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Does rotational heather burning increase red grouse abundance and breeding success on moors in northern England?

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Rotational burning of moorland vegetation is considered by grouse moor managers to create structurally diverse habitat that helps maximise red grouse *Lagopus lagopus scotica* (Lath.) abundance for shooting by increasing breeding success and adult survival. However, there is growing concern that increasing levels of burning, particularly on deep peat, are impacting upon upland ecosystems. We used linear mixed models to examine the influence of burning on heather *Calluna vulgaris* (L.) height and structure, and on grouse density and breeding success, at 36 moors in northern England which practiced driven grouse shooting and employed full-time gamekeepers to burn heather, but also to control generalist predators of grouse and their parasitic nematode worms. Variation in heather height was positively associated with burning extent on moors and the relationship between heather height and burning was similar on moors of deep (blanket bog) and shallow peat (heath). Grouse pre-breeding density was not related to burning extent, but breeding success and post-breeding density were positively associated with extent of burning on moors. Relationships between grouse and burning were similar on heath and blanket bog. Higher grouse breeding success and post-breeding density were likely to be associated with a more varied vegetation structure following burning. Rotational burning is associated with higher grouse breeding success and post-breeding densities beneficial for driven grouse shooting. Thus a conflict may exist between rotational burning to benefit grouse and potential impacts of burning on ecosystem services such as carbon storage and flood protection. Potential benefits of burning for increasing grouse breeding success and post-breeding density need to be considered carefully against any likely impacts on ecosystem services, particularly in areas of blanket peat.

Peatland, often dominated by heather moorland, is an internationally important habitat covering 17% of the land surface of the British Isles (Bather and Miller 1991). UK peatlands constitute 10–15% of total peatland areas worldwide (Milne and Brown 1997). In the British Isles, upland peatlands support contrasting land uses including forestry, sheep farming and in some regions, red grouse *Lagopus lagopus scotica* (Lath.) shooting (Ramchunder et al. 2009).

Grouse shooting has been practiced for around 150 years and provides an important source of revenue to rural communities with otherwise limited employment opportunities (McGilvary 1995, PACEC 2014). Driven grouse shooting, where birds are flushed by a line of beaters towards stationary hunters, requires high densities of grouse which are attained through intensive management of generalist predators, heather habitats and grouse parasites, the most important of which is the intestinal nematode *Trichostrongylus tenuis* (Cobbold) (Sotherton et al. 2009). Rotational

strip-burning of ericaceous-dominated vegetation creates habitat considered favourable for red grouse by preventing natural succession of scrub and woodland and by producing a mosaic of vegetation heights within each grouse territory: tall heather provides concealment from predators, younger heather provides adult grouse with more nutritious shoots for food and short heather provides higher insect availability favoured by chicks (Gardner and Usher 1989, Palmer and Bacon 2001, Buchanan et al. 2006).

Rotational burning can be a useful conservation management tool to create habitat suitable for threatened species (Pons et al. 2003, Fuhlendorf and Engle 2004, Boyles and Aubrey 2006, Vogel et al. 2007). Prescribed fire is used by conservationists to create optimal habitat for grassland bird species, and has been shown to increase abundance of threatened species on the North American prairie such as the greater prairie-chicken *Tympanuchus cupido* (L.) and upland sandpiper *Bartramia longicauda* (Bechstein), by creating high quality foraging and nesting areas and increasing nesting success (McNew et al. 2014, 2015, Sandercock et al. 2015). However, there is still controversy regarding the effect of regular burning on ecosystem processes, particularly in upland peatlands (Ramchunder et al. 2009, Davies et al. 2016).

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Rotational burning, together with other management practices carried out on grouse moors such as predator control (Fletcher et al. 2010, Newey et al. 2016), can benefit ground-nesting bird species such as golden plover *Pluvialis apricaria* (L.) and curlew *Numenius arquata* (L.) (Tharme et al. 2001, Pearce-Higgins and Grant 2006). Regular burning has also been shown to increase the abundance of peat-forming plants such as *Eriophorum vaginatum* (L.) and *Sphagnum* spp. (Lee et al. 2013a, b). However, there is increasing concern that burning at high frequencies can impair ecosystem functions, such as carbon and water storage (Garnett et al. 2000, Ramchunder et al. 2009), especially on sites with deep peat (blanket bog) rather than shallow peat (heath). Frequent burning may contribute to erosion of peat (Yeloff et al. 2006), with associated increases in dissolved organic carbon in rivers leading to increased sedimentation and declines in diversity of riparian macroinvertebrates (Brown et al. 2013, Ramchunder et al. 2013). A recent increase in extent of burning on northern English moors and on sites of national and international conservation importance has increased concerns regarding rotational strip-burning to favour red grouse (Yallop et al. 2006, Douglas et al. 2015).

