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DOI: 10.1016/j.biocon.2011.10.014

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Linking nest histories, remotely sensed land use data and wildlife crime records to explore the impact of grouse moor management on peregrine falcon populations

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ARTICLE INFO

Article history:

Received 14 July 2011

Received in revised form 4 October 2011

Accepted 11 October 2011

Available online xxxx

Keywords:

Source-sink dynamics

Persecution

Predation

Climate change

Hunting

Wildlife crime

ABSTRACT

Wildlife crime can be difficult to quantify, and its true impact on populations can be underestimated if rates are under-recorded. The illegal killing of birds of prey is an important form of wildlife crime, which in the UK, is often associated with land managed for the recreational shooting of red grouse *Lagopus lagopus scoticus*. In the UK, increases in peregrine falcons *Falco peregrinus* following recovery from organo-chlorine pesticides have not been uniform, with slow growth and localised declines in some areas, including those managed for red grouse shooting. In this study, we combined 1081 peregrine nest histories across northern England between 1980 and 2006 with a remotely sensed map of grouse moor management, to test whether breeding performance was lower in areas with active management for grouse shooting. Productivity of pairs on grouse moors was 50% lower than pairs breeding on non-grouse moor habitat. However, clutch size and brood size of successful nests did not differ between habitat types, suggesting that food constraints were unlikely to explain this difference. Population models suggested source-sink dynamics, with populations on grouse moors unable to sustain themselves without immigration. Population data confirmed that growth rates were indeed lower on grouse moors than on non-grouse moor sites. Analysis of wildlife crime data confirmed that persecution of the species was more frequent on grouse moors than in other habitat types. This population will be more secure, and better able to function as a barometer of environmental health and climate change, if illegal persecution of the species ceases on areas of land managed for grouse shooting.

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1. Introduction

Populations of top predators, including raptors, are vulnerable to direct anthropogenic control (Newton, 1979; Helldin, 2000; Rodriguez and Delibes, 2004). Despite many raptor species being protected across their range by legislation (Mclean et al., 1999), illegal activity often continues, but as with most wildlife crimes, quantifying the true level of these activities can often be difficult (Gavin et al., 2009). Uncertainty over the amount of unreported or undiscovered crime, described as 'dark-figures' by criminologists, is one of the greatest obstacles in tackling wildlife crime globally (Akella and Cannon, 2004; Wellsmith, 2011). It is clear however, that in some circumstances illegal persecution of raptors is sufficient to limit their breeding success (Etheridge et al., 1997; Whitfield et al., 2008), survival (Oro et al., 2008; Real and Manosa,

1997; Smart et al., 2010; Whitfield et al., 2004a), territorial occupancy (Redpath et al., 2010; Villafuerte et al., 1998; Whitfield et al., 2004b), and population size (Whitfield et al., 2006; Smart et al., 2010).

Raptors are often persecuted because of their perceived impacts on gamebirds (Park et al., 2008; Valkama et al., 2005; Villafuerte et al., 1998). In the British uplands, the management of moorland areas for recreational sport shooting of red grouse is a widespread and economically important land use in Scotland and northern England (Sotherton et al., 2009). However grouse shooting, and in particular 'driven' grouse shooting (grouse flushed toward a static row of shooters) which requires a high densities of grouse to be economically viable, remains associated with the illegal killing and disturbance of raptors (Redpath et al., 2010; Thompson et al., 2009) and these activities are a major impediment to the conservation of several species (Anderson et al., 2009; Etheridge et al., 1997; Fielding et al., 2011; Sim et al., 2007; Whitfield et al., 2006).

Populations of peregrine falcon across Europe and North America suffered dramatic declines caused by secondary poisoning from organo-chlorine pesticides such as DDT in the 1950s and

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1960s (Hickey, 1969). Following the ban on their use, and in some cases management intervention, populations have recovered (Cade et al., 1988; Ratcliffe, 1993). The UK is now of international importance for the species, holding 12–14% of the European population, with 1530 occupied nesting ranges in 2002 (Banks et al., 2010). The species has few natural predators, but has long been persecuted by humans (Mearns and Newton, 1988). Although the species is now fully protected in the UK (Wildlife and Countryside Act 1981, as amended) it remains the target of illegal killing and nest destruction, particularly on grouse moors where peregrines are perceived as a threat to grouse stocks (Court et al., 2004; Hardey et al., 2003). The species was recently identified by the UK government as a priority for targeting wildlife crime enforcement resources (DEFRA, 2011).

Motivated in part by these continuing conservation threats, volunteer observers monitor many raptor species across the UK (e.g. Wernham et al., 2008). The accumulated information includes 30 years of data on the breeding success of peregrine falcons collected by the Northern England Raptor Forum. These data, collected across landscapes varying in grouse management intensity, provide an opportunity to test whether peregrine falcon breeding success is limited by persecution associated with grouse moor management. Banks et al. (2010) recently stressed the need for such research to accurately establish the current importance of persecution of peregrine populations in the UK.

In this study, we test whether measures of breeding performance of peregrine falcons differed between grouse moor and non-grouse moor habitats. We predict that if persecution associated with grouse moor management was widespread, breeding parameters such as hatching success and overall breeding success would be lower in areas surrounded by active grouse moor. For comparison, we also examine differences in clutch size and brood size (of fledged broods), parameters which are unlikely to be affected by illegal persecution (because persecution usually results in complete breeding failure), but may be affected if grouse moor management is influencing the food resources available.

Using the breeding parameters found on grouse moors and in non-grouse moor habitats, we then construct stochastic population models, to test whether productivity on grouse moors is sufficient for the population to be self sustaining or whether these populations are being sustained by immigration from areas of higher productivity. We also explore whether trends in the number of occupied nesting ranges on grouse moors differed from that on non-grouse moor habitats over time. Finally, we explore directly whether incidents of peregrine persecution are associated with grouse moor management in northern England. For this we use the Royal Society for the Protection of Birds' (RSPB) Wild Bird Crime Database to examine the incidents of peregrine persecution in our study area, and to explore whether the frequency of persecution incidents was higher in grouse moor areas.

