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Working with stakeholders to reduce conflict – modelling the impact of varying hen harrier *Circus cyaneus* densities on red grouse *Lagopus lagopus* populations

David A. Elston[1], Luigi Spezia[1], Dave Baines[2] and Stephen M. Redpath[3]*

[1]Biomathematics and Statistics Scotland, Craigiebuckler Aberdeen AB15 8QH, UK; [2]Game & Wildlife Conservation Trust, The Coach House, Eggleston Hall, Barnard Castle, Co. Durham DL12 0AG, UK; and [3]Institute of Biological and Environmental Sciences, Zoology Building, University of Aberdeen, Aberdeen AB24 2TZ, UK

Summary

1. Conflict management is difficult and may benefit from scientists working closely with stakeholders. We worked with conservation and moorland management interests, to consider the potential use of a quota system to address the long-standing conflict arising from hen harrier *Circus cyaneus* predation on red grouse *Lagopus lagopus scoticus*.

2. We modelled the impact of different harrier densities on grouse populations using a stochastic population dynamics model to inform the debate over the consequences of a quota system. The stakeholders commissioned the work and agreed on the underlying principles, the data sets and the approach.

3. The model covers the recovery phase from low grouse densities to a level at which driven shooting can recommence, as this phase is of paramount concern to the managers of grouse moors.

4. The model incorporated uncertainty in parameter values as well as for temporal and spatial variation in demographic rates. Multiple runs of the model enabled us to construct probability distributions, both for the population sizes in the first 2 years following cyclic lows in the grouse populations and for the number of years to recommencement of driven grouse shooting.

5. The model results quantified the extent to which high densities of harriers pose challenges for grouse management. At harrier densities of or below 0·025 km^2, harrier impacts were predicted to reduce autumn grouse densities by $<10\%$, suggesting that a quota scheme could theoretically support coexistence between grouse shooting and harrier conservation.

6. *Synthesis and applications*. Conflict management requires dialogue between conflicting parties and can benefit from objective inputs from scientists using an agreed evidence base and transparent derivation of relevant information from that evidence base. By discussing the principles of model development and eligibility of data sets with a stakeholder group in advance of producing model results, we achieved buy-in from all parties involved. Our model informs the debate: whether this additional information will lead to the development and testing of a quota system in practice remains to be seen.

Key-words: conflict management; estimated demographic rates; modelled predation rates; resumption of driven shooting; simulated autumn grouse densities; stakeholder engagement, hen harrier, red grouse; stochastic population dynamics model

Introduction

The resolution of conflicts over wildlife species presents difficult challenges to ecologists (Sullero-Zubiri, Sukumar & Treves 2008). Such conflicts can be seen across the world (Woodroffe, Thirgood & Rabinowitz 2005). Robust solutions are notoriously hard to achieve and success stories are few. Typically, parties become polarized and unable to have meaningful dialogue (Redpath *et al.* 2013). Participatory and deliberative approaches are used as a

*Correspondence author. E-mail: s.redpath@abdn.ac.uk

way of breaking down these barriers and are considered a positive way forward in conflict management (e.g. Chase *et al.* 2000). Indeed, there is evidence that such stakeholder engagement improves relationships, increases trust and reduces conflict (Beierle & Konisky 2001; Ansell & Gash 2008; Jones-Walters & Cil 2011), provided that the arguments and trade-offs are explicitly considered (McShane *et al.* 2011; Salafsky 2011).

Models provide a constructive way of evaluating alternative management solutions in a neutral framework that can reduce animosity and mistrust (Redpath *et al.* 2004). Various modelling approaches have been used to understand conflict, from game theory (Colyvan *et al.* 2011) to Bayesian approaches (New *et al.* 2011), whilst others have been used together with stakeholders to explore the systems and alternative solutions, such as management strategy evaluation (Smith *et al.* 2008) and multi-criteria decision modelling (Redpath *et al.* 2004).

Here we engaged with stakeholders over a specific conflict in the UK and developed a stochastic population dynamics model to explore a potential mitigation technique. We incorporated all relevant data and the uncertainties in a framework agreed upon by all parties. The conflict we consider is between game managers and conservation organisations in the UK over hen harriers *Circus cyaneus* which are predators of red grouse *Lagopus lagopus scoticus*. This conflict is both highly contentious and long-running (Thirgood & Redpath 2008). The hen harrier is a species of high conservation concern, included on the Red List of birds of conservation concern in the UK and on Annex 1 of the EU Birds Directive (79/409/EEC, now codified in 147/2009/EC). In the UK, the principal threat to the breeding population is thought to stem from illegal killing by those involved in the management of grouse. Such illegal activity limits the breeding success, numbers and range of harriers on moorland managed for grouse shooting (Etheridge, Summers & Green 1997; Stott 1998; Anon. 2000; Holmes *et al.* 2003; Sim *et al.* 2007), and the ongoing decline of the species has led to its disappearance as a breeding bird in England in 2013.

