and Wildlife Conservation Trust, Fordingbridge, Hampshire, SP6 1EF, UK - e-mail: ahoodless@gwct.org.uk

Corresponding author: Kathy Fletcher

Received 30 January 2012, accepted 24 May 2013

Associate Editor: Hans Christian Pedersen

Moorland dominated by heather *Calluna vulgaris* in the uplands of the United Kingdom is a habitat of high international conservation importance (Thompson et al. 1995). This habitat supports a unique suite of breeding birds, with species on the red list (at least 50% decline in numbers or contraction in breeding range in the last 25 years) or amber list (25-49% decline or contraction in the last 25 years) of conservation concern in the United Kingdom (Eaton et al. 2009). These species, including northern lapwing *Vanellus vanellus* (red-listed), black grouse *Tetrao tetrix* (red-listed), Eurasian curlew *Numenius arquata* (amber-listed) and red grouse *Lagopus lagopus scotica* (amber-listed), have shown widespread population declines in upland areas over the last 20 years, generally associated with habitat loss, degradation and fragmentation (Sim et al. 2005, 2008). Heather moorland comprises 25% of the British uplands and around half of it is managed by private land-owners for red grouse shooting (Hudson 1992). Numbers of red grouse available for shooting are maximised through employing gamekeepers to manage heather by rotational strip burning and to control predators and parasites of grouse (Hudson & Newborn 1995). In addition to boosting grouse numbers, this type of management is known to conserve heather habitats (Robertson et al. 2001), other ground-nesting birds (Tharme et al. 2001, Fletcher et al. 2010) and help support rural economies (Dunlop 2010).

Several factors influence grouse abundance, including heather extent and quality (Moss et al. 1975), parasitic nematodes *Trichostrongylus tenuis* (Jenkins et al. 1963, Hudson 1986), the virus louping ill (Reid et al. 1978) and social effects (Watson et al. 1994). Predation by a range of avian and mammalian

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

species may also be a key influence on grouse breeding success and abundance. Predation can be reduced by culling generalist predators, such as red foxes *Vulpes vulpes* (hereafter fox), carrion crows *Corvus corone* (hereafter crow), stoat *Mustela erminea* and least weasel *M. nivalis* (hereafter weasel), and it has been experimentally shown to increase numbers of grouse (Fletcher et al. 2010). Some raptors also prey upon grouse (Kenward 1982, Graham et al. 1995, Redpath & Thirgood 1999), and are legally protected in the United Kingdom although illegal killing occurs on some moors (Etheridge et al. 1997). A study on a single moor where hen harriers *Circus cyaneus* and peregrine *Falco peregrinus* were naturally increasing suggested that raptor predation could prevent grouse population increasing (Thirgood et al. 2000). However, no previous study has examined the influence of raptors on grouse whilst simultaneously manipulating the abundance of other avian and mammalian predators. Here, we use data from a nine-year experiment (Fletcher et al. 2010) to examine the relative importance of different guilds of controlled predator species on grouse, and test whether grouse breeding success and abundance were limited by an increase in the number of raptors.

Material and methods

Study site

Four study plots were located in Northumberland, United Kingdom (Plot A (centre 55°17'N 2°9'W), Plot B (55°19'N 2°18'W), Plot C (55°12'N 2°04'W) and Plot D (55°15'N 2°25'W)), at altitudes of 220-470 m a.s.l., with each study plot 6.1-6.9 km from its nearest neighbour. Plots were 9.3-14.4 km^2 in size and consisted of similar mosaics of habitats of which heather-dominated heath and heath/acid grassland mixtures were most common at higher altitudes, with grasses and rushes more extensive on lower slopes. Each plot was split into surveying blocks (on average of 1.5 km^2), with only those blocks dominated by heather and heath/acid grassland mixtures providing suitable habitat for red grouse considered here. Heather-dominated plot areas considered within our study were 5.5-10.2 km^2 (mean ± SE: 8.3 ± 1.0 km^2), on average 69% of the total plot area. Plots were grazed by sheep, typically at summer densities of 1.0-1.5 ewes ha^{-1}, and approximately 2% of heather area was burnt annually (Hudson & Newborn 1995).