Whilst moorland burning is a widespread practice that moor managers consider benefits red grouse, few studies have described or quantified this perceived benefit (but see Picozzi 1968, Tharme et al. 2001). Picozzi (1968) compared burning patterns to numbers of red grouse shot on Scottish grouse moors and Tharme et al. (2001) examined the effect of different management and environmental variables on grouse abundance, but neither examined the effect of burning extent on grouse breeding success or compared the effect of burning on grouse on heath-dominated and blanket bog moors. We improved upon previous studies by examining the relationship between burning extent and grouse demographic parameters, density and breeding success, on both heath and blanket bog moors using data from 36 moors in northern England that practiced driven grouse shooting and employed full-time gamekeepers. We predict that:

- 1) rotational burning is associated with increased diversity in heather structure ;
- 2) more burning creates habitat that may support more grouse territories and hence higher breeding densities;
- 3) burning is linked to higher grouse breeding success and higher post-breeding densities.

Material and methods

Study areas

Habitat data were collected at 36 different moors in northern England in 1997 and 2010. Data were collected in both years at 20 of these moors, while for 16 moors data were collected in only one year (Fig. 1). Hence, a total of 56 data points were available for moors surveyed over two years. Grouse demographic data were collected at the same moors between 1995–1999 and 2008–2012. Intensification in moor management practices such as prescribed burning occurred in northern England between 1997 and 2010 (Yallop et al.

2006, Douglas et al. 2015). We compared data collected in years before and during a general increase in extent of prescribed burning in the northern English uplands in order to describe any potential effects of increased burning extent on vegetation and grouse.

Data were collected from single study areas, approximately 1 km² in size (range 0.5–1.9 km²), located on privately owned moors averaging 31 km² in size (range 6–60 km²). Study areas were selected from areas with habitat and management intensities regarded as typical of the whole moor. Moors had a mean altitude of 467 m a.s.l. (range 235–680 m). All study moors were managed for driven grouse shooting and employed full-time gamekeepers. Both shooting and sheep farming were the principal rural land uses on study moors, with sheep grazing of the moorland typically restricted to spring through to early autumn. Burning on moors was conducted solely to benefit grouse and larger grass-fires typical of those to benefit grazing sheep were not conducted. Gamekeepers legally killed predators of grouse and their eggs on moors, such as the red fox *Vulpes vulpes* (L.), stoat *Mustela erminea* (L.) and carrion crow *Corvus corone* (L.). Raptors are legally protected in the UK, but some species are still illegally killed on some moors (Amar et al. 2011). No data were available on total number of predators controlled or culling effort in each of our 1 km² study areas.

Infestation of grouse by the intestinal nematode *T. tenuis* can reduce their survival and breeding success (Hudson et al. 1992a, Newborn and Foster 2002). Effective control of the parasite is carried out through the provision of grit coated with a layer of fat containing an anthelmintic drug (fenbendazole hydrochloride prior to 2007, after which the active drug used was flubendazole) in grit boxes deployed on moorland approximately every 100–200 m depending on grouse density (Newborn and Foster 2002, Adam et al. 2011). Prior to 2007, the drug used to control *T. tenuis* (fenbendazole) was less effective than that used from 2007 (flubendazole) and no data on level of usage prior to 2007 are available. Specific information regarding the quantity of grit deployed or density of grit boxes provisioned by each estate is only available for study areas in 2010, hence we were unable to include data on intensity of parasite control in analyses. As we purposely selected moors which employed full-time gamekeepers, study areas may be expected to have adequate levels of predator and parasite control.

Red grouse demographic data

Red grouse were surveyed annually at each study area in late-March or early-April to record indices of pre-breeding density (no. of grouse km⁻²), and in July to estimate indices of breeding success (ratio of young to adult birds (males and females)) and post-breeding density (total no. of young and adult birds km⁻²) using pointing dogs that systematically flushed grouse within the study area (Jenkins et al. 1963). Indices of grouse densities were derived by dividing the total no. of individuals observed from six equally spaced line transects within each 1 km² area by size of study area. Density indices recorded using several line transects within an area have been shown to be closely correlated with density derived from distance sampling, although grouse densities

