Scotland's Rural College

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Illegal killing associated with gamebird management accounts for up to three-quarters of annual mortality in Hen Harriers *Circus cyaneus*

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ABSTRACT

Predators are frequently victims of wildlife crime due to conflicts with human interests. Where predators are protected, killing may occur covertly and novel methods, including satellite tracking, are often required to assess population consequences. Wildlife crime persists in the British uplands, where raptors are illegally killed on moorland managed for Red Grouse *Lagopus lagopus scotica* shooting. To understand impacts on one such species, the Hen Harrier *Circus cyaneus*, we analysed data from 148 individuals tracked across Britain between 2014 and 2021. Using remotely sensed land-use data and continuous-time survival methods, we quantified survival rates, contributions of natural causes and illegal killing to mortality, and spatial and temporal associations between mortality and land managed for grouse shooting. Annual survival was low, especially among first-year birds (males: 14 %; females: 30 %), with illegal killing accounting for 27–43 % and 75 % of mortality in first-year and subadult (1-2 years) harriers respectively. Illegal killing is likely attributable to grouse moor management because i) a 10 % increase in grouse moor use resulted in a 43 % increase in mortality risk; ii) a strong overlap existed between mortality and grouse moor extent in 20 km squares, identifying hotspots of illegal killing in northern England and northeast Scotland; iii) death due to natural causes showed different spatial and temporal patterns; and iv) timing of mortality peaked around the shooting season and during breeding territory establishment. Governments have failed to reduce illegal killing of Hen Harriers and other raptors in Britain and our results emphasise that further legislative reform is needed to tackle this enduring criminality.

1. Introduction

Conservation conflicts are an increasing challenge facing conservation practitioners, commonly arising where wild animals pose a perceived or actual threat to human livelihoods, safety, or economic activities (Woodroffe et al., 2005; Redpath et al., 2013). Predators lie at the heart of some of the most intractable conflicts due to their impacts on livestock or wild species exploited by humans (e.g., Gusset et al., 2009; Cummings et al., 2019). Many predators are of high conservation concern and legally protected (e.g., Wipple et al., 2014), but illegal killing may continue where human interests are perceived to be compromised by predator conservation (Redpath et al., 2013).

Illegal killing of predators is typically carried out covertly to minimise chances of detection and prosecution, and quantifying its magnitude is challenging. Limited evidence suggests that such killing can contribute significantly to overall mortality. Liberg et al. (2012) found that 50 % of wolf *Canis lupus* mortality in Scandinavia was attributable to illegal killing, although only one third of this was directly verifiable,

whilst Whitfield and Fielding (2017) discovered that covert killing accounted for 74 % of mortality of young Golden Eagles *Aquila chrysaetos* in Scotland. Another difficulty when predators are killed covertly is determining whether this mortality is additive, compensatory, or partially compensatory to natural mortality, which is also key to understanding population impacts (Murray et al., 2010).

To tackle the challenges posed by covert wildlife crime, researchers increasingly apply tracking and biologging technologies. Tracking devices on albatrosses have been used to monitor illegal fishing (Weimerskirch et al., 2020) and as an early warning system to alert authorities to poaching activities based on the movements of tracked non-target species (De Knegt et al., 2021). Modern tracking methods also hold promise for quantifying illegal killing in predator populations, as they permit near constant, real-time monitoring of individuals and can yield insights on where and when mortality occurs (Whitfield and Fielding, 2017; Murgatroyd et al., 2019; Sergio et al., 2019a).

Recreational shooting of Red Grouse *Lagopus lagopus scotica* occurs across large parts of the British uplands. The high post-breeding numbers of grouse desired by this form of shooting requires the use of uniquely intensive game management, including habitat management, predator and disease control (Thompson et al., 2016; Mustin et al., 2018). Raptor predation can reduce the number of grouse available for shooting (Thirgood et al., 2000). As the capital value of shooting estates is determined by the number of grouse shot per annum (Knight Frank, 2014), there is a strong economic incentive to reduce losses of grouse to raptor predation. Illegal killing of raptors is thus widespread on grouse shooting estates and limits the distribution and population size of several species in Britain (Etheridge et al., 1997; Whitfield et al., 2003; Whitfield et al., 2004a; Whitfield et al., 2004b; Whitfield et al., 2008a; Smart et al., 2010; Fielding et al., 2011; Amar et al., 2012; Whitfield and Fielding, 2017; Melling et al., 2018; Murgatroyd et al., 2019; Newton, 2021).