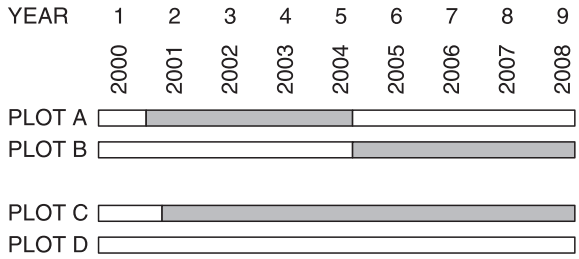


Figure 1. Design of study indicating plot years without predator control (□) and plot years with predator control (■).

Our experiment commenced in spring 2000 when all plots were monitored for a base-line breeding season with no predator control. In September 2000, treatments were implemented at the plot scale using a paired plot approach (Fig. 1). Within the first pair of plots (A and B), year-round predator control ran from September 2000 to September 2004 on Plot A and from September 2004 to March 2008 on Plot B. The second pair of plots (C and D) remained under the same treatment throughout; Plot C with year-round predator control and Plot D with no predator control. The assignment of treatments was randomised. Access restrictions during a foot-and-mouth disease outbreak prevented predator control activities on Plot C (2001 = no predator control for analyses). Data were not collected across all plots in spring 2001 (predator abundance indices and red grouse breeding numbers).

Predators were culled year-round by two full-time gamekeepers (1/plot) using legally sanctioned techniques. For further details of predator control activities, which targeted foxes, crows, stoats and weasels, see Fletcher et al. (2010). When a plot was subjected to predator control, these activities occurred within the plot and within a 2-km buffer around each plot. Legally protected predators (11 raptor species, badger *Meles meles* and otter *Lutra lutra*) that occurred in study plots were not killed.

Monitoring red grouse

Breeding numbers of red grouse (mid-March-mid-April) were recorded in 2000 and then from 2002 to 2008 and post-breeding numbers (mid-July-mid-August) from 2000 to 2007. Parallel transects within each block (ca 150 m apart) were walked with pointing dogs systematically working both sides of the transect to cover the whole block. This method provides reliable density and productivity estimates at this scale (Jenkins et al. 1963, Evans et al. 2007). When grouse were located, the sex (for adults only),

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and in the summer, the age (adult or juvenile) were recorded. Care was taken to ensure that flushed birds were not recounted along the survey line by watching where the birds resettled, and counts were only conducted in good weather with light winds and good visibility. From surveys, we calculated four demographic variables: proportion of hens with broods (measure of clutch survival), mean brood size (measure of chick survival), change in numbers of adults during the breeding season (measure of adult survival) and the young to adult ratio (overall reproductive success incorporating losses at all stages).

Monitoring predator abundance

We calculated abundance indices for generalist predators across each plot and year (excluding 2001). Fox abundance during the breeding season (March-June) was monitored monthly, by collecting scats from set routes (18.2-26.0 km on each plot) that followed fence lines, walls and river banks following an initial clear-up visit in February (units: mean scats km^{-1}; Baines et al. 2013).

The abundance of stoats and weasels was monitored in April in each year (excluding 2001). We deployed 50 tracking tunnels for two weeks in each plot and the proportion of tunnels with footprints recorded (King & Edgar 1977, Graham 2002). Stoat abundance indices were too low for analysis across all plot years (range: 0-2% tunnels with prints). The numbers of stoat and weasel culled over the 16 plot years within the experiment were correlated ($r_s = 0.67$, $P = 0.002$); therefore, we used the proportion of weasel prints in April to represent small mustelid abundance during the grouse breeding season.

We calculated abundance indices for crows and raptor species by recording all sightings during four timed transect counts per plot between April and June (predominantly undertaken during 06:00-09:00; transect distance = 137 ± 5 km and duration = 53 ± 2 hours on each plot; units: birds seen $hour^{-1}$). From 2000 to 2007 (data from 2001 unavailable), the 279 raptor sightings comprised common buzzard *Buteo buteo* (35%), common kestrel *Falco tinnunculus* (24%), merlin *Falco columbarius* (14%), peregrine falcon (9%), short-eared owl *Asio flammeus* (9%), northern goshawk *Accipiter gentilis* (4%) and hen harrier (4%). Within these analyses, we focus on species known to eat adult red grouse regularly, i.e. hen harrier, peregrine falcon, northern goshawk and common buzzard (Kenward 1982, Graham et al. 1995, Redpath & Thirgood 1999). The total number of sightings for these species across all plot years was 147.