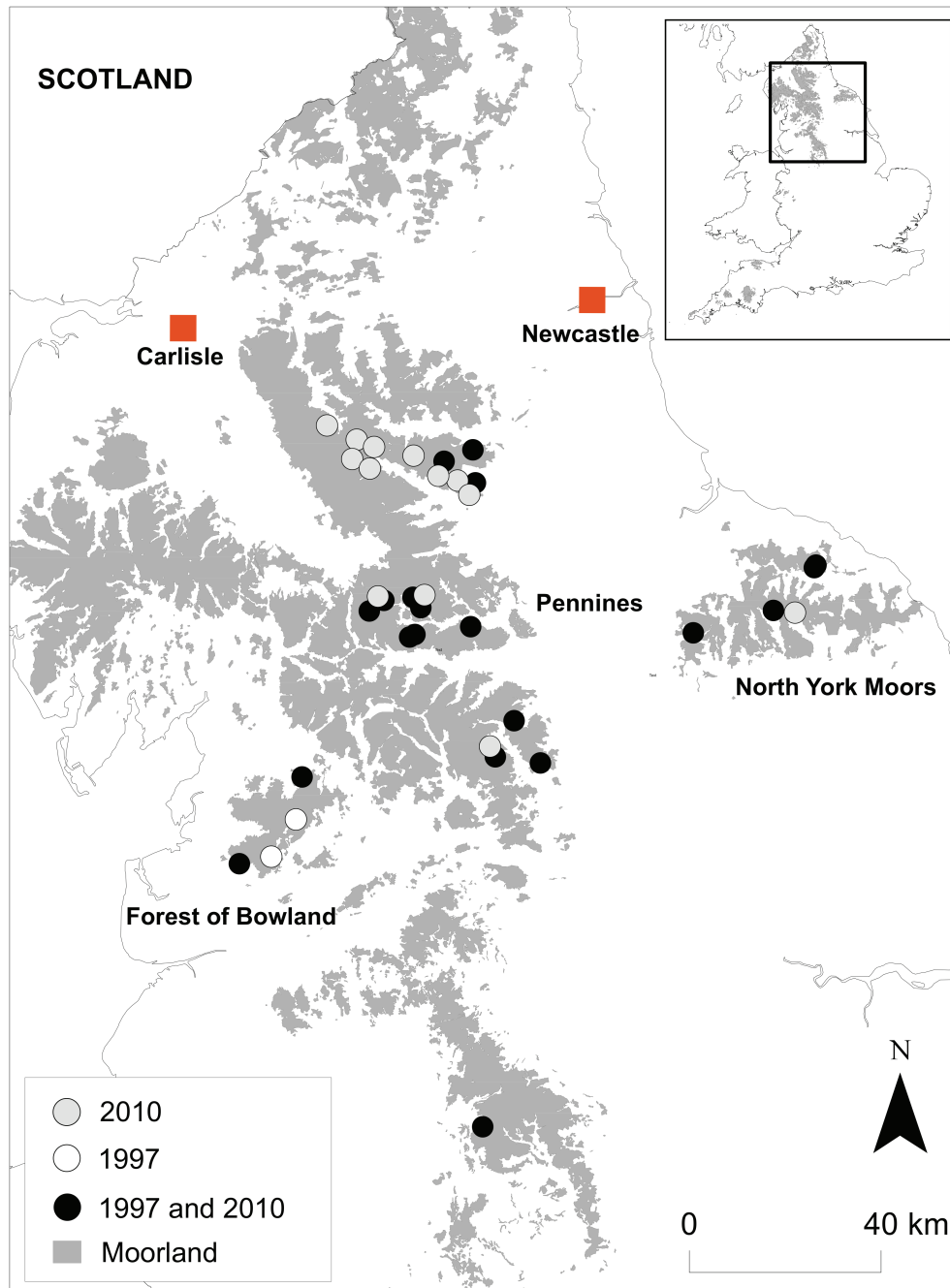


Figure 1. Locations of study moors in northern England and years in which habitat surveys were carried out. Grouse counts took place on each moor from March–April and July from 1995–1999 and 2008–2012 .

derived using lines transects have been shown to be 65% lower than those derived using distance sampling (Warren and Baines 2011). Whenever possible, surveys were carried out by the same observer on each study area between years to reduce potential observer bias. In post-breeding surveys, grouse were categorised as either adult or young when young were typically 6–9 weeks old, and could be differentiated on size and freshly-grown primary and tail feathers. Male red grouse were still with the brood at this time so we used ratio of young to adult birds to quantify breeding success rather than ratio of young to females as used in other species (Baines 1996, Watson and Moss 2008). Counts occurred

before shooting, thus age ratios were not influenced by harvesting age ratios (Flanders-Wanner et al. 2004, Hansen et al. 2012).

All grouse demographic data were averaged for two five-year periods; 1995–1999 and 2008–2012, whose median years coincided with years when habitat data were collected (1997 and 2010). Grouse abundance fluctuates in a quasi-cyclical manner approximating five years in relation to *T. tenuis* parasite abundance (Hudson et al. 1998), so we calculated mean grouse density and breeding success to reflect the average duration of grouse cycles in northern England.