2. Methods

2.1. Study areas and peregrine breeding surveys

Peregrine breeding data were obtained by volunteers from seven regions of northern England (Fig. 1, Table 1) between 1980 and 2006, although the span of years varied between regions (Table 1). Data were available for the majority of upland areas in the north of England, with the exception of the Lake District; however a study on the dynamics of this population covering a similar period to our study has been previously published (Horne and Fielding, 2002). Field methods followed those described for monitoring peregrine populations (Court et al., 2004; Hardey et al., 2006). Known peregrine nesting ranges were monitored by

fieldworkers throughout the study period and new nesting ranges were located from visits to potentially suitable nesting areas or by following up reports of possible breeding attempts. Several visits to check for occupancy at each site were made from mid-March to late April, followed by further visits in May to record evidence of breeding (presence of a clutch) from direct observations or the presence of incubating females, and where possible to record clutch size. Subsequent visits determined hatching success, eventual outcome of the breeding attempt and fledging brood size. Because volunteers carried out most work, data are not available for all site-year combinations. A foot- and-mouth disease outbreak reduced access and therefore monitoring effort in 2001.

Nest locations were recorded as six figure UK Ordnance Survey (OS) grid references (i.e. to the nearest 100 m). Some nesting ranges have a series of alternative nests sites and we allocated a unique identifier ('range') to nests within the same nesting territory, as describe by Steenhof and Newton (2007) and Newton and Marquiss (1982). Altitude of each nest site was recorded as six 100 m height bands as follows: <100 = 1; 100–199 = 2; 200–299 = 3, 300–399 = 4, 400–499 = 5, >500 = 6. Fieldworkers were asked to classify the main habitat surrounding each nest site as coastal, urban/suburban, farmland, forestry, grass moor, heather moor managed for grouse shooting (grouse moor), and heather moor not managed for grouse shooting. Very few coastal ($n = 6$) and urban/suburban ($n = 18$) sites were monitored so nests in these habitats were excluded from any further analysis. Where possible, pairs occupying a nesting range were aged based on their plumage colour, and classified as 'adult' or 'immature' (where either one or both were 1st year birds).

2.2. Quantifying surrounding grouse moor management

Heather on moorland managed for red grouse is burned in strips to perpetuate a mosaic of young nutritious heather as a food source for grouse (Hudson, 1992). This produces a characteristic pattern that is readily apparent from satellite images, enabling the identification of areas with active grouse moor management. This approach has been used in numerous studies to explore various spatial relationships with grouse moor management (Amar et al., 2011; Anderson et al., 2009; Whitfield et al., 2003). We used recent satellite images (mainly 2005–2006 <http://earth.google.com>; see Anderson et al., 2009) to classify grouse moor management across our study regions using a 1×1 km OS grid. We selected 1 km squares with heather habitat (Target Level 1 categories Dwarf Shrub Heath) as classified by Land Cover Map 2000 (Fuller et al., 2005). We then classified each square which contained heather, as either burnt or un-burnt depending on whether strip burning was present from the satellite images. Finally, to derive a measure of grouse moor activity (hereafter Ground Moor Index – GMI) for each nest site, we calculated the percentage of ground strip-burned in the land area encompassed by the 1 km square in which the nest site was located and the surrounding eight 1 km squares.

We compared the GMI with the habitat classification of nest sites provided by fieldworkers (Fig. 2). The average GMI for nests classified as grouse moor was close to 50%, whereas for nests in other habitats it was well below 20% (Fig. 2). Thus, for the purpose of our subsequent analysis we categorised nest sites as being on grouse moors if they were surrounded by over 20% strip burning, and classified sites as non-grouse moor habitat if they were surrounded by less than 20% strip burning. Using this approach we found there was close agreement between the subjective (fieldworkers) classifications and the objective (GMI) classification; 82% of sites that were classified as grouse moors and 91% that were classified as non-grouse moor habitats from fieldworker classification were classified as such using the 20% GMI threshold.