Grouse shooting is an important land-use in the UK uplands, providing economic and social benefits (Fraser of Allender Institute 2010), as well as benefits to upland conservation (Thompson *et al.* 1995; Robertson, Park & Barton 2001; Tharme *et al.* 2001). At high density, grouse are flushed and shot as they fly over butts or blinds – so called driven shooting – and this can create substantial revenue for moorland owners (Fraser of Allender Institute 2010). Evidence suggests that predation by high densities of harriers can make driven shooting uneconomic, but there is scope for low densities of harriers being compatible with shooting (Redpath & Thirgood 1999; Thirgood *et al.* 2000).

Legislation and continued efforts at enforcement have so far been unsuccessful at increasing harrier numbers on managed grouse moors, especially in England. Partly as a result of this lack of progress, the government agency responsible for harrier conservation, Natural England, initiated a dialogue process in 2005, facilitated by an independent NGO, the Environment Council (http://www.the-environment-council.org.uk/). This forum provided an opportunity for the main hunting and conservation stakeholders together with the statutory agencies to meet a few times per year to search for solutions that would lead to improved harrier conservation status in England without the loss of driven grouse shooting.

A variety of alternative technical solutions to this conflict have been proposed (see Thirgood *et al.* 2000; Redpath *et al.* 2010). One technique, initially put forward by Potts (1998), is that of a quota scheme. The main mechanism discussed was that excess clutches or broods would be moved away from grouse moors and the young reared in captivity, before being allowed to rejoin the wild population at fledging. Such an approach has been used successfully in continental Europe to deal with the problems of harriers being killed during harvesting in arable habitats (Amar, Arroyo & Bretagnolle 2000; Arroyo, Garcia & Bretagnolle 2002). Stakeholders agreed that an objective, evidence-based assessment was required to explore the consequences of different quota levels of nesting harriers on grouse populations and commissioned this work.

Materials and methods

MODELLING APPROACH

We developed a model to assess the consequences of particular levels of harrier densities on grouse populations. This immediately posed a number of difficulties: the causes of the cyclic dynamics of grouse are the subject of a long-standing debate (Martínez-Padilla *et al.* 2014); the dynamics of grouse populations over full cycles are far from straightforward (e.g. Haydon *et al.* 2002); and harvesting decisions, such as how many days to shoot on, are likely to vary widely between estates.

Initial discussions with stakeholders revolved around finding an approach that would be transparent and which all stakeholders would be able to agree with and defend amongst their constituencies. We agreed to focus on a realistic problem for managers: how long it took a grouse population to recover from low density to numbers sufficient for driven shooting in the presence of different densities of nesting harriers. This approach avoided the need to model the population cycles, specify relationships between grouse density and numbers of birds shot, and enabled us to focus on the time period of principal concern to grouse managers.

EVIDENCE USED AND MODELLING ASSUMPTIONS

Step 1: Reproduction

Game and Wildlife Conservation Trust (GWCT) provided data sets from grouse moors in three regions in northern England (Northern Pennines, Southern Pennines, North York Moors), summarized in Table 1. Data available to us consisted of counts

Table 1. Percentage of observed July broods of sizes ranging from 0 to 15 chicks, pooled across estates and years for each of three regions: Northern Pennines (NP), Southern Pennines (SP) and North York Moors (NYM)

	Brood sizes															
Region	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
NP	11·4	4·1	4·8	7·3	9·9	10·7	11·8	11·3	11·2	6·8	4·9	3·0	1·4	0·7	0·4	0·3
SP	5·3	1·0	2·4	7·3	16·0	17·5	17·5	16·5	8·7	4·9	2·9	0·0	0·0	0·0	0·0	0·0
NYM	7·5	2·5	3·5	12·0	18·5	30·0	26·5	24·0	16·5	6·0	3·5	1·5	0·0	0·0	0·0	0·0

of brood sizes in 4 years. Although these counts were made in July, they give a good indication of brood sizes following mortality of grouse chicks immediately after hatching.

Step 2: Chick predation

Adult harriers of both sexes take grouse chicks to feed their own young during June and July. We used 9 years of data from Scotland, excluding supplementary feeding trials, to estimate grouse chick predation by harriers (Redpath & Thirgood 1997, Redpath, Thirgood & Leckie 2001). The data consisted of numbers of grouse chicks brought back to each observed nest and numbers of observation hours per nest: an analysis of data from seven of these years has been published by Redpath & Thirgood (1999), using a model that assumes no chicks are caught when the chick density is zero.

Step 3: Winter mortality

The GWCT also provided data for the survival of 100 radio-tagged grouse over the winters of 1999/2000, 2000/2001 and 2001/2002 from three moors in the North Pennines (Table 2). We based our analysis on birds that had died of natural causes rather than being shot.

Step 4: Adult predation

Female harriers kill adult grouse in spring, in contrast to male harriers. We have no observational data from which to estimate the relationship between grouse density and predation rates at this time of year, although it is plausible to regard the predation rate as being an increasing function of grouse density. In the absence of data, three predation curves (termed low, medium and high adult predation) were agreed on with stakeholders. All three predation curves had upper asymptotes at 30 grouse, corresponding to female harriers taking one adult grouse each per day during the month following their return to breeding areas and before incubation. At low grouse density (5 pairs km^{-2}), the mean numbers of grouse taken per female harrier were set to be 1, 2 and 4 for the low, medium and high spring predation curves, respectively. At higher grouse density (20 pairs km^{-2}), the corresponding mean numbers of grouse taken per female harrier were set to be 5, 10 and 20.