Statistical analysis

Initially, we assessed which aspects of red grouse demography were influencing annual changes in grouse abundance. Change was measured over the whole year (as the log-transformed ratio of spring numbers in year t+1 to those in year t). We thus sought to examine whether this change variable was related to change over the non-breeding period (as the log-transformed ratio of spring numbers in year t+1 to post-breeding numbers in year t), change over the breeding period (as the log-transformed ratio of post-breeding adult numbers in year t to spring numbers in year t) and grouse productivity, measured in three ways: proportion of hens with broods, mean young/brood and young to adult ratio. The number of plot years of data available varied owing to the restrictions to access across all plots imposed on data collection in spring 2001 due to a foot-and-mouth disease outbreak.

Furthermore, we analysed the following three topics to consider effects of predators at differing scales on grouse breeding demographic variables: 1) influence of broad-scale predator control on grouse demography and raptor abundance; 2) influence of aggregated abundance of controlled predators and of raptors on grouse demography; 3) influence of the abundance of fox, crow and small mustelids separately. For 1), predator control was a two-level factor (control/no control). We assumed that any effect of predator control would become apparent in the year of treatment, and no lag was considered when predator control ceased on Plot A in September 2004 (Fletcher et al. 2010). The rationale for 2) was that the abundance indices of fox, crow and small mustelid were expected to be influenced by predator control and were therefore unlikely to be independent. As these indices were expressed in different units, they were combined (after transformation to natural logarithms) using the first Principal Component to represent a 'controlled predator index' (loadings: fox = 0.721, crow = 0.66 and small mustelid = 0.192). This index was considered in addition to a 'raptor index' comprising the sum of sightings/hour of hen harrier, peregrine falcon, northern goshawk and common buzzard. For 3), the abundance indices of fox, crow and small mustelids were transformed to natural logarithms and considered separately in univariate models (multivariate models were not used owing to the likely correlation among indices).

All the above analyses took into account the experimental design (see Fig. 1), which was a nested design with four levels of variation. These were, from top to bottom, the Pair stratum (df = 1), the Plot

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

within Pair stratum (df = 2), the Year within Pair stratum (df = 14) and the Plot-Year stratum (df = 14, of which one was allocated to the predator control treatment). Hypothesis testing proceeded using multilevel modelling within the analytical framework of generalised linear mixed models. Ideally such models would have included a variance component for each of the top three levels of variation. However, the number of degrees of freedom available in the top two strata was too low to permit this, and the single Pair effect and two Plot within Pair effects were modelled explicitly as fixed effects. The specification of the generalised linear mixed model varied according to the dependent variable y_{ijk} as follows:

Response variable: proportion of hens with broods

y_{ijk} is number of broods, number of hens is binomial denominator and error is binomial;

Response variable: mean number of young/brood

y_{ijk} is total number of young, ln(brood) is an offset and error is Poisson;

Response variables: change in adult numbers between years, change in adult numbers over the breeding period, young to adult ratio

y_{ijk} is log-transformed response variable and error is Normal;

$f(y_{ijk}) = c + p + s_i + \pi_{ij} + a\, x_{jk}$ (linear predictor), with $\pi_{ij} \sim \text{Normal}(0, \sigma^2)$,

where y_{ijk} is the response variable, f is the canonical link function, c is a constant, p is the Pair effect, s_i is the effect of Plot within Pair i, π_{ij} is the random