Habitat and vegetation data

Habitat and vegetation data were collected every 20 m along 4–7 parallel transects, 1 km long and spaced 250 m apart within each study area in late-autumn/winter 1997 and 2010, giving a mean of 218 points per area, or two samples ha⁻¹. Peat depth up to 1 m (measured to the nearest 5 cm) was recorded by pushing a 1-m probe vertically into the substrate. If $\geq 50\%$ of sample points had peat depth ≥ 40 cm, the moor was categorised as blanket bog-dominated (hereafter ‘blanket bog’), $< 50\%$ of points as heath-dominated (hereafter ‘heath’) (Natural England 2010). Of the 36 moors, 19 were defined as heath and 17 as blanket bog. Blanket bog may also be categorised by vegetation composition, including prevalence of species such as *Sphagnum* and *Eriophorum*.

Recently burnt vegetation was recognisable as either burnt that spring, due to the charred black colouration (black burns), or burnt within the last 2–4 years, due to the presence of grey burned heather stems (grey burns). Proportions of black and grey burns were combined to create a single measure of burning extent for each moor (proportion of sample points with evidence of burning). Burning rotations (length of time between successive burns of the same ground) were estimated from the proportion of moor burned annually (e.g. proportion of moor burned per year = 0.1, burning rotation = 10 years). Mean annual burning extent was calculated by dividing total proportion of moor burned by 4 (maximum number of years in which burning could have occurred). As we calculated mean annual burning extent over four-year periods, we account for potential inter-year variation in burning extent. For moors with evidence of burning, proportion of burns known to have been made that year (black burns) were significantly correlated with proportion of both grey and black burns on moors (linear regression: $F_{1,44} = 27.0$, $R^2 = 0.38$, $p < 0.001$). Hence we may be confident in our estimations of burning rotations using proportion of black and grey burns.

Height (to nearest 5 cm) of dominant vegetation species was recorded within a 0.3×0.3 m quadrat. On all study sites heather *Calluna vulgaris* (L.) was the dominant species. Heather cover was calculated for each study moor as the proportion of sample points covered by heather. To quantify diversity in heather structure, variation in heather height was estimated from heather height by calculating the coefficient of variation ((standard deviation / mean) $\times 100$) for each quadrat measurement. Parameters measured are summarised in Table 1.

Rainfall data

To account for potential effects of rainfall on burning rates and grouse demographics on moors, we estimated rainfall (mm) for each moor for the month of March when most burning occurs (Tucker 2003) and when most grouse chicks hatch in May (Fletcher et al. 2013). Rainfall was calculated using 5×5 km gridded observation database (Perry and Hollis 2005, Met Office 2015).

Statistical analyses

As most moors were surveyed for habitat conditions twice, once in 1997 and again 13 years later in 2010, we used linear mixed models (LMMs) with normal error distributions and with moor as a random factor to account for non-independence amongst data points. LMMs were used to determine which environmental factors explained variation among moors in heather height (prediction 1), pre-breeding grouse density (prediction 2) and breeding success and post-breeding density (prediction 3).

We assessed covariates for collinearity using Pearson’s product-moment correlation coefficients. There was high collinearity between altitude and peat depth ($r = 0.74$), hence altitude was excluded from models. Other variables showed little evidence of correlation ($r < 0.45$; Dormann et al. 2012).

Table 1. Summary of explanatory variables included in analyses with definitions. ‘+’ indicates inclusion of a variable in a model. ‘P’ represents prediction tested.

Explanatory variables	Description	Response variables			
		P1 Variation in heather height (cm)	P2 Pre-breeding density (grouse km ⁻²)	P3 Breeding success (ratio young to old birds)	P3 Post-breeding density (grouse km ⁻²)
Variation in heather height (cm)	Estimated from heather height by calculating coefficient of variation for each 0.3×0.3 m quadrat	N/A	N/A	N/A	N/A
Heather cover	Proportion of sample points with <i>Calluna vulgaris</i>	+	+	+	+
Burning extent	Proportion of sample points with evidence of burning	+	+	+	+
Altitude (m)	Height above sea level of each study area				
Rainfall (mm)	Mean monthly (March or May) precipitation estimated for each study area from 5×5 km gridded observation data	+	+	+	+
Mean heather height (cm)	Recorded to the nearest 5 cm, within a 0.3×0.3 m quadrat	N/A	+	+	+
Year	1997 and 2010	+	+	+	+
Habitat type	Blanket bog or heath. Calculated from peat depth (cm)	+	+	+	+
Random factor					
Study moor	Thirty-six individual moors from which data from repeated quadrats were collected	+	+	+	+

To test the prediction that burning was associated with diversity of heather structure, we used a model with variation in heather height as the response variable and burning extent, heather cover, mean rainfall in March, year and habitat type as explanatory variables. Two-way interactions between burning extent and habitat type and heather cover and habitat type were included. As mean heather height was used to calculate variation in heather height, it was excluded from this model.