Table 2. Data used to inform overwinter survival rates, summarizing records from 100 radio-tagged birds from three moors in the North Pennines

	Numbers alive on		
Winter	1st August	1st October	1st April (next year)
1999/2000	54	54	41
2000/2001	27	26	15
2001/2002	19	19	12

Further modelling assumptions

The following assumptions, discussed with stakeholders, were made in addition to those implicit in the annual cycle stated above to simplify the modelling approach:

a) the sex ratios in grouse and harriers were fixed at 1:1;
b) the modelled grouse populations were closed in terms of total size;
c) the total predation of grouse chicks by adult harriers for each nest occurred over 900 h – 60 days from hatching to dispersal for 15 h per day; and
d) natural mortality of adults only takes place in winter.

Apart from evidence from one moor (Langholm), there has been little evidence of harrier polygyny on grouse moors, especially when densities are low (assumption a). Assumption (b) was considered plausible for large grouse moors. Assumption (c) is based on published data (Redpath & Thirgood 1997). Assumption (d) was based on the finding that harriers during the breeding season took only grouse chicks rather than adult birds (Redpath & Thirgood 1997).

Modelling context

In discussion with stakeholders, we determined that the modelling would be in the context of:

a) when present, harrier nest densities were set from 0·0125 to 0·2 km^{-2} and remained unchanged during each simulation;
b) the area of the grouse moor was set at 80 km^{2} (8000 ha, c.19800 acres);
c) grouse densities started at population lows of either 10 or 20 pairs km^{-2};
d) modelling of the grouse population started at the time of spring counts, and the predation rate of adult grouse by female harriers was evenly split before and after that time; and
e) each simulation would be summarized by the grouse densities in autumn of years 1 and 2, and the first year in which autumn grouse densities were sufficiently high that driven grouse shooting could resume.

The grouse moor area was chosen to enable integer values for numbers of harrier nests at the minimum nonzero harrier density. The threshold for driven shooting was set by analysis of data provided by the GWCT (see below), consisting of estimates of

July grouse densities derived using distance sampling methods from repeat transect samples across the whole or most of the moor. These density estimates were all from within the last 10–12 years and were accompanied by the decision of whether or not to have driven shooting in the corresponding autumn.

CONSTRUCTION OF A SIMULATION MODEL FROM THE AVAILABLE EVIDENCE

Having determined the evidence we would use for our modelling, we then had to define how exactly we would use that evidence. In doing so, we wished to be as transparent as possible and to allow both the variation and uncertainty in supporting evidence to manifest itself in the results.

Step 1: Reproduction

Simulations were performed using reproduction data from just one English region in turn, the results for each region being compared by way of a sensitivity analysis. Mean numbers of chicks per brood varied between regions, with mean values of 5·6, 5·4 and 5·2 for Northern Pennines, Southern Pennines and North York Moors, respectively, but there was substantial variation between combinations of moors and years giving corresponding ranges of 3·5 to 7·6, 3·9 to 6·6 and 4·0 to 6·6. In each year of each simulation, one combination of year and moor was selected at random, and thereafter, all requisite brood sizes were selected at random according to the frequencies in the corresponding data. This ensured simulated brood sizes were integer-valued and followed the distribution of observed brood sizes.

Step 2: Chick predation

We used the same form of empirical relationship as published by Redpath & Thirgood (1999), but with estimation of parameters informed by two additional years of data and making explicit allowance for the different sources of variation underlying these data. Our analysis involved treating the data on observed number of grouse chicks, O_{ij}, brought back to nest i in year j as following a Poisson distribution, with mean value M_{ij} given by the equation:

$$M_{ij} = H_{ij} * R_{ij},$$

where H_{ij} was the number of hours for which nest i in year j was observed and R_{ij} was the corresponding provisioning rate which is also the predation rate for that nest on the population of grouse chicks. Following Redpath & Thirgood (1999), we treated the provisioning rate as a nonlinear function of chick density, C_j, in year j, but with the introduction of random effects to allow for variation between years and variation between nests within years. The resulting equation we used was:

$$R_{ij} = \exp(a + y_j + n_{ij}).(C_j/b)^c/[1 + (C_j/b)^c]$$

with random effects y_j and n_{ij} assumed to follow normal distributions with zero mean and variances v_y and v_n, respectively. The model parameters, and their role, are: a, a scaling parameter for predation rate, modulated by year and nest effects; b, a scale parameter for chick density which removes the effects of the dimensionality of density; and c, a shape parameter which controls the relationship between standardized chick density and the provisioning rate. This generalized nonlinear model was fitted using a Markov chain Monte Carlo (MCMC) sampling algorithm in WinBUGS. The following vague priors for four of the parameters were used to ensure information in the estimation came from the data rather than the priors: $a \sim N$ (0; 10 000); $c \sim N$ (0; 10 000); sqrt(v_y) $\sim N_+$(0; 10 000); sqrt(v_n) $\sim N_+$(0; 1000), where N (m; v) stands for the normal distribution with mean m and variance v, N_+(0; v) stands for the normal distribution left-truncated at 0 and hence taking only positive values. A gamma prior distribution with mean 51 and variance 1020 was used for b, to reflect the fixed value of 51 used in Redpath & Thirgood (1999) but allowing for considerable uncertainty in this figure. Following a conservatively large burn-in period of 1 000 000 updates, we iterated the sampler a further 2 500 000 times, saving the sampled value at every 500th iteration to give 5000 combinations of values of a, b, c, v_y and v_n for use in the simulations. Data and the fitted curve are shown in Fig. 1; point and interval estimates for the parameters informed by the data are presented in Table S1 (Supporting information).