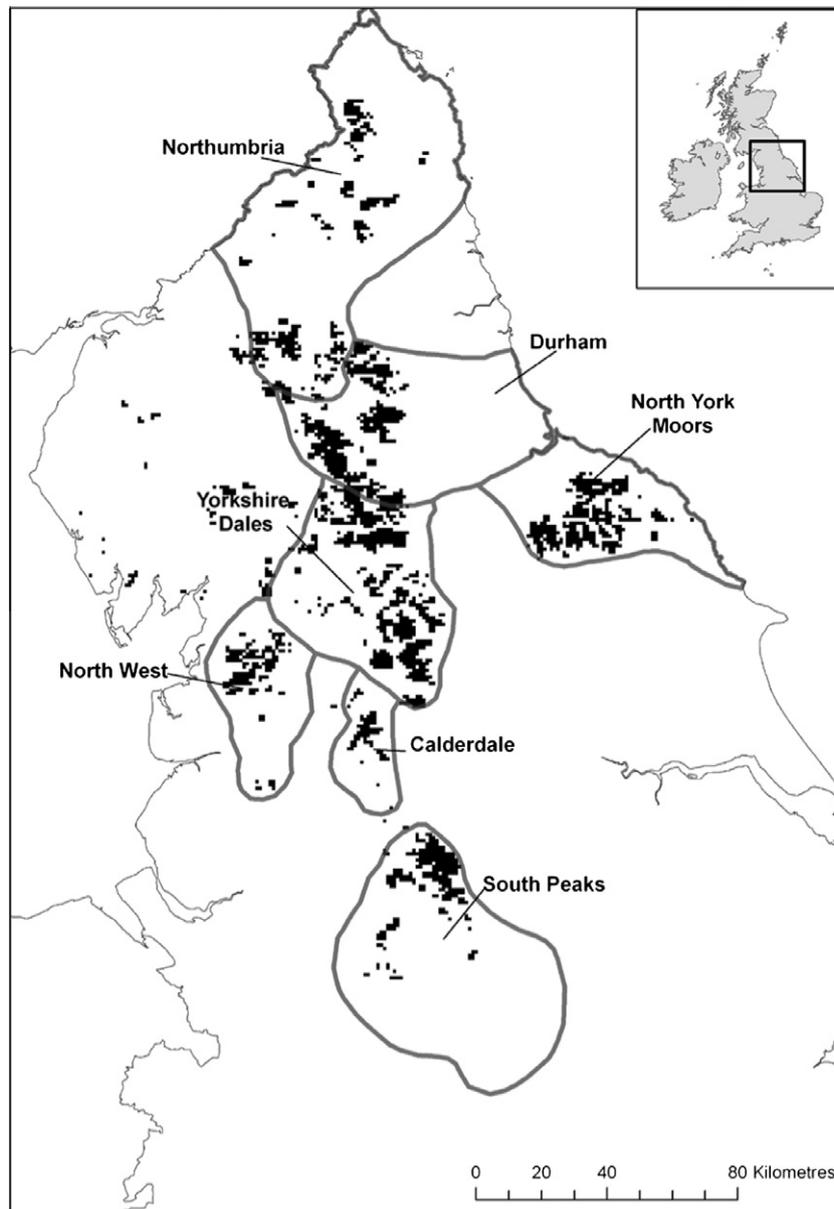


Fig. 1. Map showing the location of our study area and the boundary of our study regions, and the prevalence of grouse moors as shown by the 1 km squares which were classified as containing strip burning.

Table 1

Regional summaries of the data used in the analysis for each of the seven regions, and the average \pm S.E. (sample size) of the various breeding parameters analysed. Due to small sample sizes, these data exclude information from coastal or urban/suburban sites, and from pairs where one bird was immature.

Study region	Span of years (<i>n</i>)	Nesting ranges (total occupied years)	Burnt within 1 km (%)	Probability of laying (%)	Clutch size	Hatching success (%)	Fledged brood size	Breeding success (%)
Calderdale	1998–2006	8 (32)	2 \pm 1	100 \pm 0 (32)	3.30 \pm 0.12 (30)	71 \pm 8 (32)	2.43 \pm 0.18 (23)	71 \pm 8 (32)
Northumbria	1980–2006	31 (216)	3 \pm 1	90 \pm 2 (213)	3.29 \pm 0.06 (154)	81 \pm 3 (163)	2.39 \pm 0.08 (129)	61 \pm 3 (213)
South Peaks	1984–2006	27 (152)	19 \pm 3	91 \pm 2 (149)	2.91 \pm 0.08 (85)	86 \pm 3 (132)	2.42 \pm 0.10 (106)	71 \pm 4 (148)
Yorkshire Dales	1980–2006	33 (263)	19 \pm 1	90 \pm 2 (212)	3.25 \pm 0.17 (35)	81 \pm 3 (180)	2.46 \pm 0.08 (131)	53 \pm 3 (251)
Durham	1992–2006	9 (71)	21 \pm 3	79 \pm 5 (71)	3.06 \pm 0.11 (52)	58 \pm 6 (56)	2.25 \pm 0.17 (31)	44 \pm 6 (71)
North York Moors	1992–2006	5 (17)	43 \pm 4	44 \pm 1 (9)	3 \pm 0 (3)	33 \pm 33 (3)	2 \pm 0 (1)	7 \pm 7 (14)
North West	1980–2006	28 (282)	52 \pm 1	98 \pm 1 (261)	3.18 \pm 0.06 (199)	56 \pm 3 (241)	2.15 \pm 0.09 (98)	37 \pm 3
Total	1980–2006	141 (1033)	25 \pm 1	91 \pm 1 (947)	3.17 \pm 0.04 (559)	72 \pm 2 (807)	2.36 \pm 0.04 (519)	52 \pm 2 (990)

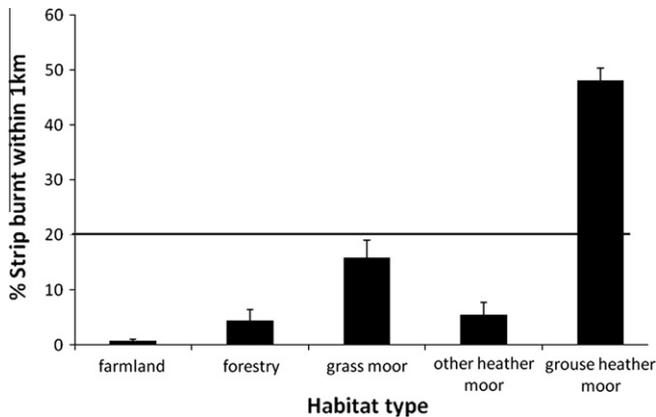


Fig. 2. Mean ($\pm 95\%$ C.I.) percentage of area with strip burning (Grouse Moor Index: GMI) within a 1 km of nests located in different habitat types as classified by field data. Line shows the 20% level, which was our threshold value for classifying sites as either grouse moor sites or non-grouse moor sites.

2.3. Rainfall data

Previous research has found that peregrine breeding success in the UK is inversely related to rainfall in May, the month when most clutches hatch and when young chicks are most vulnerable (Horne and Fielding, 2002; Mearns and Newton, 1988). We therefore extracted estimated May rainfall levels for each year from 1980 to 2006 from the monthly 5 km gridded UKCIP dataset (Perry and Hollis, 2005), and allocated rainfall in each year to nests within each 5 km cell.