To test the predictions that burning extent was positively related to grouse demographics (pre-breeding density, breeding success and post-breeding density), we used models incorporating these variables in relation to burning extent, heather cover, mean heather height, mean rainfall in May, period and habitat type. Pre-breeding density was included as an explanatory variable in the breeding success model to test for density-dependence. Pre- and post-breeding densities were \log_e -transformed to improve the fit of models. As burning extent was found a posteriori to explain variation in heather height (Table 3), burning extent was chosen over variation in heather height for inclusion as an explanatory variable. It was expected a priori that relationships between habitat and grouse variables may differ between blanket bog or heath moors, so we included the two-way interactions of habitat type \times burning extent and habitat type \times heather cover.

We used Wald tests (distributed approximately as χ^2) to assess whether interactions explained a significant amount of variation in response variables. Interactions were not significant in explaining variation in either heather height or grouse demographic parameters, so models were refitted without interactions and each main effect was tested for significance after taking into account other environmental variables using Wald-statistics.

We tested that residuals were normally distributed and homoscedastic by plotting histograms of residuals and residual versus fitted values. We tested for nonlinearity in covariates by examining plots of model residuals versus burning extent, heather cover, mean heather height and monthly rainfall respectively. No nonlinear relationships involving grouse density or breeding success and burning extent were apparent. There was no evidence of spatial correlation in response variables among study moors (Mantel-test p values > 0.05). Analyses were implemented in the program R ver. 3.1.2 using the 'lme4' R package (Bates et al. 2014, <www.r-project.org>).

Data accessibility

Grouse demographic data and habitat and vegetation data used in analyses are archived by the Game and Wildlife Conservation Trust and can be made available on request.

Results

Heather height was more variable in 1997 and on heath-dominated moors (coefficient of variation (CV) 1997 = 36%, 2010 = 31%; heath = 42%, blanket bog = 28%) and differed significantly between years and habitat types. Variation in

Table 2. Means \pm SE of response variables and covariates included in analyses for each year and habitat type. Results of Wald chi-square tests are displayed for LMMs including the response variable and year or habitat as explanatory variables. Pre- and post-breeding density were log-transformed and burning extent and heather cover were expressed as proportions and logit-transformed.

	Variation in heather height (cm)	Pre-breeding density (grouse km ⁻²)	Breeding success (young:old)	Post-breeding density (grouse km ⁻²)	Burning extent (%)	Heather cover (%)
1997	49.1 \pm 2.4, n = 22	76.4 \pm 6.2, n = 20	2.3 \pm 0.1, n = 20	179.4 \pm 16.6, n = 21	10.1 \pm 2.1, n = 22	65.7 \pm 2.6, n = 22
2010	40.2 \pm 2.1, n = 34	104.9 \pm 5.5, n = 34	2.7 \pm 0.1, n = 34	303.7 \pm 13.1, n = 34	20.0 \pm 2.4, n = 34	62.3 \pm 2.1, n = 34
Wald test	$\chi^2_1 = 9.72$, p = 0.002	$\chi^2_1 = 29.76$, p < 0.001	$\chi^2_1 = 11.11$, p = 0.001	$\chi^2_1 = 78.60$, p < 0.001	$\chi^2_1 = 8.48$, p = 0.004	$\chi^2_1 = 0.54$, p = 0.46
Blanket bog	35.9 \pm 1.6, n = 29	91.6 \pm 4.8, n = 28	2.6 \pm 0.1, n = 27	266.7 \pm 16.7, n = 28	9.7 \pm 1.9, n = 29	62.2 \pm 2.2, n = 29
Heath	52.1 \pm 2.0, n = 27	97.3 \pm 8.0, n = 26	2.5 \pm 0.1, n = 27	245.3 \pm 20.4, n = 27	23.1 \pm 2.3, n = 27	65.1 \pm 2.3, n = 27
Wald test	$\chi^2_1 = 33.27$, p < 0.001	$\chi^2_1 = 0.06$, p = 0.80	$\chi^2_1 = 1.89$, p = 0.17	$\chi^2_1 = 0.87$, p = 0.35	$\chi^2_1 = 23.56$, p < 0.001	$\chi^2_1 = 0.82$, p = 0.37

Table 3. Results of Wald tests from LMMs examining the effect of burning extent on variation in heather height (cm), accounting for variation in heather cover, rainfall, year and habitat type. Coefficients were calculated using restricted maximum likelihood (REML). Random factor = Study moor (n = 36). n = 56. Random factor variance for full model = 23.43, standard deviation = 4.84.