At the start of each simulation, one of the final 1000 combinations of values of a, b, c, v_y and v_n was drawn at random, with values of y_j and n_{ij} then drawn at random and independently as required, using one random draw for y_j for all nests in a particular year. Values for M_{ij} were then calculated deterministically, using a, b, c, y_j and n_{ij}, treating the number of hours H_{ij} as being 900, after which the simulated number of chicks taken by that nest, P_{ij}, was drawn at random from a Poisson distribution with mean M_{ij}. For each simulation year, summation of P_{ij} across nests gave the total number of chicks taken by harriers. For years in which the simulated total number of chicks predated exceeded the number of chicks available, it was assumed that all chicks were predated.

Step 3: Winter mortality

We assumed the observed (see Table 2) winter survival rates, S, of grouse would follow beta distributions with probability density functions proportional to $S^{\alpha-1}(1\text{-}S)^{\beta-1}$. For such a distribution, the mean survival rate is $s_M = \alpha/(\alpha + \beta)$ and its variance is $s_V = \alpha\beta/[(\alpha + \beta)^2\ (\alpha + \beta + 1)]$. These equations for mean and variance can be inverted to give: $\alpha = [s_M{}^2\ (1\text{-}\ s_M)/s_V]\ \text{-}\ s_M$ and $\beta = \alpha\ s_V\ (\alpha + s_M)/s_M{}^3$. This approach was necessary during

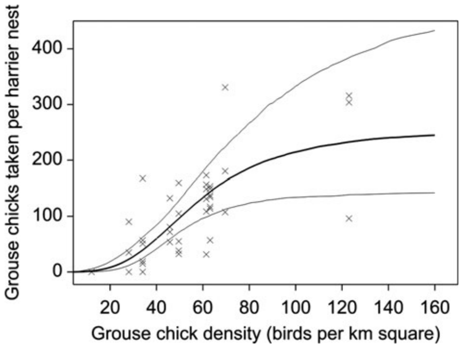

Fig. 1. The observed numbers of grouse chicks taken per harrier nest (×) after scaling up to 900 available hours, and the corresponding modelled relationship (thick line) and 95% credible intervals (thin lines).

preliminary modelling, when means and standard errors were the only figures available, and we subsequently elected to continue with this approach. For each year of each simulation, we selected one of the beta distributions at random, drew a mortality rate at random from that distribution and then estimated the number of birds dying from the corresponding binomial distribution.

Step 4: Adult predation

The fixed points on the low, medium and high predation rate curve were interpolated uniquely according to an asymptotic curve of the form $N_j = 30\ A_j^q\ (r + A_j^q)$ where N_j is the expected number of adult grouse taken by a female harrier in the spring of year j, and A_j is the corresponding density of adult grouse. The approximate parameter values for (q, r) achieving this interpolation were (1·268, 537·6), (1·404, 354·7) and (1·852, 460·4) for the low, medium and high spring predation curves, respectively.

Simulations were performed using each predation rate curve (Fig. 2) in turn, the results for each being compared by way of a sensitivity analysis. The probability of each adult grouse being predated was estimated by reading off the chosen predation rate curve at the current grouse density, multiplying this figure by the number of female harriers to get the total expected number of adult grouse predated and then dividing this figure by the number of grouse to get the expected probability of predation per bird. The number of adult grouse predated was then a random draw from the corresponding binomial distribution. In the first year of each simulation, the probability of predation per bird was divided by two to allow for the spring count taking place mid-way during the period of adult predation.

Resumption of driven shooting

For the 75 combinations of year and moor for which data were available, driven shooting took place on 59 occasions (Fig. 3). We treated the decision to have driven shooting as a binary response variable and modelled this using a generalized linear model with logistic link function using grouse density as a covariate: the need for more complex models was assessed by replacing the linear covariate by a smoothing spline with four degrees of freedom, but this increase in complexity was not supported by the data. The fitted response curve had $\log(p/(1\text{-}p)) = 0{\cdot}341 + 0{\cdot}0412\ (G\text{-}150)$, where G is the population estimate of density (birds km^{-2}) obtained in June but assumed to remain constant throughout the summer: the estimates of intercept and slope had standard errors of 0·409 and 0·00110, respectively, and a correlation of −0·051. These estimates of intercept and slope give a fitted probability of $P = 0{\cdot}5$ with a density of 133 birds km^{-2} following predation of chicks. Initial simulation runs were performed using this value of 133 birds km^{-2} as a fixed threshold, with driven shooting assumed to recommence as soon as it was exceeded. Subsequently, we decided to allow for uncertainty in the parameter estimates, setting a new threshold for each simulation run. This was done by drawing new values from the bivariate normal distribution with mean and variance–covariance parameters derived from the above, calculating the density corresponding to a fitted value of $P = 0{\cdot}5$, and then using this as a threshold to define the year in which driven shooting would resume. To avoid the possibility of unrealistic thresholds being set, we constrained the thresholds to lie between the lowest density at which driven shooting had occurred and the largest density at which driven shooting had not occurred (respectively, 73 and 237 birds km^{-2}).