The magnitude of Hen Harrier mortality due to illegal killing on grouse moors has previously been difficult to quantify due to steps taken by perpetrators to conceal their crimes. Annual recorded incidences of illegal killing are widely accepted to represent only a fraction of the number of individuals persecuted (McMillan, 2011; RSPB, 2021). Now, however, satellite transmitters afford new insights into the pervasive impacts of illegal killing. A recent study found that only 17 % of satellite-tracked Hen Harriers survived their first year, the probability of mortality rose with increasing use of grouse moors and was highest in protected areas comprising a proportionately greater area managed for grouse shooting (Murgatroyd et al., 2019). Our study extends these previous findings and greatly enhances our understanding of illegal killing by presenting results from the largest programme of Hen Harrier tracking globally. This dataset includes individuals tagged in nests across a large proportion of the species' distribution in Britain and the Isle of Man, and both individuals known or suspected to have died of natural causes and those illegally killed. This enables a novel comparison of the relative contribution of natural causes and illegal killing to mortality rates, as well as an examination of spatial and seasonal patterns of mortality and whether these are related to land management for grouse shooting. Specifically, in this study, we address the following questions:

1. What is the survival probability of Hen Harriers, and how does this differ between sexes and age classes?
2. What is the relative contribution of natural causes and illegal killing to mortality, and how does this differ between sexes and age classes?
3. What are the seasonal patterns of survival, and how do these differ between natural causes and illegal killing?
4. Is weekly survival associated with use of grouse moors, and does this relationship vary between birds that died of natural causes or that were killed illegally?

5. What are the spatial patterns of survival, and do associations with grouse moors vary between birds that died of natural causes or that were killed illegally?

2. Methods

2.1. Hen Harrier and environmental data

2.1.1. Satellite tagging

Hen Harrier breeding attempts were monitored by experienced fieldworkers at traditional nesting grounds across Britain and the Isle of Man between 2014 and 2020 (Fig. 1). Nest locations were pinpointed using either observations of adult behaviour ($n = 91$) or fixes from individuals tagged as chicks, which were now breeding ($n = 8$). Nests were visited under licence when chicks were between 26 and 32 days old to fit satellite tags. We tagged between 1 and 4 chicks per nest (mean = 1.7), selecting individuals heavy enough to meet licence conditions, and, where possible, tagging an equal number of males and females. Sexes were separated in the nest based on iris colouration (Picozzi, 1981; Hardey et al., 2009).

We fitted satellite transmitters to 148 harriers (65 males, 83 females;
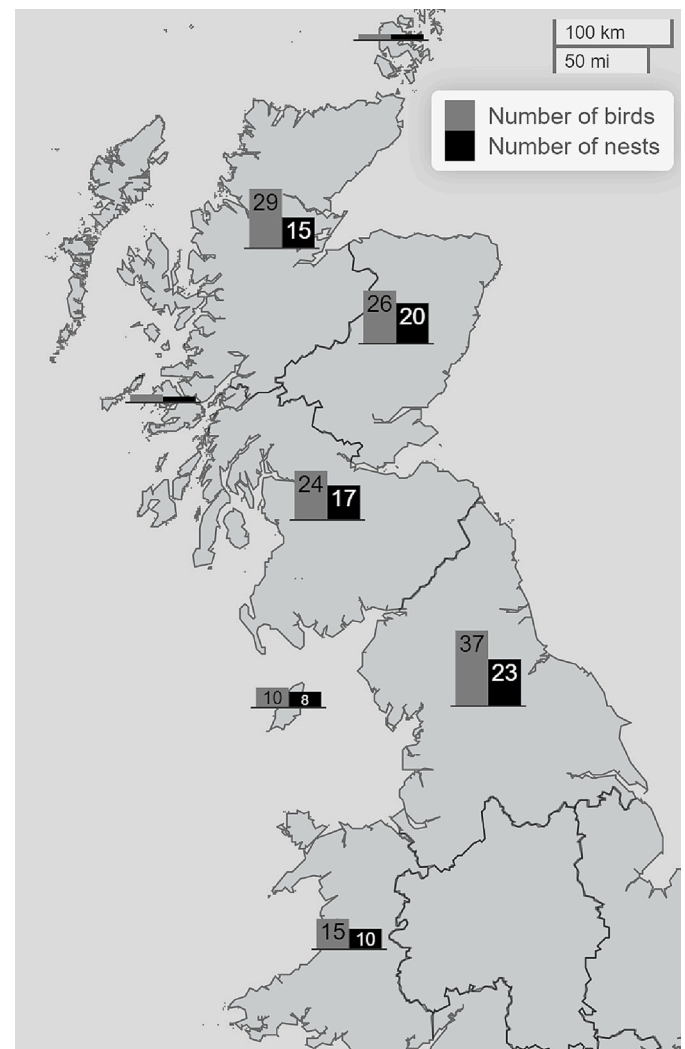