P1: Variation in heather height	Coefficient	SE	χ^2	df	p <
Interactions					
Intercept	44.97	9.68	–	–	–
Habitat type × Burning extent	–2.34	16.72	0.02	1	0.89
Habitat type × Heather cover	21.37	17.64	1.63	1	0.20
Main effects					
Intercept	37.51	7.67	–	–	–
Burning extent	43.90	9.22	25.37	1	0.001
Heather cover	0.39	7.90	0.003	1	0.96
March rainfall	0.01	0.04	0.04	1	0.85
Year	–10.85	1.90	36.74	1	0.001
Habitat type	9.27	3.36	8.51	1	0.004

Values displayed for year and habitat type are given relative to 1997 and blanket bog respectively.

heather height (cm) was 22% greater on moors in 1997 than in 2010 and was 45% greater on heaths compared to blanket bogs (mean \pm SE 1997 = 49.1 \pm 2.4, 2010 = 40.2 \pm 2.1; heath = 52.1 \pm 2.0, blanket bog = 35.9 \pm 1.6). Percentage of area burnt was 138% greater on heath moors than on blanket bog (heath = 23.1 \pm 2.3, blanket bog = 9.7 \pm 1.9) and was more variable in 2010 and on heath moors (CV: 1997 = 91%, 2010 = 70%; heath = 52%, blanket bog = 90%). Variation in burning extent was high for both years and habitat types. Pre-breeding grouse densities (grouse km⁻²) were 37% greater during the period 2008–2012 than 1995–1999 (1995–1999 = 76.4 \pm 6.2, 2008–2012 = 104.9 \pm 5.5) and showed greater variation from 2008–2012 (CV: 1995–1999 = 23%, 2008–2012 = 30%). Post-breeding densities (grouse km⁻²) were 70% greater during the period 2008–12 than 1995–99 (1995–99 = 179.4 \pm 16.6, 2008–12 = 303.7 \pm 13.1) and showed greater variation from 1995–1999 (CV: 1995–1999 = 42%, 2008–2012 = 25%). Grouse breeding success (ratio of young to old birds) was 17% higher in 2008–2012 than in 1995–1999 (1995–1999 = 2.3 \pm 0.1, 2008–2012 = 2.7 \pm 0.1) and showed little variation between years and habitat types (CV: 1997 = 20%, 2010 = 16%; heath = 19%, blanket bog = 18%). Grouse densities and breeding success were similar on heath and blanket bog (Table 2).

Variation in heather height was positively related to burning extent, hence moors with greater proportions of burnt areas had a more variable heather structure (Table 3, Fig. 2). Neither burning extent nor any of the other explanatory variables were associated with grouse pre-breeding density (Table 4a). Breeding success was positively associated with burning extent, so moors with greater proportions of burnt areas had higher grouse breeding success (Table 4b, Fig. 3). No significant relationship between breeding success and burning extent was found using data collected in 1997 alone ($\chi^2_1 = 1.5$, p = 0.22, n = 20; estimate \pm SE = 2.07 \pm 1.72), while there was a significant relationship between these variables in 2010 ($\chi^2_1 = 8.7$, p = 0.003, n = 34; estimate \pm SE = 1.86 \pm 0.63). Post-breeding grouse density was positively associated with burning extent using data from both years, so moors which were burned more frequently had higher post-breeding densities (Table 4c, Fig. 4).

Discussion

Grouse shooting can be an important source of income for upland communities in parts of the UK (specifically, northern England and Scotland), but heather burning as a component of grouse moor management may conflict with the provision of ecosystem services, such as carbon sequestration (McGilvary 1995, Bonn et al. 2008, PACEC 2014). We found a positive association between burning extent and post-breeding density of red grouse. This was most likely due to the positive effect of burning on breeding success of grouse by creating heterogeneous habitat suitable for rearing chicks.

Our results confirm prediction 1, that rotational burning is associated with a structurally diverse habitat preferred by red grouse (Palmer and Bacon 2001), but rejects prediction 2, with burning extent not being associated with higher pre-breeding densities of grouse. Thus the notion held by

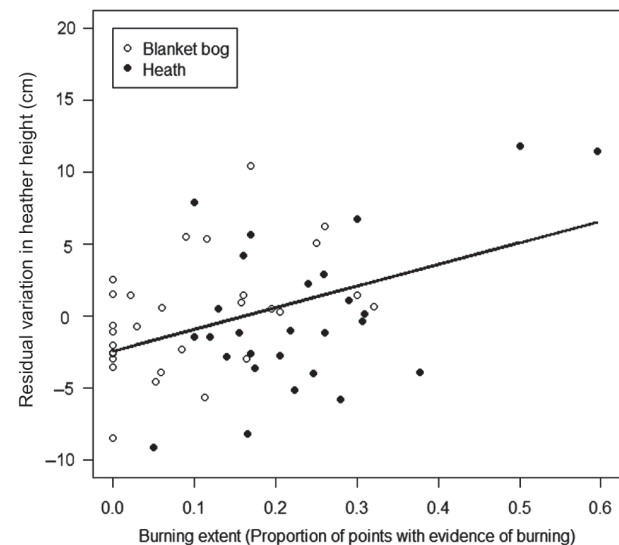


Figure 2. Partial residual plot showing the relationship between residuals of LMM examining change in variation in heather height (cm) and burning extent (proportion of sample points with evidence of burning) (n = 56). The straight line represents a linear regression between residuals of LMM and burning extent.