2.4. Persecution data

The RSPB's Wild Bird Crime Database assigns persecution incidents into three categories: confirmed, probable and possible, depending on the amount of available evidence (RSPB, 2010). We obtained all confirmed and probable incidents of persecution on peregrines between 1990 and 2006 within our study areas, defined by the boundaries in Fig. 1. This time period was slightly shorter than the full span of years when our monitoring work occurred, but covered the years when monitoring occurred in most of the regions. Only those incidents assignable to a 1 km square were used, and to avoid issues of pseudo-replication, the few incidents ($n = 4$) involving multiple persecution cases at the same locality (e.g. where birds were shot and their nests also destroyed) were classified as single incidents. Repeated cases of persecution between years at the same locality were however treated as separate incidents. The proportion of strip burning surrounding each incident

was then calculated in the same manner as for peregrine nests, and sites were again classified as being 'grouse moors' if GMI was $>20\%$.

2.5. Statistical analysis

Breeding performance measures from each site in each year were as follows: (i) Clutch Production: whether an occupied site produced a clutch; (ii) Hatching Success: whether a pair producing a clutch went on to successfully hatch that clutch; (iii) Fledging Success: whether a hatched brood successfully fledged; (iv) Breeding Success: whether a site occupied by a pair produced any fledged young. All these measures were binary (success/failure) and were analysed in our models with a binomial error structure and logit link function. We also analysed (v) Clutch Size; (vi) Fledged Brood Size: the number of young fledged by a successful nest; and (vii) Overall Productivity: the number of young produced per occupied site. These last three variables were analysed with a Poisson error structure and log link function.

Data on breeding performance were analysed using Generalised Linear Mixed Models (GLMMs), incorporating nest site, range, study region and year as random terms to control for non-independence of data collected at these levels, and to account for the unbalanced nature of our data. On occasions when models failed to converge with all random terms, we removed 'site' from the model, enabling convergence. Denominator degrees of freedom were calculated using the Kenward Rogers method and the significance value of fixed effects was taken from a Type III analysis. All GLMMs were carried out in SAS version 9.1 (SAS Institute Inc., 2004).

The key explanatory variable in our analyses was that describing whether a site was classified as grouse moor ($GMI \geq 20\%$) or not ($GMI < 20\%$). Models also included the nest site's altitude band (scored 1–6) as a covariate to control for a positive association between altitude and burning. For hatching, fledging and breeding success we also included May rainfall as a covariate. If persecution occurred disproportionately on grouse moors, then effects of weather conditions on breeding performance may be masked, thus we also tested for an interaction between habitat type and May rainfall. We also examined whether any difference in breeding success between habitats was consistent across regions, for this analysis we used the same models but fitted region, habitat and region * habitat type interaction as fixed effects (removing the random region term). Pairwise comparisons between habitat types within regions were then made using the differences in least squared means.

We used a Chi-square test (with Yates' correction) to explore whether persecution incidents occurred on grouse moors (sites

Table 2
Results of a generalised linear mixed models, testing whether each variable differed on grouse moor and non grouse moor habitats (together with the mean model estimate for each habitat type) after controlling for Altitude and May rain (where appropriate). Results in bold are those which were significant at $P < 0.05$.

Variable	Altitude	May rainfall	Habitat type	Non-grouse moor habitat (\pm SE)	Grouse moor (\pm SE)
% Singletons ^a	$F_{1, 89} = 0.09, P = 0.76$		$F_{1, 85} = 0.26, P = 0.60$	$2.3 \pm 1.8\%$	$3.1 \pm 2.4\%$
% Immature pairs	$F_{1, 102} = 0.33, P = 0.56$		$F_{1, 60} = 0.08, P = 0.78$	$4.2 \pm 2.1\%$	$5.0 \pm 2.9\%$
Clutch production	$F_{1, 91} = 0.04, P = 0.84$		$F_{1, 78} = 14.38, P = 0.0003$	$96 \pm 2\%$	$83 \pm 8\%$
Hatching success	$F_{1, 116} = 2.10, P = 0.15$	$F_{1, 803} = 2.31, P = 0.13$	$F_{1, 80} = 12.90, P = 0.0006$	$82 \pm 4\%$	$58 \pm 8\%$
Fledging success	$F_{1, 95} = 0.04, P = 0.83$	$F_{1, 42} = 0.14, P = 0.70$	$F_{1, 35} = 4.47, P = 0.04$	$92 \pm 2\%$	$82 \pm 5\%$
Overall breeding success	$F_{1, 111} = 0.04, P = 0.83$	$F_{1, 28} = 0.48, P = 0.49$	$F_{1, 47} = 26.59, P < 0.0001$	$67 \pm 4\%$	$33 \pm 5\%$
Overall productivity ^b	$F_{1, 113} = 5.59, P = 0.02$		$F_{1, 57} = 25.39, P < 0.0001$	1.51 ± 0.15	0.76 ± 0.09
Clutch size	$F_{1, 78} = 0.01, P = 0.93$		$F_{1, 40} = 0.67, P = 0.41$	3.09 ± 0.09	3.19 ± 0.11
Brood size ^c	$F_{1, 516} = 0.06, P = 0.81$		$F_{1, 516} = 0.81, P = 0.36$	2.40 ± 0.08	2.26 ± 0.13

^a % of territories with any birds present which only held a single bird.

^b GLMM would not converge with altitude and habitat type in the model – this result is therefore for altitude fitted separately in the model. GLM modelling (fitting Year, Region, Altitude, May Rainfall and Habitat type) confirmed that habitat type remained significant with altitude included in the model.

^c Models would only converge after the exclusion of the random term 'territory', and would not converge with May rainfall.

with GMI > 20%) more frequently than expected, given the proportion of nesting peregrines in that habitat type. To calculate this proportion, we used data from nests monitored between 1990 and 2006, covering the period when the persecution data were recorded and ensured greatest representation across the regions.