Fig. 1. The number of Hen Harriers fitted with transmitters and the number of nests at which tagging occurred in different regions of Britain. Bar charts for Mull and Orkney were too small to label and the relevant figures are four individuals and three nests tagged on Mull and three individuals and three nests tagged on Orkney.

mean = 21 per year, range = 6–37). Most were solar-powered Argos PTT transmitters with a duty cycle of 4 h of transmission and 19 h switched off (*n* = 123; Microwave Telemetry Inc., Columbia, MD, USA; 9.5 g tags on males (*n* = 58, although two 12 g tags were inadvertently deployed on males early in the project) and 9.5 g (*n* = 28) or 12 g (*n* = 35) tags on females), with a smaller cohort fitted with either 11.5 g (*n* = 14, females only; Pathtrack Ltd., Otley, UK) or 10 g (*n* = 11, 5 males & 6 females; Ornitela, Vilnius, Lithuania) GPS-GSM tags. Transmitters were fitted using 6 mm Teflon-ribbon thoracic cross-strap single weak-point back-pack harnesses (Anderson et al., 2020) mounted on neoprene bases. Approval for use of 9.5 g harness-mounted devices on males between 290 and 400 g and 9.5 g or 12.0 g devices on females between 390 and 750 g was granted by the Special Methods Technical Panel of the British Trust for Ornithology (endorsement number 2673), reviewed annually following an assessment of the previous year's tagging returns. The combined weight of the tag and harness constituted 2.48 % (9.5 g tag) or 2.96 % (12 g tag) of average adult female body mass and 3.7 % of average male body mass (9.5 g tag, Scharf and Balfour, 1971).

Argos transmitters estimated locations in this study based on Doppler shift of signals received during passes of polar-orbiting satellites and did not have on-board GPS functionality due to weight constraints. The accuracy of Argos transmitter locations is generally lower than that of GPS and depends particularly on the number of signals (Costa et al., 2010). With individual location estimates, the Argos system yields a location class that summarises expected positional error. Location classes 3, 2, 1, and 0 correspond to spatial errors of <250 m, 250–500 m, 500–1500 m and > 1500 m respectively, while the A, B and Z classes are associated with unquantified errors. Following Murgatroyd et al. (2019), the latter three location classes were excluded from consideration in this study due to low positional accuracy. The expected operational lifespan of these Argos transmitters is at least three years, but they often last well beyond this deployment period (Whitfield and Fielding, 2017; Sergio et al., 2019a).

2.1.2. Allocation of fates to Hen Harriers

Bird locations and tag engineering data were downloaded and scrutinised daily. Where data suggested a harrier was stationary or that a tag had ceased transmitting, one or more field visits were made to relocate the individual or retrieve the tag and/or remains and gather evidence of circumstances of death. In cases where we had reason to believe that a tag had stopped working in suspicious circumstances, we first informed the police and then made attempts to recover the bird as soon as it was practicable to do so. Search areas initially focused on ground immediately surrounding the final Argos location, but these were widened where initial recovery attempts failed, and in the end often covered several square kilometres. We used a Goniometer RXG-134 receiver and AXG-134 antenna to aid recovery of actively transmitting Argos tags, which enabled a relatively high recovery rate of 36 % (e.g., Sergio et al., 2019b). Remains of recovered birds were sent for veterinary post-mortem examination to diagnose cause of death (Supplementary Materials 1). Using all available evidence, we assigned tracked harriers to six fate categories using a modified version of the classification in Murgatroyd et al. (2019; see Supplementary Materials 2 Fig. S1).