Table 4. Results of Wald tests from LMMs examining the effect of burning extent on log-transformed grouse pre- and post-breeding density (grouse km⁻²) and breeding success (ratio of young to old birds) accounting for variation in heather cover, rainfall, mean heather height, year and habitat type. Coefficients were calculated using restricted maximum likelihood (REML). Random factor = Study moor (n = 36). Random factor variance pre-breeding density full model = 0.03, standard deviation = 0.18; Breeding success variance = 0.06, standard deviation = 0.25; Post-breeding density variance = 0.07, standard deviation = 0.27.

	Coefficient	SE	χ^2	df	p ≤
a) P2: Pre-breeding density (n = 54)					
Interactions					
Intercept	4.50	0.46	–	–	–
Habitat type × Burning extent	0.54	0.71	0.68	1	0.41
Habitat type × Heather cover	0.89	0.72	1.80	1	0.18
Main effects					
Intercept	4.24	0.37	–	–	–
Burning extent	-0.27	0.39	0.52	1	0.47
Heather cover	0.55	0.32	3.18	1	0.07
May rainfall	-0.003	0.003	1.12	1	0.29
Mean heather height	-0.004	0.007	0.26	1	0.61
Year	0.35	0.09	17.71	1	0.001
Habitat type	0.02	0.13	0.04	1	0.85
b) P3a: Breeding success (n = 54)					
Interactions					
Intercept	1.70	0.75	–	–	–
Habitat type × Burning extent	-0.06	1.07	0.14	1	0.71
Habitat type × Heather cover	-1.85	1.09	2.65	1	0.10
Main effects					
Intercept	2.70	0.59	–	–	–
Pre-breeding density	0.0001	0.002	0.01	1	0.93
Burning extent	1.71	0.54	9.21	1	0.002
Heather cover	-0.46	0.50	0.76	1	0.38
Year	0.27	0.15	5.10	1	0.02
May rainfall	0.003	0.004	0.64	1	0.42
Mean heather height	-0.02	0.01	2.34	1	0.13
Habitat type	-0.28	0.19	2.03	1	0.15
c) P3b: Post-breeding density (n = 55)					
Interactions					
Intercept	5.07	0.50	–	–	–
Habitat type × Burning extent	0.81	0.70	1.61	1	0.20
Habitat type × Heather cover	-0.60	0.78	0.82	1	0.37
Main effects					
Intercept	5.39	0.41	–	–	–
Burning extent	0.75	0.40	4.22	1	0.04
Heather cover	0.43	0.36	1.56	1	0.21
Year	0.49	0.09	31.28	1	0.001
May rainfall	-0.005	0.003	2.70	1	0.10
Mean heather height	-0.01	0.008	1.09	1	0.30
Habitat type	-0.25	0.14	3.65	1	0.06

Values displayed for year and habitat type are given relative to 1995–1999 and blanket bog respectively.

grouse moor managers that rotational burning is associated with more red grouse territories in spring would, on the surface, appear not to be supported.

Our results support prediction 3, that burning extent on moors is associated with higher ratio of young to old birds (of both sexes), so that increasing proportion of burned area on moors by 10% increases ratio of young to old birds by approximately 0.2 (almost a quarter of a chick per pair). Regular strip-burning may provide better breeding habitat for red grouse by creating a mosaic of different vegetation heights providing food and cover for chicks (Miller 1964, Gardner and Usher 1989, Palmer and Bacon 2001, Buchanan et al. 2006). Our results also show that extent of burning on moors is associated with higher post-breeding grouse densities, so that increasing the proportion of burned area on moors by 10% may increase post-breeding density by approximately 10 grouse km⁻².

Although we selected moors with similar gamekeeper densities, there may be other between-moor differences not accounted for in this study, e.g. variation in effort by keepers. We found a significant relationship between breeding success and burning extent in the year in which more burning was carried out (2010), but there was no significant relationship in 1997. Moors which were burned more frequently may have had more efficient gamekeepers who also managed grouse predators and parasites more effectively. Without detailed information on indices of individual predator species abundance and associated trapping effort, together with parasite data, it is difficult to disentangle the relative contribution of these variables and burning. However we deliberately restricted the inclusion of study moors to those where gamekeepers were employed full-time to remove predators and to manage strongyle parasites. Management intensities influence grouse abundance on moors (Hudson et al. 1992b,