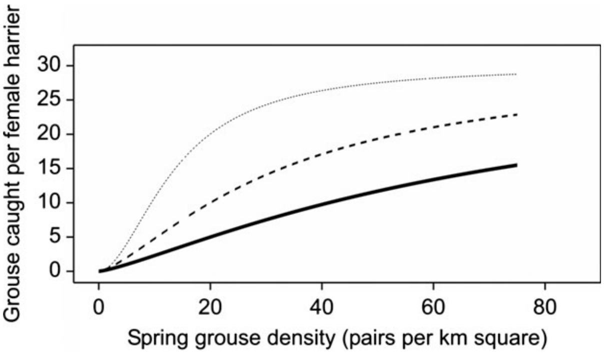

Fig. 2. The three curves assumed for predation of adult grouse in spring by female harriers, indicating the expected numbers of grouse taken per female harrier as a function of grouse density in spring, A. The curves each have an upper asymptote of 30 grouse and are described in the text as high (dotted, top), medium (dashed, middle) and low (solid, bottom) spring predation.

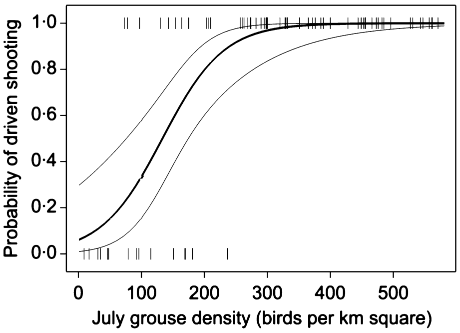

Fig. 3. Observed decisions as to whether (response = 1) or not (response = 0) to conduct driven shooting as a function of grouse density G, along with the fitted relationship and 95% confidence intervals from a logistic regression treating log (p/(1-p)) as a linear function of G.

Simulation strategy

Each simulation involved looping through the four demographic and predation steps above up to 11 times. Random draws were always assumed to be mutually independent. Each simulation ran until at least the autumn of year 2: if the threshold density for resumption of driven shooting had yet to be exceeded, then simulations continued until this happened or the autumn of year 11 was reached. We performed 100 000 simulations per situation to provide a reasonably precise estimate of the likely distribution of outcomes for each situation. Some pseudo-code describing the structure of the simulations is given as Appendix S1 (Supporting information). The simulations were summarized by grouse densities in years 1 and 2 and the year of first exceedance of the threshold density, these values being presented as tables of means, tables of percentages or graphs of the associated frequency distributions.

Results of simulations

In the absence of breeding harriers, simulated grouse densities in the autumn of year 1 were mostly between 50 and

100 birds km^{-2} when spring densities were set to 10 pairs km^{-2} (Fig 4a, 1st row) and between 100 and 200 birds km^{-2} when spring densities were set to 20 pairs km^{-2} (Fig 4a, 2nd row). Grouse densities in the autumn of year 2 were increased to between 80 and 330 birds km^{-2} when spring densities were set to 10 pairs km^{-2} and between 170 and 600 birds km^{-2} when spring densities were set to 20 pairs km^{-2} (Fig 4b, 1st and 2nd rows, respectively). Using the brood size data from the Northern Pennines gives a slightly longer upper tail than using brood size data from other regions, due to the higher mean brood sizes in Table 1, but overall the differences between regions were small (Fig 4a&b, comparison of columns).

In the presence of harriers, the distributions of simulated grouse densities in the autumns of years 1 and 2 were reduced, the scale of the reduction depending strongly on the density of harrier nests (Fig 4). With a harrier density of 0·0125 nests km^{-2} and using the medium spring predation curves, the reduction in mean grouse densities in the autumn of year 1 varied from 2·4 to 2·5%: with a density of 0·1 nests km^{-2}, the corresponding reductions were in the range 18–19% (Fig 5). By the autumn of year 2, these reductions had increased to 3–5% and 21–34% for harrier densities of 0·0125 and 0·1 nests km^{-2}, respectively. The type of spring predation curve made only a small difference to the results compared with the effect of harrier nest density (Tables S2a–c, Supporting information).