2.1.3. Grouse moor distribution

Grouse moor managers burn patches of moorland on a rotation of 10–25 years to create a mosaic of different ages of heather *Calluna vulgaris* used by grouse as food and shelter (Thompson et al., 2016). The resulting strip burns are detectable on remotely sensed images, and here we use the burning map of Douglas et al. (2015) to represent the spatial distribution of grouse moor habitats, defining a 1 km square as being subject to grouse moor management if it contained strip burns (see also Chapman et al., 2010; Allen et al., 2016).

2.2. Statistical analysis

(1) What is the survival probability of Hen Harriers, and how does this differ between sexes and age classes?

We estimated annual survival for male and female harriers using Kaplan-Meier survival analysis (Table S1). The survival dataset was configured i) specifying staggered entry of individuals into the study on their tagging date and ii) using a recurrent annual timescale (Fieberg and DelGiudice, 2009) from 1 June to 31 May, permitting separate estimation of survival for first-years (0–1 years), subadults (1–2 years) and adults (>2 years). Annual survival was specified as a binary variable, with '0' indicating survival/censored and '1' indicating death. Other variables recorded the time an individual entered and exited the tagged population, measured in days since 1 June. The small number (*n* = 4) of individuals suffering tag technical failures were right-censored on the date of their final fix.

(2) What is the relative contribution of natural causes and illegal killing to mortality, and how does this differ between sexes and age classes?

We created aggregate fate classes to examine the relative contributions of natural causes and illegal killing to mortality (Fig. S1). Illegally killed (IK) individuals were combined with the Stop No Malfunction fate class under 'known or probable illegal killings' (e.g., Whitfield and Fielding, 2017), whereas the natural and unknown classifications were pooled as 'known or probable natural deaths'. We strongly suspect that most individuals with unknown fates died naturally. For example, remains and/or tags were recovered for 9 of 32 Hen Harriers in this fate class. The fact that these individuals were available for recovery is circumstantial evidence for natural causes of death, as attempts are often made to conceal acts of illegal killing. Furthermore, there was no evidence from tag engineering data or circumstances surrounding the disappearance of the remaining unrecovered harriers indicating death due to anything other than natural causes. We estimated mortality rates due to illegal killing and natural causes for two different age classes (first-years and subadults) of male and female Hen Harriers by deriving cause-specific cumulative incidence functions (Table S1, Murray and Bastille-Rousseau, 2020) using the *survival* package (Therneau, 2022) in R (R Core Team, 2022). Mortality rates were not calculated for adults (> 2 years) due to the small number of individuals contributing to these age classes.

(3) What are the seasonal patterns of survival, and how do these differ between natural causes and illegal killing?

Seasonal patterns of mortality were examined using the *cyclomort* package in R (Gurarie et al., 2020), which fits a flexible parametric periodic hazard function to identify multi-modal mortality peaks from continuous time survival data (Table S1). We tested whether birds dying of natural causes and those illegally killed differed in the seasonal timing or number of mortality peaks. We first examined seasonal timing using the entire cohort of tracked harriers and fitted models that assumed different numbers of seasonal peaks (0–4), which were compared using Akaike's Information Criteria (AIC, Burnham and Anderson, 2002). This analysis revealed that a three-peak model was optimal. We then tested for differences in the timing of mortality of harriers dying of the two causes by contrasting the fit of models specifying either common or cause-specific three-peak periodic hazard functions using a Likelihood Ratio (LR) test. We also examined whether the two causes differed in the number of seasonal mortality peaks by fitting models with different numbers of seasonal peaks to the two groups separately and compared these using AIC.

(4) Is weekly survival associated with use of grouse moors, and does this relationship vary between birds that died of natural causes or that were killed illegally?

Associations between weekly mortality and use of grouse moor habitats were investigated using competing-risks Cox proportional hazards models implemented in the *survival* package in R (Table S1, Murray and Bastille-Rousseau, 2020). This approach is appropriate when deaths have been attributed to multiple causes and insights are desired on cause-specific influence of covariates (Murray and Bastille-Rousseau, 2020).