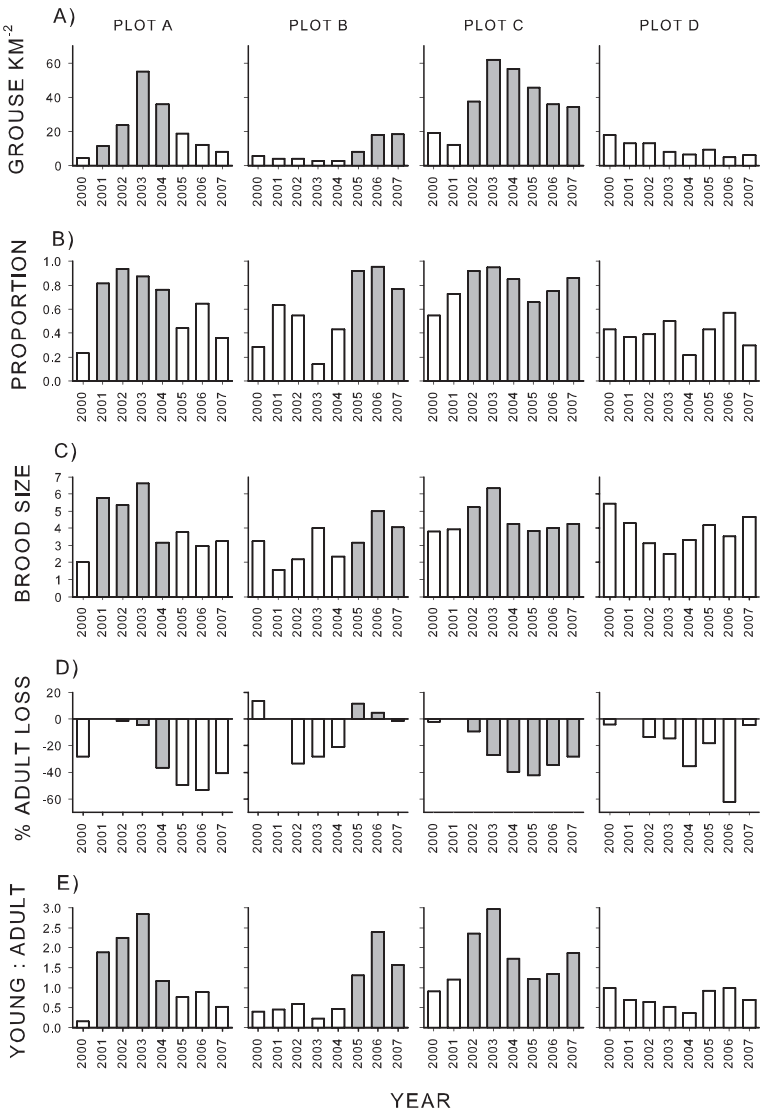


Figure 2. Red grouse parameters during 2000-2007: A) Post-breeding density, B) Proportion of hens with broods, C) Mean brood size, D) Survival of adult grouse during the breeding season and E) Young to adult ratio on four study plots in years with predator control (■) and years without predator control (□). Data from 2001 were not available for survival of adult grouse during the breeding season.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. Effect of grouse demography variables on the annual change in grouse numbers, taking into account the experimental design through multilevel modelling (see Methods section).

Response variable	N	Error structure	Link	Explanatory variable	Coefficient	± S.E.	F	P
Annual change in grouse numbers	24	Normal	Identity	Proportion of hens with broods	0.37	± 0.20	3.45	0.080
Annual change in grouse numbers	24	Normal	Identity	Mean brood size	0.93	± 0.29	10.64	0.005
Annual change in grouse numbers	24	Normal	Identity	Change in adults numbers during breeding season	1.27	± 0.18	47.73	< 0.001
Annual change in grouse numbers	24	Normal	Identity	Young to adult ratio	0.45	± 0.03	11.77	0.005
Annual change in grouse numbers	24	Normal	Identity	Change in numbers during non-breeding season	0.19	± 0.06	0.30	0.592

effect of Year j within Pair i, x_{jk} is an explanatory variable with values for every combination of Year j and Plot k, with estimated coefficient a. Depending on the hypotheses being considered, the model may contain more than one explanatory variable. The significance of explanatory variables in the model was evaluated using Wald tests (Stroup 2012). Confidence limits around back-transformed means were obtained through back-transformation of the 95% confidence interval on the scale of the linear predictor. All analyses were undertaken in GENSTAT 11.1.

Results

Grouse abundance, breeding success and survival

On plots subject to predator control, grouse numbers increased during initial years of predator control. For example, the first three years of predator control on Plot A and the first two years on Plots B and C saw the largest percent increases in grouse post-breeding numbers (mean ± SE: 139 ± 20% $year^{-1}$; Fig. 2). In later years of predator control (Plot C during 2005-2008), grouse numbers declined (-16 ± 6% $year^{-1}$) at a rate that was comparable with plot years with no predator control (-23 ± 6% $year^{1}$). Annual change in numbers between consecutive springs was not explained by change in numbers over the non-breeding period but was explained by grouse breeding season parameters (Table 1).

Grouse clutch and chick survival (proportion of hens with broods and mean brood size), in plot years with predator control, were significantly greater (1.5-1.8 times) than in plot years with no predator control (Table 2A; see Fig. 2). Losses of adult grouse during the breeding season were also significantly smaller in plot years with predator control (-12%), compared to plot years with no predator control (-32%; see Table 2A and Fig. 2). The overall reproductive success (young to adult ratio) was 3.2 times greater in plot years with predator control than in plot years with no predator control (see Table 2A and Fig. 2).