2.6. Population models

We modelled growth rates of peregrine populations using VORTEX (Lacy et al., 2005) making various assumptions (Appendix A, Table A.1). We used a meta-population model, with habitat specific probability of breeding success and the mean fledged brood size (Table 2). Our initial population size of 150 individuals in each population, resulted in around 50 pairs assuming a stable age distribution, similar to the maximum number of pairs monitored per year in either habitat type ($n = 53$). Carrying capacity of each population was 400 individuals and models were run for 100 iterations over 50 years. Our first scenario assumed a closed population with no dispersal, allowing population specific growth rates to be estimated. We then specified 10% dispersal between the populations, similar to the breeding dispersal levels seen in a nearby southern Scottish population (Mearns and Newton 1984), in order to test whether productivity from one population could sustain the other, and whether this affected the overall meta-population growth.

3. Results

3.1. Prevalence of immature pairs and singletons

Over the 27 years (1980–2006), we had data from 1081 pair-occupied territories. From the 916 (85%) aged pairs, only 48 (5%) were immature pairs. Overall breeding success of immature pairs was very low, with only 3 of 48 pairs (6%) producing young. Due to this low breeding success, small sample size and uneven distribution between regions, we excluded data from immature pairs in all our subsequent analysis. There was, however, no difference in the proportion of immature pairs found on grouse moor and non-grouse moor habitats (Table 2), so this exclusion should have little influence on our principle analyses. From the territories that held any peregrines, there was no significant difference in the proportion that were occupied by single birds between grouse moor and non-grouse moor habitats (Table 2).

3.2. Clutch production, hatching and fledging success

We had data from 947 breeding attempts that were monitored sufficiently during the laying period to determine whether a clutch was laid. From these, 867 (92%) laid a clutch. Pairs on grouse moors were significantly less likely to produce a clutch than pairs on non-grouse moor habitats (Table 2). Hatching success on grouse moors was significantly lower than on non-grouse moor habitats (Table 2; Fig. 3). Rainfall in May had no significant effect on hatching success, but there was an interaction with habitat type ($F_{1, 802} = 4.33, P = 0.03$), such that rainfall had a negative effect for pairs on non-grouse moor habitat but no effect on grouse moors (Fig. 4a). Fledging success of hatched broods was significantly lower on grouse moors than on non-grouse moor habitats (Table 2; Fig. 3), although there was no May rainfall effect nor any interaction with habitat type ($F_{1, 567} = 1.92, P = 0.16$).

3.3. Breeding success and overall productivity

Breeding success of peregrines on grouse moors was substantially lower than those on non-grouse moor habitats (Table 2; Fig. 3). Again, there was no May rainfall effect on breeding success,

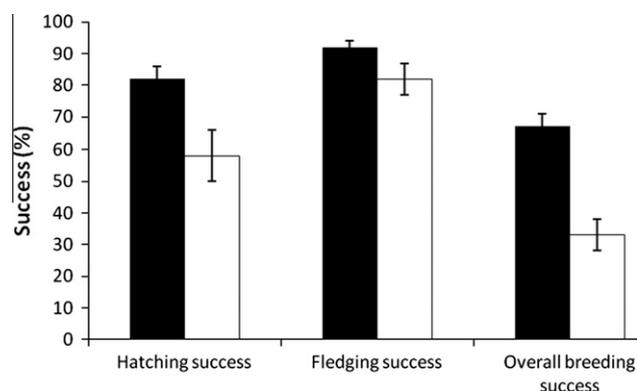


Fig. 3. Average hatching, fledging and overall breeding success (± 1 S.E.) for peregrines nesting on grouse moor (clear bars) and non-grouse moor habitat (filled bars) in Northern England. Differences between the habitat type for all three parameters were significant at $P < 0.05$.

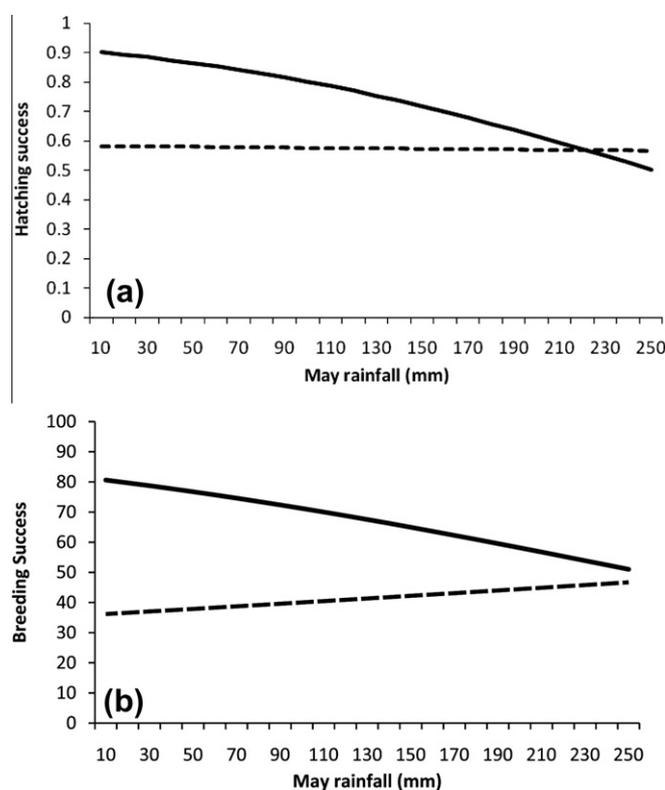


Fig. 4. Interaction between habitat type (grouse moor: dashed line; non-grouse moor habitat: solid line) and May rainfall for (a) hatching success ($P = 0.03$) and (b) brood fledging success ($P = 0.02$). May rainfall had very little influence on breeding performance for pairs on grouse moors, but showed a negative influence on breeding attempts in other habitat types.

but there was a significant interaction between rainfall and habitat type ($F_{1, 985} = 4.92, P = 0.02$), rainfall being negatively associated with breeding success on non-grouse moor habitats, but having no effect on grouse moors (Fig. 4b).