Prior to analysis, we processed the satellite-tracking dataset using the approaches set out in Supplementary Materials 3. We configured the input data by first recording information on survival during each week of life. As previously, birds entered the dataset at time of tagging, and we structured the dataset using a recurrent annual timescale (Fieberg and DelGiudice, 2009). We accommodated the competing causes of death using the data augmentation method of Lunn and McNeil (1995), which replicates data sets by the number of risk factors (i.e., two in our case to reflect natural causes of death and illegal killing). These replicates were indexed in the dataset by a *risk type* dummy variable, which we fitted in the competing-risks Cox proportional hazards models as a stratification factor (method B, Lunn and McNeil, 1995). Individuals were censored in one of the data replicates depending on which cause of death applied (Lunn and McNeil, 1995; Murray and Bastille-Rousseau, 2020).

Following Murgatroyd et al. (2019), we quantified use of grouse moor during each week by calculating the percentage of satellite fixes that overlapped 1 km squares classified as burned. This measure of *grouse moor use* was then included as a covariate in proportional hazards models to test whether it explained variation in weekly mortality risk. We also included an interaction term between *grouse moor use* and *risk type* to evaluate differences in this relationship between natural causes and illegal killing. Other covariates were *age* (two-level factor: first-year or older birds), *sex, tagging date* (number of days since 1st June) and the two-way interaction terms between *age*grouse moor use* and *sex*grouse moor use*.

We tested for violations of the Cox proportional hazards assumption using graphical checks and tests of the Schoenfeld residuals (Murray and Bastille-Rousseau, 2020). The *age* covariate did not conform to the proportional hazards assumption, so we stratified our models by *age*. We assessed the importance of individual covariates and their interaction terms using Type III Wald *p*-values derived with robust variances to account for repeated observations of weekly survival from individual harriers. Fully-specified models were simplified by iteratively removing non-significant interaction terms and then main effects.

(5) What are the spatial patterns of survival, and do associations with grouse moors vary between birds that died of natural causes or that were killed illegally?

We derived a spatial measure of mortality as the number of fixes from the final week of life in 20 km UK National Grid squares as a proportion of the total number of fixes recorded in a square across the tracking period, following Murgatroyd et al. (2019). We calculated this metric separately in each square for males and females, first-year and older birds, and birds dying of natural causes or illegal killing, resulting in replicated measures for 20 km squares. This measure of mortality was specified as the response variable in statistical models as a two-column matrix comprising the count of final week fixes and the count of non-final week fixes per square. We also derived a spatial index of *grouse management* for each 20 km square as the proportion of 1 km squares with strip burning.

Associations between the distribution of harrier final fixes and covariates were analysed using beta-binomial generalized linear models (GLMs, Table S1). We did not continue with initial attempts to use mixed models (GLMMs) to accommodate repeated observations from

individual 20 km squares, as the *square ID* random intercept accounted for negligible variance. Alongside the *grouse management* covariate, we specified three other main categorical variables, namely *fate class* (natural causes vs. illegal killing), *age* (first-year or older birds) and *sex*. We also tested interactions between these and the *grouse management* covariate. We assessed the influence of covariates and their interaction terms using *p*-values derived from Type III Likelihood Ratio (LR) Tests and simplified the model using backwards stepwise deletion of non-significant terms. Beta-binomial GLMs were fitted using the *glmmTMB* package (Brooks et al., 2017), and LR tests implemented using the *monet* package (Singmann, 2022) in R.

3. Results

(1) What is the survival probability of Hen Harriers, and how does this differ between sexes and age classes?

The median lifespan of harriers after tagging was 121 days (range = 2–2171 days). Kaplan-Meier survival analysis suggested that annual first-year (0–1 years) survival rates were 14 % for males and 30 % for females (Fig. 2, Table 1). These increased to 56 % and 58 % for male and female subadults (1–2 years), and adult female annual survival (> 2 years) was 80 %. Too few males ($n = 1$) survived past two years of age by the end of the study to allow an estimate of adult male survival.

(2) What is the relative contribution of natural causes and illegal killing to mortality, and how does this differ between sexes and age classes?