Predator abundance

For the controlled predators, predator control activities reduced the spring abundance indices of foxes (-43%) and crows (-78%), with small mustelids remaining unchanged (Fletcher et al. 2010; Fig. 3). There was a non-significant trend of higher raptor abundance index (68% greater) in years with predator control than in years with no predator control (see Table 2A). There was no consistent annual increase in raptor abundance when compared to the year in which predator control commenced (see Fig. 3).

Impact of predator groups on grouse parameters

Overall grouse breeding success (young:adult) was negatively related to the controlled predator abundance index, with clutch losses (represented by proportion of hens with broods) and adult survival showing stronger relationships than chick survival (represented by mean brood size; see Table 2B). However, only the survival of adult grouse during the breeding season showed a significant negative correlation with the abundance indices of both controlled predators and raptors (see Table 2B).

Within the suite of controlled predators, the crow abundance index significantly negatively influenced

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 2. Effect of predator control activities (A), controlled predators (first PCA of fox, crow and small mustelid indices) and raptor abundance index (hen harrier, peregrine falcon, northern goshawk and common buzzard combined; B) and indices of crow, fox and small mustelids separately on grouse demographic parameters taking into account the experimental design through multilevel modelling (C; see Methods section).

					Mean ± S.E. (N)			
A) Response variable	N	Error structure	Link	Explanatory factor	Predator control	No predator control	F	P
Raptor abundance index (ln hours as offset)	32	Poisson	Log	Predator control	0.12 ± 0.02 (13)	0.07 ± 0.02 (19)	3.74	0.073
Proportion of hens with broods	32	Binomial	Logit	Predator control	0.82 ± 0.03 (13)	0.45 ± 0.05 (19)	44.70	< 0.001
Mean brood size	32	Normal	Identity	Predator control	4.74 ± 0.39	3.14 ± 0.21	12.91	0.001
Change in number adults during breeding season	28	Normal	Identity	Predator control	-12.18 ± 7.39	-32.23 ± 0.87	5.44	0.036
Young to adult ratio	32	Normal	Identity	Predator control	1.86 ± 0.25	0.58 ± 0.06	37.88	< 0.001

B) Response variable	N	Error structure	Link	Explanatory variables	Coefficient	± S.E.	F	P
Proportion of hens with broods	32	Binomial	Logit	Controlled predators	-0.81	± 0.20	15.93	0.001
				Raptors	-0.07	± 0.26	0.07	0.788
Mean brood size	32	Normal	Identity	Controlled predators	-0.17	± 0.06	8.09	0.012
				Raptors	0.04	± 0.08	0.29	0.599
Change in number adults during breeding season	28	Normal	Identity	Controlled predators	-0.15	± 0.05	8.20	0.009
				Raptors	-0.22	± 0.07	9.59	0.005
Young to adult ratio	32	Normal	Identity	Controlled predators	-0.51	± 0.11	20.67	< 0.001
				Raptors	0.08	± 0.16	0.31	0.585

C) Response variable	N	Error structure	Link	Explanatory variables	Coefficient	± S.E.	F	P
Proportion of hens with broods	32	Binomial	Logit	Fox	-0.01	± 0.44	0.00	0.982
Mean brood size	32	Normal	Identity	Fox	-0.15	± 0.12	1.61	0.218
Change in number adults during breeding season	28	Normal	Identity	Fox	-0.06	± 0.11	0.31	0.585
Young to adult ratio	32	Normal	Identity	Fox	-0.61	± 0.26	5.73	0.025
Proportion of hens with broods	32	Binomial	Logit	Crow	-1.05	± 0.21	26.07	< 0.001
Mean brood size	32	Normal	Identity	Crow	-0.21	± 0.07	9.28	0.006
Change in number adults during breeding season	28	Normal	Identity	Crow	-0.11	± 0.07	2.80	0.114
Young to adult ratio	32	Normal	Identity	Crow	-0.68	± 0.13	25.04	< 0.001
Proportion of hens with broods	32	Binomial	Logit	Small mustelid	-0.02	± 0.25	0.01	0.939
Mean brood size	32	Normal	Identity	Small mustelid	-0.11	± 0.07	2.49	0.128
Change in number adults during breeding season	28	Normal	Identity	Small mustelid	-0.13	± 0.06	4.92	0.037
Young to adult ratio	32	Normal	Identity	Small mustelid	-0.12	± 0.17	0.45	0.507

the highest amount of variation in overall breeding success, particularly regarding proportion of hens with broods and mean brood size (see Table 2C). Fox abundance index did not explain a significant amount of variation in clutch losses or chick and adult survival, but the overall breeding success was significantly negatively related (see Table 2C). Finally the small mustelid abundance index explained a significant amount of variation in the loss of adults during the breeding season (see Table 2C).