Across the regions we found a weak but significant correlation between the average amount of strip burning surrounding occupied territories and the overall average breeding success for that region ($R^2 = 61.2, F_{1, 6} = 7.89, P = 0.03$) (Fig. 5), so regions with occupied territories surrounded by most grouse moor habitat tended to have lower breeding success. Differences in overall breeding success within each habitat type also emerge within

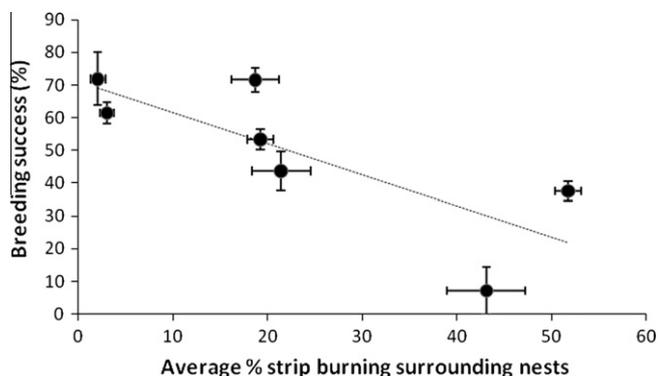


Fig. 5. Relationship between the mean percentage strip burning (± 1 SE) surrounding occupied territories in each of the seven regions and the overall mean breeding success (± 1 SE) in that region. The relationship was significant ($F_{1,6} = 7.89$, $P = 0.03$) and explained 61% of the variation in the data.

regions; breeding success on grouse moors was significantly lower than on non-grouse moor habitats in all regions with the exception of the South Peaks ($t_{63} = 0.57$, $P = 0.57$) (Fig. 6).

We found that overall productivity per pair was also significantly lower on grouse moors than on non-grouse moor habitat, with only around half the young produced per breeding attempt on grouse moors compared with non-grouse moor habitats (Table 2). Because of problems with convergence we were unable to control for altitude in this analysis; however fitting altitude as a fixed effect, whilst significant, was far less so than habitat type (Table 2). We therefore ran a Generalised Linear Model with year, region, altitude and habitat type fitted as fixed effects. This model confirmed our previous findings; altitude showed a significant negative association with productivity ($\chi^2_2 = 4.43$, $P = 0.03$), but after controlling for altitude, grouse moor habitats had significantly lower productivity than non-grouse moor habitats ($\chi^2_2 = 39.67$, $P < 0.0001$).

3.4. Factors influencing the clutch size and fledged brood size

We found no difference in clutch or fledged brood size between pairs breeding on grouse moors and in other habitat types (Table 2). The analysis of brood size of successful nests was compromised because models would not converge with range fitted as a random

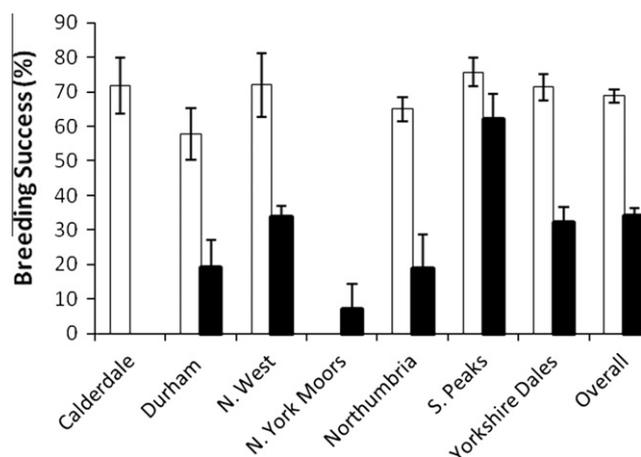


Fig. 6. Mean (± 1 SE) breeding success in the seven regions for pairs occupying territories on grouse moor (filled bars) and non-grouse moor habitats (i.e. Sites with $< 20\%$ strip burning within 1 km). Calderdale had no sites classed as grouse moors, and all sites in N. Yorkshire were on grouse moors. $P < 0.05$ for all regions, except S. Peaks ($P = 0.57$).

effect, although fitting range instead as a fixed effect did not alter the results.

3.5. Population growth rates on grouse moors and on non-grouse moor habitats

Between 1992 and 2006 (excluding 2001 (foot and mouth year), i.e. the years when all regions were monitored) there was a significantly different trend in the number of occupied ranges in the two habitat types, as revealed by the significant interaction between year and habitat type (year: $F_{1,172} = 1.48$, $P = 0.22$; habitat type $F_{1,171} = 8.82$, $P = 0.003$; year * habitat type $F_{1,171} = 8.86$, $P = 0.003$). Whilst the number of nest sites on non-grouse moor habitat increased from 19 to 53 occupied ranges, the numbers on grouse moors showed a flat trend, declining slight from 23 to 21 occupied ranges) (Fig. 7).

3.6. Population models

The closed population model showed that the peregrine population on grouse moors was unlikely to be self-sustaining. The grouse moor population had a negative growth rate ($\lambda = 0.956$) and 28% of simulations resulted in extinctions. Excluding extinction simulations, models predicted average declines over 50 years from 150 to only 20 individuals. By contrast, the non-grouse moor population had a positive growth rate ($\lambda = 1.089$), with no simulations resulting in extinction; this population was predicted to increase from 150 to 287 individuals over the 50 years (Fig. 8).

The open population model, with 10% dispersal, produced a grouse moor population with a positive growth rate ($\lambda = 1.008$), with no extinction simulations and increases predicted over the 50 years from 150 to 207 individuals. However, although the non-grouse moor population was predicted to increase (from 150 to 270) over the 50 years, the average population growth rate ($\lambda = 1.040$) was reduced in comparison with the closed models (Fig. 8).