Mortality due to illegal killing increased or remained consistent over the first two years of life (Fig. 3; males: first-years = 22.9 %, subadults = 33.3 %; females: first-years = 31.0 %, subadults = 31.6 %) but natural mortality declined (males: first-years = 62.5 %, subadults = 11.1 %; females: first-years = 40.4 %, subadults = 10.5 %). The percentage of overall annual mortality attributable to illegal killing was: first-year males (27 %), first-year females (43 %), subadult males (75 %) and subadult females (75 %). In the absence of illegal killing (and assuming causes of death act additively), annual survival rates would be 38 % and 60 % for first-year males and females, and 89 % and 90 % for subadult males females respectively.

(3) What are the seasonal patterns of survival, and how do these differ between natural causes and illegal killing?

Seasonal timing of mortality differed between natural causes and illegal killing, (LR test: $\chi^2 = 24.71$, df = 9, $p = 0.003$), as did the number of mortality peaks, with three peaks for harriers dying naturally and either zero or two (models separated by only 0.03 AIC points) for birds killed illegally (Table S2). For natural deaths, a brief peak of mortality occurred in early August, followed by another at the end of October and then a prolonged period of high mortality through the winter months (Fig. 4). For birds killed illegally, models could not distinguish whether mortality was consistent throughout the year or there was a longer peak centred on mid-October, followed by a briefer peak in early of April (Fig. 4).

(4) Is weekly survival associated with the use of grouse moors, and does this relationship vary between birds that died of natural causes or that were killed illegally?

Associations between mortality risk and use of grouse moor habitats varied significantly between causes of death (Fig. 5, Table 2a). The risk of illegal killing increased with greater use of grouse moors (hazard ratio = 5.30, 95 % CI: 2.69–10.50), with every 10 % increase in grouse moor use accompanied by a 43 % rise in mortality risk. In contrast, natural mortality decreased with increasing grouse moor use (hazard
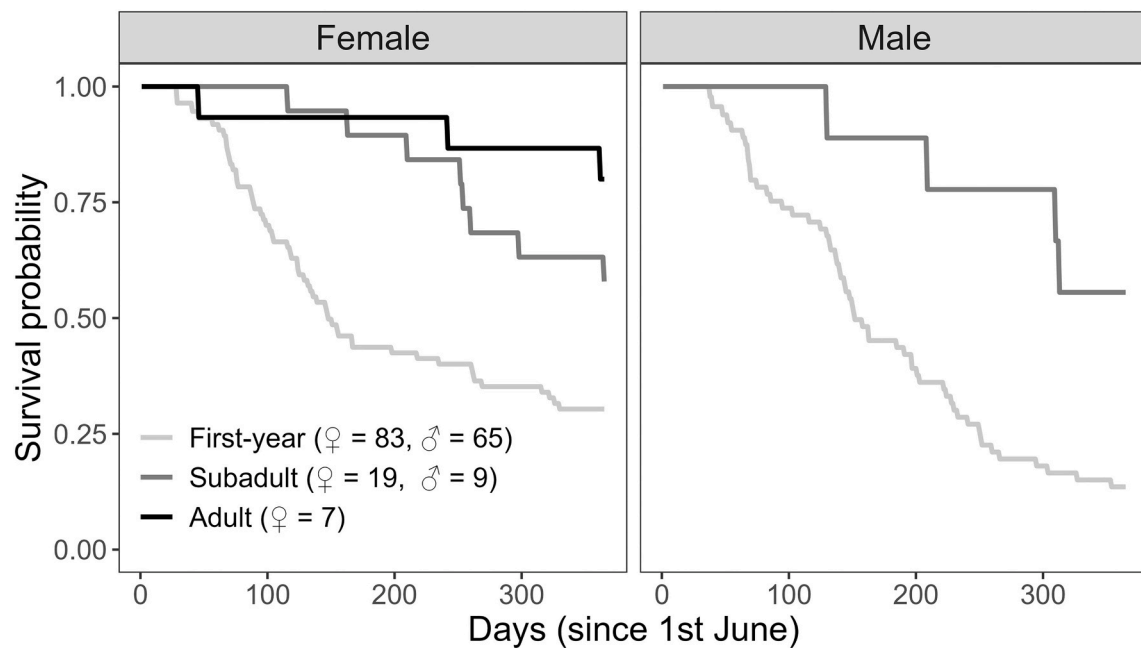
Fig. 2. Kaplan-Meier survival functions for different age-classes and sexes of Hen Harrier in Britain. The figures in the legend represent the number of harriers that contributed to estimates of survival in each class.