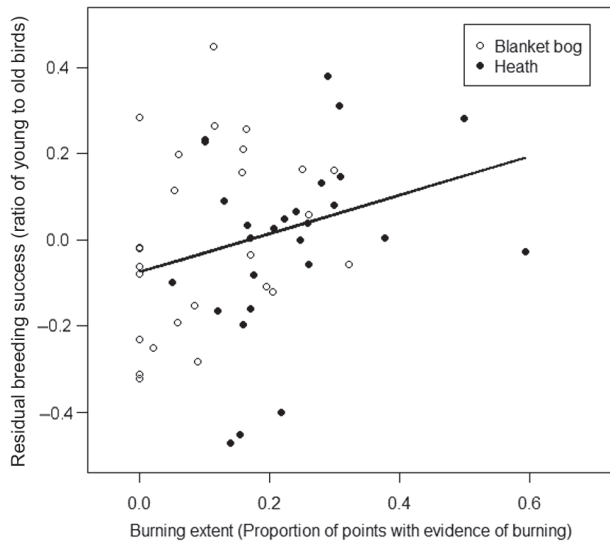


Figure 3. Partial residual plot showing the relationship between residuals of an LMM examining variation in grouse breeding success (ratio of young to old birds in July) and burning extent (proportion of sample points with evidence of burning) ($n = 54$).

Thirgood et al. 2002), but the relative effect of each component of grouse moor management on grouse demographics can only be determined by controlled experiments, which given that most grouse moors are privately owned and that grouse shooting is of high economic importance, renders such experiments extremely difficult to conduct at appropriate landscape scales.

In our analyses, we found linear relationships between response variables and burning extent which suggest that variations in heather height, grouse density and breeding success increase at a constant rate as burning on moors increases. However, linear increases in grouse density and breeding success with increasing burning extent are unlikely to hold for

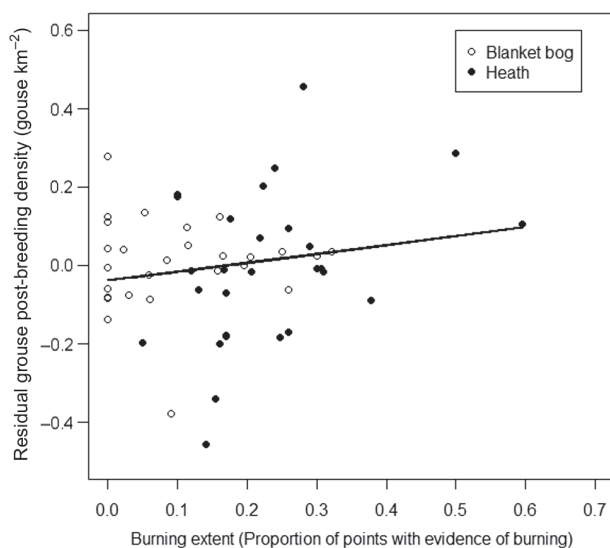


Figure 4. Partial residual plot showing the relationship between residuals of an LMM examining variation in grouse post-breeding density (grouse km^{-2}) and burning extent (proportion of sample points with evidence of burning) ($n = 55$).

moors with very high burning frequencies, and curvilinear relationships between response variables and burning extent beyond a burning extent of 0.5 (i.e. a burning rotation of ~ 8 years) are more likely. Although we found no evidence of curvilinear relationships involving breeding success, grouse density and burning extent, Fig. 3 and 4 suggest that breeding success and post-breeding density may start to decline when burning extent exceeds 0.5.

Grouse moor managers may be able to reduce the negative impacts of regular burning on peatland sites by modifying their burning practices. Best practice guidelines for prescribed burns recommend the use of controlled ‘cool’ burns, especially on blanket bog, which are less likely to ignite lower peat layers (Defra 2007, Clay et al. 2009). Using ‘cool’ burns reduces the risk of post-fire erosion and release of carbon (Maltby et al. 1990, Clay et al. 2015).

We estimated that blanket bog moors which were burned had average burning rotations of 25-years and we found that 34% of blanket bogs surveyed in 1997 or 2010 had no evidence of recent burning in the last 2–4 years. Heath moors had shorter burning rotations of approximately 17-years. Increasing the length of burning rotations could mitigate the negative effects of burning and moor managers are encouraged by Defra (2007) to increase intervals between burns, especially on blanket bog.

This study is the first to examine the association between rotational burning and grouse density and breeding success on blanket bog and heath-dominated moors. Our results suggest that moors which were burned more frequently had higher breeding success which resulted in greater grouse densities in July, thus maximising grouse abundance for autumn shooting on both heath-dominated moors and on blanket bog. However, the linear relationships we observed between burning extent and grouse demographics may only apply to moors with burning rotations > 8 years (although more data are required to confirm this) and burning at higher frequencies may have negative impacts on grouse and other bird species which prefer heterogeneous vegetation structures as well as on the wider peatland environment.

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