Discussion

Within an experimental framework, we examined correlations between predator abundance indices and grouse breeding parameters to determine if predator abundance explained the grouse trends. We focused on the breeding season period as productivity and adult survival during this period were correlated with annual change in grouse numbers but no correlation was found with the changes in

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

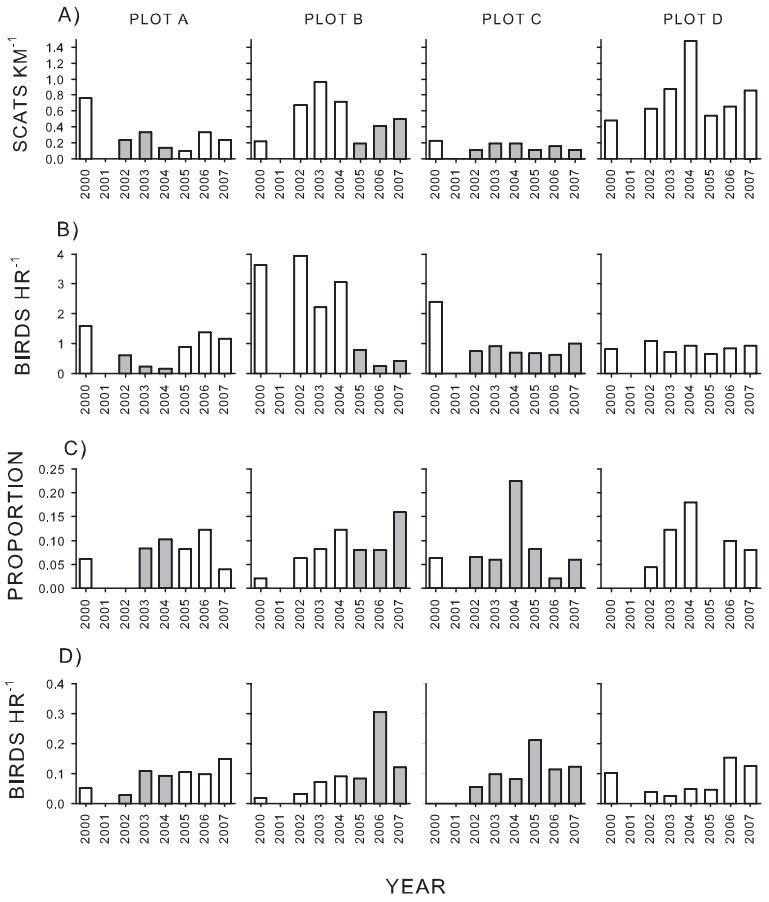


Figure 3. Spring abundance indices for predator species or groups during 2000-2007: A) foxes (scats km^{-1}), B) crows (birds seen hour^{-1}), C) small mustelids (proportion of tunnels with prints) all reproduced from Fletcher et al. (2010) and D) raptors (birds seen hour^{-1}; for hen harrier, peregrine falcon, northern goshawk and common buzzard) on four study plots in years with predator control (■) and years without predator control (□). Data from 2001 were not available.

numbers of grouse during the non-breeding period. We showed that this level of predator control was correlated with higher grouse productivity and reduced declines in grouse numbers during the breeding season (using a combined index for all controlled species). The crow abundance index explained greater variation in grouse productivity than other predator groups, which is consistent with crows showing the largest reduction in abundance from predator control activities. Of the controlled predators, small mustelids were negatively correlated with adult survival during the breeding season even though the predator control activities did not significantly alter their abundance. It may be that small mustelid predation of adult birds became more important as fox abundance was lowered as predicted by the mesopredator release hypothesis (Ritchie & Johnson 2009).