Table 1
Estimates of annual survival for different sexes and age classes of Hen Harrier derived from Kaplan-Meier survival analysis based on an annual recurrent timescale from 1st June-31st May.

Sex	Age class	Annual survival estimate	95 % CIs	# harriers
Female	First-year	0.303	(0.218–0.423)	83
	Subadult	0.579	(0.395–0.850)	19
	Adult	0.800	(0.621–1.000)	7
Male	First-year	0.135	(0.074–0.249)	65
	Subdult	0.556	(0.310–0.997)	9

ratio = 0.32, 95 % CI: 0.13–0.82), declining by 7 % with each 10 % rise in use. Mortality risk was also higher for birds tagged later in the breeding season and differed significantly between years (Table 2a).

(5) What are the spatial patterns of survival, and do associations with grouse moors vary between birds that died of natural causes or that were killed illegally?

The proportion of final-week fixes of birds killed illegally increased with the proportion of grouse moor in the landscape (Table 2b, Fig. S2a & b). Males were almost six times and females three times more likely to be illegally killed in 20 km squares where grouse moors were a dominant (≥50 %) land use compared to squares not managed for grouse (females: $emm_0 = 0.018$, 95 % CI: 0.012–0.025; $emm_{0.5} = 0.055$, 95 % CI: 0.032–0.092; males: $emm_0 = 0.007$, 95 % CI: 0.004–0.012; $emm_{0.5} = 0.039$, 95 % CI: 0.020–0.075). Areas with high levels of illegal killing included the Pennines in northern England, and in and around the Cairngorms National Park in northeast Scotland (Figs. 6, S3a & b). The proportion of final-week fixes of birds dying naturally was not related to the proportion of grouse moor in the landscape in either sex (Fig. S2a & b). Significant differences in the relationship between grouse moor management and harriers dying naturally and illegally were only found in males (males: est. = 5.30, s.e. = 1.28 $p < 0.001$; females: est. = 1.81, s. e. = 1.04, $p = 0.300$).

4. Discussion

### 4.1. Hen Harrier survival estimates and potential impacts of tags

Annual survival of first-year Hen Harriers reported by this study was 14 % for males and 30 % for females, which is consistent with the 17 % of individuals that survived their first year in a smaller cohort of satellite-tracked Hen Harriers tagged in northern England and southern Scotland (Murgatroyd et al., 2019). Picozzi (1984) and Rothery (1985) estimated age-dependent survival of Hen Harriers on the Orkney Isles, where there is no grouse moor management, but where individuals do migrate to the mainland outside the breeding season. They derived estimates of apparent survival between 0 and 2 years of 14 % and 29 % for males and females respectively. When first-year and subadult age classes are pooled in this study, comparable estimates of (true) survival between 0 and 2 years were lower for both males and females (males = 8 %, 95 % CI: 3.3–17.9 %; females = 17 %, 95 % CI: 10–29 %). Survival increased with age, and our estimates for adult females was similar to or above those documented previously by studies on mainland Scotland (40 % and 78 %, Etheridge et al., 1997), but below that for the population on Orkney (90 %, Picozzi, 1984, Rothery, 1985).

We selected the largest individuals in Hen Harrier broods for tracking to comply with licence conditions. A consequence of this preferential selection of larger individuals for tagging is that estimates of survival, particularly of juveniles, may not be fully representative of the wider population, which may be lower than estimated here.