3.7. Persecution data

Between 1990 and 2006 there were 46 confirmed or probable peregrine persecution incidents within our study regions, 39 (85%) of which took place at or close to nest sites. Seventy percent of cases took place on grouse moors (defined by $> 20\%$ GMI),

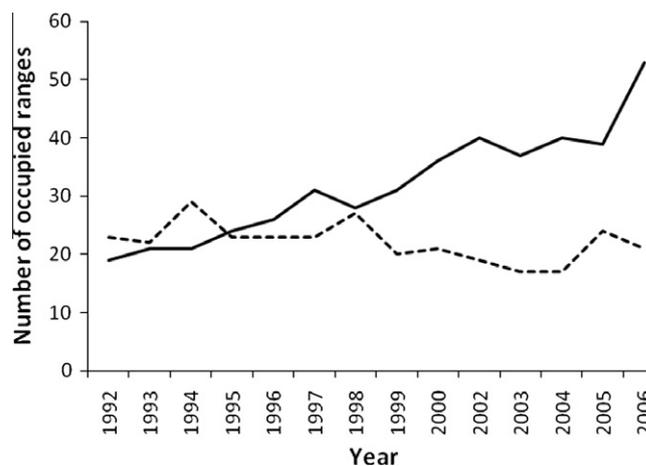


Fig. 7. Number of occupied nesting ranges on grouse moor habitat (dashed line) and non-grouse moor habitat (solid line) between 1992 and 2006 (the years when all study regions were monitored). 2001 data are excluded because of the paucity of data due to foot and mouth.

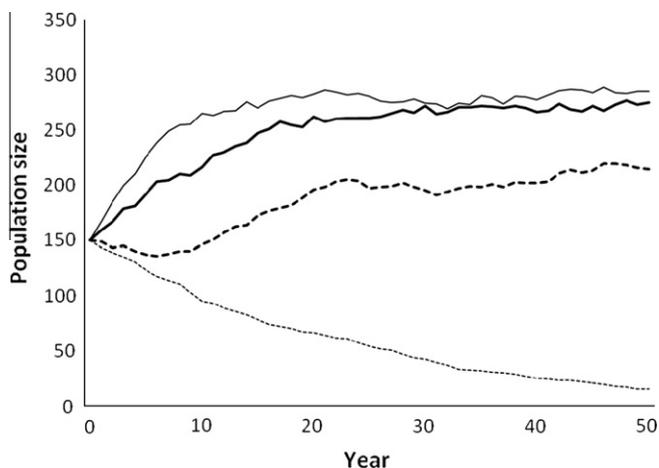


Fig. 8. Graphical output for the VORTEX population models, simulated population size over 50 years, for population on grouse moor (dashed lines) and non-grouse moor habitat (solid lines), according to whether the populations were either closed (thin lines), with no immigration or emigration; or open with 10% dispersal between populations (thick lines). Lines show the mean output for 100 simulations run for each model over a 50 year period. See supplementary Table 1 for the full parameter estimates.

whereas from our study during 1990–2006 only 42% of peregrine nests were found on grouse moors. This proportion was significantly higher than expected if persecution was occurring in proportion to the distribution of peregrines nesting in the two habitat types from our study ($\chi^2_1 = 13.8$, $P < 0.01$).

4. Discussion

Breeding performance of peregrine falcons was considerably lower on grouse moors than in other habitats, and these differences were consistent across almost all of the regions within our study area. Clutch production, hatching success and fledging success were all lower on grouse moors, and consequently overall breeding success and productivity of pairs was only half the level found in other habitat types. Only one third of pairs occupying grouse moor territories went onto produce any young, whereas on non-grouse moors over two thirds produced young. However, clutch size and brood size of successful nests did not differ between grouse moor and non-grouse moor habitats. Food supplies are more likely to affect these two measures (Aparicio, 1994; Newton, 1979; Redpath et al., 2002a) and this suggests that food supplies differed little between grouse moor and non-grouse moor habitats, and were unlikely to explain the overall differences in breeding performance in this study. This is not surprising given that we know that many peregrine prey species occur at similar or higher densities on grouse moors than on non-grouse moors (Tharme et al., 2001).

Productivity levels on non-grouse moor habitats in this study (1.51 ± 0.15 per pair) were similar to other comparable studies in the UK (Hardey et al., 2003; Horne and Fielding, 2002; Ratcliffe, 1993) and elsewhere (Gainzarain et al., 2000; Tordoff and Redig, 1997; Olsen and Olsen, 1989). Productivity on grouse moors (0.76 ± 0.09) however, was far lower than those recorded in these other studies, and was closer to those found during the era of organo-chlorine pesticides use (Hickey, 1969; Cade et al., 1988; Ratcliffe, 1993). For example, productivity in northern England during the 1960s, a period when organo-chlorine pesticides were reducing productivity, was between 0.45 and 0.99 young per occupied territory, very similar to that found for grouse moors in the same area in this study.

Our analysis of data held in the RSPB's wild bird crime database revealed that peregrine persecution incidents occurred far more frequently on grouse moors, than would be expected from the occurrence of peregrine territories in that habitat type. We believe that human persecution, associated with the practice of grouse moor management, was the most likely explanation for the disparities in breeding performance between the different habitats. A similar analysis considering only illegal wildlife poisoning also confirmed the close link between illegal poisoning and land managed for grouse shooting (Whitfield et al., 2003). High levels of human persecution of peregrines on grouse moors have been suggested from several other studies. For example, Hardey et al. (2003) suggested that the lower productivity of peregrines near grouse moors in Scotland was due to persecution associated with grouse moor management. A quasi-experimental study in southern Scotland revealed that when raptors on a grouse moor were fully protected from persecution, peregrine numbers doubled (Redpath and Thirgood, 1999; Amar et al., 2008). Court et al. (2004), whilst acknowledging the difficulties of detection, suggested that a minimum of 13% of nesting attempts in their study failed due to deliberate human interference on grouse moors.