Without harriers, and with a starting grouse density of 10 pairs km^{-2}, the majority (78–81%) of simulations first exceeded their thresholds for the resumption of driven shooting in the autumn of year 2 (Fig. 6, first row and Table S3a–c, Supporting information). The bulk of the remainder did so in year 3, with <1% of simulations

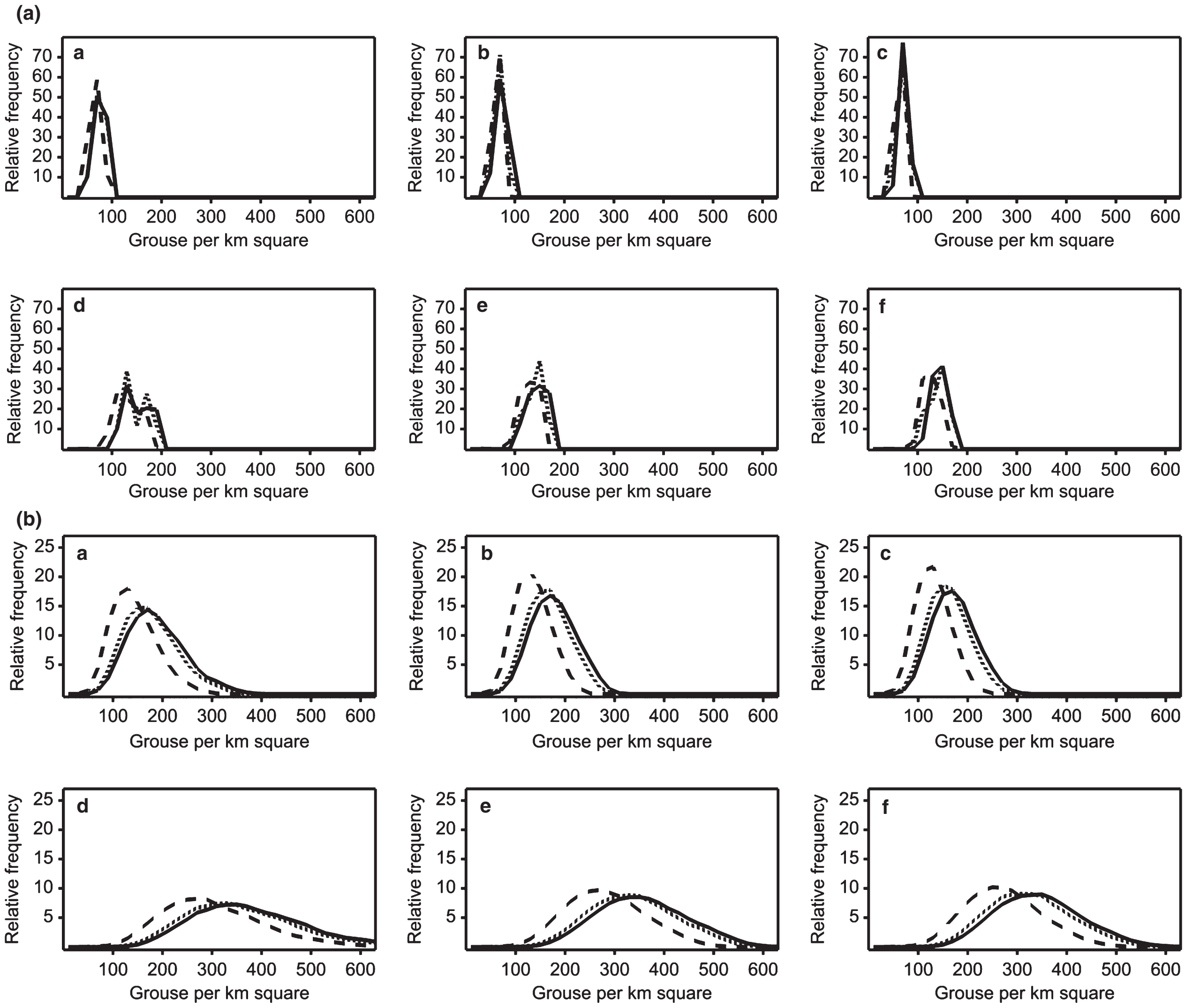

Fig. 4. Distributions of simulated grouse densities in (a) autumn of year 1 and (b) autumn of year 2, produced using the medium spring predation curves. Figures arranged in rows according to initial grouse density (top, 10 pairs km^{-2}; bottom, 20 pairs km^{-2}) and in columns according to region (left, Northern Pennines; centre, Southern Pennines; right, North York Moors). Line styles indicate hen harrier nest densities km^{-2} (0, continuous; 0·025, fine dots; 0·1 long dashes).

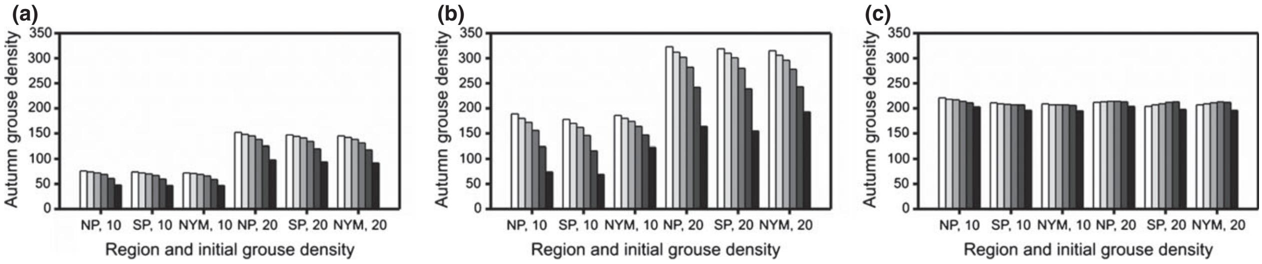

Fig. 5. Mean population densities (birds km^{-2}) of red grouse in the autumn of simulation year 1 (a), year 2 (b) and also for the year in which the threshold for resumption of driven shooting was first exceeded (c). Simulations used the medium spring predation curves, with a spring grouse density in year 1 of either 10 or 20 pairs per km^2. Brood size data used was for one of Northern Pennines (NP), Southern Pennines (SP) or North York Moors (NYM). Shading of bars indicates harrier nest densities, from 0 (white) through 0·0125, 0·025. 0·05 and 0·1 to 0·2 (black) pairs km^{-2}. Results using other spring predations curves are summarized in the Supporting Information Tables S2a-c.