Control of predators such as foxes and crows has been shown to lead to higher abundance of prey species including certain ground-nesting birds (Fletcher et al. 2010). This could result in functional or numerical responses of other predator species. The raptor abundance index was 68% greater in plot years with predator control relative to those with no predator control; however, this difference was not statistically significant and there was no consistent annual increase when compared to the year in which predator control commenced. In certain conditions, raptor predation may limit gamebird populations but the number and extent of such studies are too modest to draw firm conclusions (Valkama et al. 2005). In our study, the abundance of raptors was not significantly related to variation in grouse breeding success but plot years with higher raptor abundance were also those with greatest adult red grouse loss during the breeding season. This is consistent with data collected on Langholm Moor, Scotland, where raptors were deemed responsible for 90% of early summer mortality of adult grouse (Thirgood et al. 2000). Unfortunately, the numbers of sightings of

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

each raptor species were insufficient to allow analyses of individual species.

In addition to predation, there are other possible factors that could have influenced the grouse numbers. A comprehensive range of vegetation measures showed that there had been no change in habitat within our study (Fletcher et al. 2010). Therefore, habitat changes at the scale measured by Fletcher et al. (2010) can be excluded as a contributory factor in the grouse abundance declines seen, although habitat loss and degradation can influence grouse trends over longer timescales (Hudson 1992, Robertson et al. 2001). The virus louping ill, transmitted to grouse through infected sheep ticks *Ixodes ricinus,* may cause high levels of mortality in juvenile grouse (Reid et al. 1978). However, louping ill was absent from the study sites (K. Fletcher, unpubl. data), so it can also be discounted. Many red grouse populations exhibit cyclic patterns (Mackenzie 1952, Potts et al. 1984), but more years of data are required to confirm this for our study sites. These cycles may be caused by intrinsic processes acting through aggressiveness and spacing behaviour (Mougeot et al. 2003, 2005) and from extrinsic processes such as parasitic nematode infections (Hudson et al. 1998). Insufficient samples were available to assess the levels of nematodes throughout the experimental period; therefore, they cannot be excluded as a possibly influencing factor.

Abundance indices for the controlled generalist predators: foxes, crows and small mustelids were all negatively correlated with measurers of grouse demography. Therefore managing all these species of predators is recommended to enhance the breeding success of red grouse and is likely to benefit other ground nesting birds in this habitat (Fletcher et al. 2010). As raptors are legally protected in the UK, management to maintain the economic and conservation benefits of grouse shooting should focus on control of other generalist predators, habitat management and reduction of parasites.

Acknowledgements - we thank N.J. Aebischer, J.C. Coulson, R.E. Green, X. Lambin, I. Newton and R. Moss for critical discussions at all stages of the study's development and progress. The commitment of C. Jones, his game keeping team and all field staff is gratefully acknowledged. We are indebted to the landowners (Ministry of Defence, M. Edgar, Viscount Devonport and the Duke of Northumberland) and their tenant farmers. Our work was funded by grants donated to the Game and Wildlife Conservation Trust by the Uplands Funding Appeal and the Sir James Knott Trust.

References

Baines, D., Aebischer, N.J., Macleod, A. & Woods, J. 2013: Pine marten and red fox sign indices in Scottish forests: population change and reliability of field identification of scats. - Wildlife Biology 19(4): doi: 10.2981/13-030.

Dunlop, S. 2010: An economic survey of Scottish grouse moors. - University of Strathclyde, Game and Wildlife Conservation Trust, Perth, UK, pp. 30-38.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Gibbons, D.W., Evans, A. & Gregory, R.D. 2009: Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. - British Birds 6: 296-341.

Etheridge, B., Summers, R.W. & Green, R.E. 1997: The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier in Scotland. - Journal of Applied Ecology 34: 1081-1105.

Evans, S.A., Mougeot, F., Redpath, S.M. & Leckie, F. 2007: Alternative methods for estimating density in an upland game bird: the red grouse *Lagopus lagopus scoticus*. - Wildlife Biology 13(2): 130-139.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. 2010: Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. - Journal of Applied Ecology 47: 263-272.

Graham, I.M. 2002: Estimating weasel *Mustela nivalis* abundance from tunnel tracking indices at fluctuating field vole *Microtus agrestis* density. - Wildlife Biology 8(4): 279-287.

Graham, I.M., Redpath, S.M. & Thirgood, S.J. 1995: The diet and breeding density of common buzzards *Buteo buteo* in relation to indices of prey abundance. - Bird Study 42: 165-173.

Hudson, P.J. 1986: The effect of a parasitic nematode on the breeding production of red grouse. - Journal of Animal Ecology 55: 85-92.

Hudson, P.J. 1992: Grouse in space and time: the population biology of a managed gamebird. - The Game Conservancy Trust, Fordingbridge, UK, pp. 5, 195-198.