Persecution levels on grouse moors were apparently so high in our study that they were sufficient to obscure the natural influence that weather can have on this species' breeding performance (Mearns and Newton, 1988; Horne and Fielding, 2002). Thus, on non-grouse moors the expected negative influence of May rainfall was apparent, whereas nests located on grouse moors consistently had lower breeding and hatching success irrespective of May rainfall, such that hatching and breeding success on grouse moors were similar to levels seen in other habitats in the wettest May conditions. This finding has considerable implications for research using raptors as the model organism to examine the impacts of climate change (e.g. Redpath et al., 2002b; Wichmann et al., 2003), since the true influence of any changes in climate may be masked by human persecution.

Our closed population model suggested that the grouse moor population was not self-sustaining, whereas productivity on non-grouse moors was sufficiently high to allow rapid population growth. Because of this, our open population model with 10% dispersal between populations indicated that the meta-population had a positive population growth rate and should increase at approximately 2.7% per annum. Using this modelled growth rate to predict recent population changes we would estimate that the inland population in northern England would have increased from 160 in 1991 to 218 in 2002, which is reassuringly close to the 226 pairs observed in 2002 (Banks et al., 2010). The population therefore likely exists as a meta-population with source-sink dynamics (Pulliam, 1988). Grouse moors are operating as sinks, maintained through the continual immigration of birds from other habitat types which are acting as sources. Trends in the numbers of occupied territories in the different habitat types further reinforced the findings for these models. Numbers more than doubled on the non-grouse moor habitats (19–53), but stagnated and actually declined slightly on grouse moors (23–21). These results further reinforce the idea that persecution levels were sufficient to have population level impacts. This lack of growth on grouse moors cannot simply be explained through insufficient nesting opportunities on grouse moors, because these data on grouse moors come from 56 separate nesting territories.

Whilst our results are consistent with the hypothesis that persecution on grouse moors was the cause of the poor breeding performance in this habitat, could there be other explanations? It seems unlikely. Our evidence already suggests food supplies are unlikely to be different between grouse moors and non-grouse moor habitats. Moreover, the few predators of peregrines in the UK (e.g. goshawk *Accipiter gentilis*, golden eagle *Aquila chrysaetos*,

red fox *Vulpes vulpes* and corvids) are all likely to be found at lower densities on moorland managed for grouse than in other habitat types (Fletcher et al., 2010; Tharme et al., 2001; Whitfield et al., 2004b). Therefore, the most logical explanation for these differences is that illegal persecution associated with grouse moor management is responsible.

Various solutions have been proposed to resolve the conflict between raptor conservation and management for red grouse shooting (Thirgood et al., 2000; Thirgood and Redpath, 2008; Thompson et al., 2009), and it is important that a solution is found given the socio-economic importance of both birds of prey and red grouse shooting (Sotherton et al., 2009). At present however, considerable sums of money are being spent by conservation NGOs and government statutory agencies, and considerable time invested by dedicated volunteers, in trying to shield protected raptors from persecution (Natural England, 2008; RSPB, 2010), and by the police in trying to enforce existing legislation (e.g. Her Majesty's Inspectorate of Constabulary, 2008) with relatively little success. Redpath and Thirgood (1999) found that peregrines show a type II functional response to grouse densities, such that they pose the greatest threat to grouse stocks when grouse are at low densities; however, they concluded that peregrines hunting in the absence of other predators would not limit grouse numbers. However, peregrine predation in addition to harrier predation is likely to reduce the ability of low density grouse populations to increase (Redpath and Thirgood, 1999), and is behind the motivation for the species' persecution on grouse moors. The use of diversionary feeding to reduce grouse predation rates by hen harriers has received considerable attention (Amar et al., 2004; Redpath et al., 2001); whereas, although a similar technique exists for peregrines (Phillips, 1990), it has yet to be rigorously tested. Establishing novel techniques such as this may be vital in reducing the motivation behind the illegal persecution of this species.

Understanding and acknowledging the scale of persecution on wild raptor populations is vital to tackling this issue (Wellsmith, 2011) and this paper contributes directly to our understanding in that respect. Persecution levels are often debated by the protagonists in the conflict between raptor conservation and management for red grouse shooting, although from a conservation perspective it is the population level impact that is important, rather than the number of confirmed persecution cases. This study suggests that persecution of peregrines on grouse moors is on a scale sufficient to have an impact at the population level. The approach outlined in this study whereby demographic data are combined with remotely sensed data on management practices may be useful for other studies to quantify levels of illegal activities which can be difficult to measure directly (Gavin et al., 2009) and to monitor changes in these levels following implementation of new policies or enforcement initiatives.

Acknowledgements

We are hugely grateful to Sophie Eastwood and Sally Fisher for help in organising and checking the data, and to Liz Hoffman, Will George and Dave Fouracre whom carried out the GIS analyses. Thanks are also due to Garry Marchant for compiling the data from the North York Moors. We are also grateful to Jeremy Wilson, Murray Grant, Pat Thompson, Alistair Crowle, Jen Smart, Staffan Roos, Steve Redpath, David Hoccom, Phil Whitfield and an anonymous reviewer who provided useful comments on this paper. We thank Ian Thomson and Guy Shorrocks who helped with the provision of the persecution data. Thanks are also due to Staffan Roos for use of his collated survival data. This research would not have been possible without the dedication and time of numerous NERF fieldworkers who have contributed their data to this Project. This research was made possible by funding to AA from the RSPB and

by support from the Percy Fitz Patrick Institute of African Ornithology, DST / NRF Centre of Excellence, University of Cape Town.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.10.014.

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