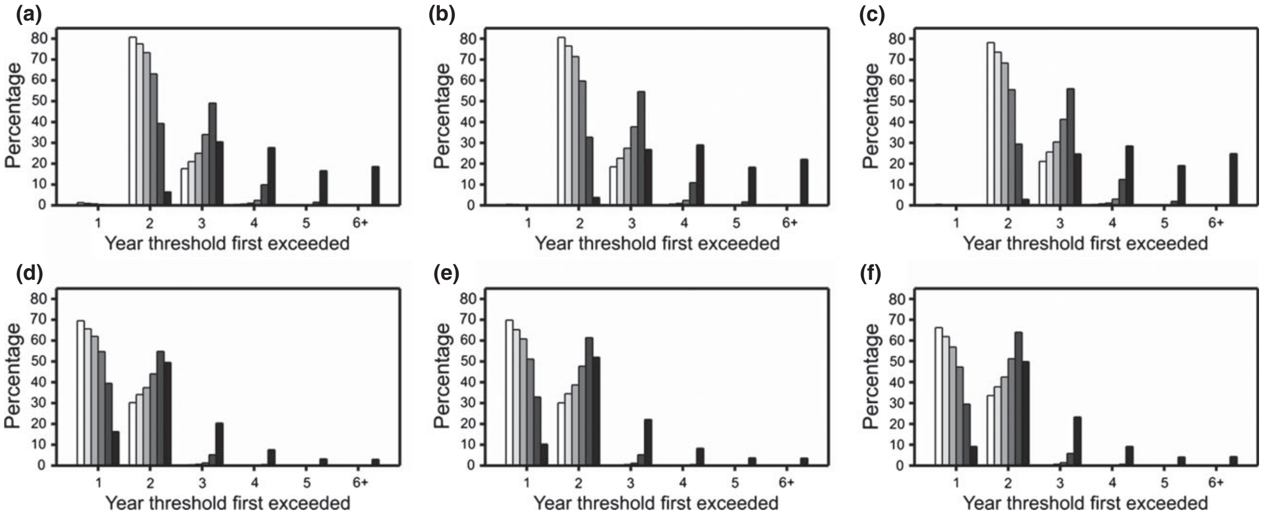

Fig. 6. For each combination of region and harrier density, this figure shows the percentage of 100 000 simulations in which driven shooting would have started in the stated year when spring grouse density in year 1 was either 10 pairs per km^2 (a,b,c) or 20 pairs per km^2 (d,e,f). Brood size data used was for one of Northern Pennines (a,d), Southern Pennines (b,e) or North York Moors (c,f). Shading of bars indicates harrier nest densities, from 0 (white) through 0·0125, 0·025, 0·05 and 0·1 to 0·2 (black) pairs km^{-2}. Simulations used the medium spring predation curve: results using other spring predations curves are summarized in Supporting Information Tables S3a-f.

requiring 4 or more years. With a starting grouse density of 20 pairs km^{-2}, the simulations first exceeded their thresholds for the resumption of driven shooting mainly (66–70%) in the autumn of year 1 (Fig. 6, second row and Tables S3d–e, Supporting information). The bulk of the remainder did so in year 2, with <1% of simulations requiring a third year.

In the presence of harriers, the time to first exceedance of the thresholds lengthened. Using the medium spring predation curves, with a starting grouse density of 10 pairs km^{-2}, the absolute difference in the percentages of simulations exceeding their thresholds by the end of year 2 averaged 4, 9 and 21% for harrier nest densities of 0·0125, 0·025 and 0·05 nests km^{-2}, respectively (Fig. 6, first row and Table S3a–c, Supporting information). Similarly, with a starting grouse density of 20 pairs km^{-2}, the absolute difference in the percentages of simulations exceeding their thresholds by the end of year 1 averaged 4, 9 and 17% for harrier nest densities of 0·0125, 0·025 and 0·05 nests km^{-2}, respectively (Fig. 6, second row and Tables S3d–e, Supporting information). Higher harrier densities had more substantial impacts. At the harrier nest density of 0·2 km^{-2}, over 60% of simulations required at least 4 years to exceed their thresholds from a starting grouse density of 10 pairs km^{-2} and over 30% required at least 3 years from a starting grouse density of 20 pairs km^{-2}.