Hudson, P. & Newborn, D. 1995: A manual of red grouse and moorland management. - The Game Conservancy Trust Limited, Fordingbridge, UK, 169 pp.

Hudson, P.J., Dobson, A.P. & Newborn, D. 1998: Prevention of population cycles by parasite removal. - Science 282: 2256-2258.

Jenkins, D., Watson, A. & Miller, G.R. 1963: Population studies on red grouse in north-east Scotland. - Journal of Animal Ecology 32: 317-376.

Kenward, R.E. 1982: Goshawk hunting behaviour and range size as a function of food and habitat availability. - Journal of Animal Ecology 51: 69-80.

King, C.M. & Edgar, R.L. 1977: Techniques for trapping and tracking stoats; a review, and a new system. - New Zealand Journal of Zoology 4: 193-212.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Mackenzie, J.M.D. 1952: Fluctuations in the numbers of British tetraonids. - Journal of Animal Ecology 21: 128-158.

Moss, R., Watson, A. & Parr, R. 1975: Maternal nutrition and breeding success in red grouse (*Lagopus lagopus scoticus*). - Journal of Animal Ecology 44: 171-190.

Mougeot, F., Piertney, S.B., Leckie, F., Evans, S., Moss, R., Redpath, S.M. & Hudson, P.J. 2005: Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. - Journal of Animal Ecology 74: 488-497.

Mougeot, F., Redpath, S.M., Moss, R., Matthiopoulos, J. & Hudson, P.J. 2003: Territorial behaviour and population dynamics in red grouse *Lagopus lagopus scoticus*. I. Population experiments. - Journal of Animal Ecology 72: 1073-1082.

Potts, G.R., Tapper, S.C. & Hudson, P.J. 1984: Population fluctuations in red grouse: analyses of bag records and a simulation model. - Journal of Animal Ecology 53: 21-26.

Redpath, S.M. & Thirgood, S.J. 1999: Numerical and functional responses of generalist predators: hen harriers and peregrine falcons on Scottish grouse moors. - Journal of Applied Ecology 68: 879-892.

Reid, H.W., Duncan, J.S., Phillips, J.P., Moss, R. & Watson, A. 1978: Studies on louping ill (Flavivirus group) in wild red grouse (*Lagopus lagopus scoticus*). - Journal of Hygiene 81: 321-329.

Ritchie, E.G. & Johnson, C.N. 2009: Predator interactions, mesopredator release and biodiversity conservation. - Ecology Letters 12: 982-998.

Robertson, P.A., Park, K.J. & Barton, A.F. 2001: Loss of heather *Calluna vulgaris* moorland in the Scottish uplands: the role of red grouse *Lagopus lagopus scoticus* management. - Wildlife Biology 7(1): 11-16.

Sim, I.M.W., Eaton, M.A., Setchfield, R.P., Warren, P.K. & Lindley, P. 2008: Abundance of male Black Grouse *Tetrao tetrix* in Britain in 2005, and change since 1995-96. - Bird Study 55: 304-313.

Sim, I.M.W., Gregory, R.D., Hancock, M.H. & Brown, A.F. 2005: Recent changes in the abundance of British upland breeding birds. - Bird Study 52: 261-275.

Stroup, W.W. 2012: Generalized Linear Mixed Models: Modern Concepts, Methods and Applications. - Chapman & Hall, London, UK, 161 pp.

Tharme, A.P., Green, R.E., Baines, D., Bainbridge, I.P. & O'Brien, M. 2001: The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. - Journal of Applied Ecology 38: 439-457.

Thirgood, S.J., Redpath, S.M., Rothery, P. & Aebischer, N.J. 2000: Raptor predation and population limitation in red grouse. - Journal of Animal Ecology 69: 1-14.

Thompson, D.B.A., MacDonald, A.J., Marsden, J.H. & Galbraith, C.A. 1995: Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. - Biological Conservation 71: 163-178.

Valkama, J., Korpimäki, E., Arrayo, B., Beja, P., Bretagnolle, V., Bro, E., Kenward, R., Mañosa, S., Redpath, S.M., Thirgood, S. & Viñuela, J. 2005: Birds of prey as limiting factors of gamebird populations in Europe: a review. - Biological Review 80: 171-203.

Watson, A., Moss, R., Parr, R., Mountford, M.D. & Rothery, P. 1994: Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. - Journal of Animal Ecology 63: 39-50.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use