Discussion

A quota scheme offers a potential, if contentious, solution to this long-term conflict (Redpath *et al.* 2010). However, stakeholders are cautious about agreeing to this approach. Grouse managers are cautious because of the perceived consequences for grouse shooting and conservationists are cautious partly because of the perceived consequences for setting a precedent for the active management of birds of prey, considering that other approaches to harrier recovery should be tested first (Thompson *et al.* 2009). However, currently, there is stalemate in this conflict and the harrier populations on grouse moors continue to be severely limited (Thirgood & Redpath 2008). This paper is the result of a long-term process that recognizes the role played by stakeholder discussion and agreement in searching for a lasting solution (Emerson *et al.* 2009).

Conflict management will benefit from dialogue between conflicting parties that incorporates objective inputs from scientists using an agreed evidence base and transparent derivation of relevant information from that evidence base (Redpath *et al.* 2013). In this study, we discussed the principles of model development and eligibility of data sets with relevant stakeholders. Although all involved recognized that additional data would be beneficial, the group accepted that we had to operate within the constraints of the data available. Throughout the process, we recognized the need to focus on outcomes identified as important to the stakeholders, and the limitations of the data available. On this basis, we developed a stochastic model allowing for variation and uncertainty, to inform the debate in as objective and transparent a manner as possible.

The results highlight that there is room for negotiation. High densities of harriers (above 0·1 nests km^{-2}) are clearly identified as a problem for grouse management, as mean autumn grouse densities in the second year of the recovery phase are predicted to be reduced by at least 20%. Yet at harrier densities of 0·025 km^{-2} or less, impacts are predicted to be relatively low (mean autumn grouse densities predicted to be reduced by no more than 10% in each of the first two years of recovery). Given that there are approximately 2800 km^2 of managed grouse moor in England (Moorland Association data quoted in Grant *et al.* 2012), this would be equivalent to 70 pairs of harriers, in contrast to the low numbers that have bred recently, culminating in there being no harriers that were known to successfully breed in England in 2013. Even the lowest hen harrier density considered here, 0·0125 km^{-2} would be equivalent to 35 pairs of harriers breeding in England.

A negotiated solution will require both groups of stakeholders to be explicit about their goals – what level of impact are grouse managers prepared to tolerate, and what densities of harriers can conservation organisations live with? If stakeholders can negotiate a solution, they will also need to recognize that a number of uncertainties remain about the impact of harriers on grouse and the design of a quota scheme. First, we have a poor understanding of the impact of harriers on grouse populations overwinter, when birds are moving more widely around the country (Etheridge & Summers 2006). Second, grouse managers are concerned that hen harriers flying over grouse moors during the shooting season will disturb birds during organized shoots and thereby affect the numbers of grouse shot. Third, diversionary feeding, whereby carrion is provided to breeding harriers to reduce predation rates on grouse chicks, could be used in combination with a quota scheme. In an experimental trial, supplementary feeding was successful at reducing predation on grouse chicks by 86% (Redpath, Thirgood & Leckie 2001). However, concerns about the long-term impact of diversionary feeding on harrier numbers and numbers of generalist predators persist and have prevented the technique from being widely taken up (Redpath *et al.* 2010). Fourth, as parasites are an important driver of cycles in autumn numbers, grouse managers increasingly use anthelmintics to improve grouse abundance (Newborn & Foster 2002). Should such management lead to a cessation in population cycles; then theoretically, grouse moors could sustain higher densities of harriers, so the quota could be raised. Fifth, there is considerable temporal and spatial variation in grouse productivity and survival (Watson & Moss 2008) outside the parameters employed in this model. Demographic rates will affect how quickly grouse populations can recover, so a quota may need to be regionally specific. Sixth, predation rates on grouse are affected by polygyny, that is, the number of females breeding per male harrier (Redpath *et al.* 2006) and availability of alternative prey (New *et al.* 2012). More grouse are caught by bigamous than monogamous birds and in situations where alternative prey are scarce, so these factors would need to be considered in the design of any trial. Lastly, the distance birds are moved from grouse moors would need to be considered as this may affect post-fledging predation and disturbance rates and subsequent return rates of harriers to the grouse moors.

These uncertainties could be important and suggest that these seven points would need to be considered and their effectiveness be monitored during a trial, before they could be widely adopted. Moreover, we suggest that any trial quota scheme should incorporate two approaches. First, it may be advisable to initially take a precautionary approach, as grouse managers are more likely to favour building up from low densities of harriers. Second, any field test of the technique would need to incorporate these aspects into a monitoring programme and an adaptive framework, so that management learns and adapts as new data emerge.

This paper provides an example of how scientists can work with stakeholders to explore solutions to conflicts over wildlife. Ultimately, any decision about how to use this model in the management of predators will depend as much on politics as on science. However, this model does present a framework for those political negotiations to take place, should both sides be interested in pursuing a quota scheme as a possible solution.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Mean values of parameters used in modelling the numbers of chicks brought back to harrier nests as a function of chick density, together with summaries of the samples of values obtained during implementation of the MCMC inference scheme in WinBUGS.

Tables S2a-c. Summaries of simulations in terms of mean population densities of red grouse in the autumn.

Tables S3a-f. Summaries of simulations in terms of year of commencement of driven shooting.

Appendix S1. Pseudo-code for implementation of the population dynamics model for red grouse in the presence of hen harriers.