Tracking devices can sometimes detrimentally affect the survival of tagged organisms (Bodey et al., 2018). Post-mortem examinations of recovered harriers ($n = 53$; up to and including October 2022) provided little evidence for deleterious effects of tags on harriers in this study, with all either reporting no ($n = 29$) or only superficial impacts such as feather loss or damage ($n = 8$; remaining 16 birds were too decomposed to allow any assessment). We also found that male Hen Harriers had lower survival in their first year than females. Between-sex differences in survival are generally rare in raptors (Newton et al., 2016), so it is possible that the sex difference in mortality could indicate an adverse impact of tags primarily in males, the lighter sex (but see later). An ongoing programme of colour-ringing to estimate survival for untagged birds will be used to test for tag impacts on survival rates when sufficient
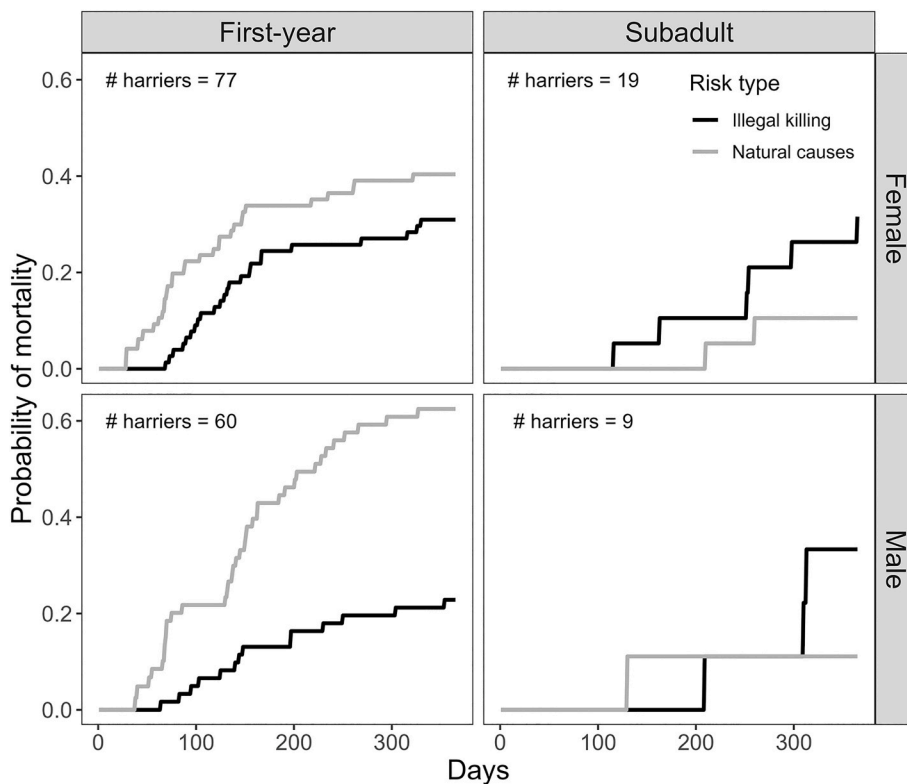
Fig. 3. Cumulative incidence functions for different age classes (first-year and subadult) of male and female Hen Harriers in Britain showing the probability of birds dying separately from natural causes and illegal killing. No incidence functions were calculated for adult males or females due to the small number of individuals surviving past two years of age. Figures at the top-left of each plot indicate the number of harriers at risk in each of the sex and age classes. The numbers of birds dying of natural causes (N) and illegal killing (IK) in each sex and age class were: first-year females: N = 28, IK = 24; first-year males: N = 37, IK = 14; subadult females: N = 2, IK = 6, subadult males: N = 1, IK = 3).
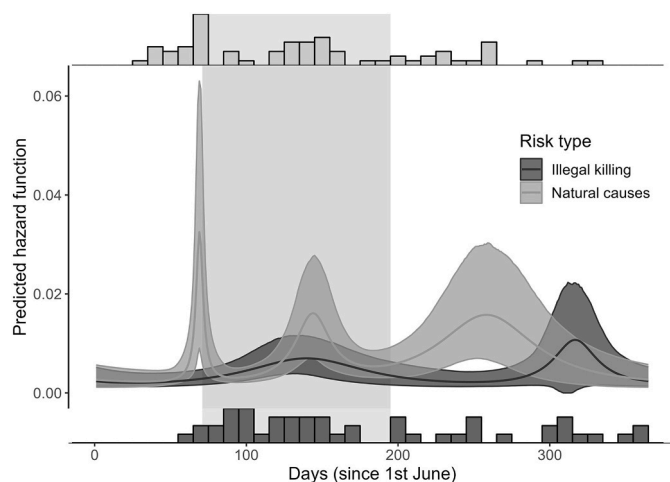
Fig. 4. Predicted seasonal peaks in mortality risk (plus 95 % confidence intervals) calculated from periodic hazard models for subsets of birds dying due to natural causes and illegal killing. Marginal histograms also denote the numbers of birds dying in each time period. Grey shaded area marks the grouse shooting season.

resighting data becomes available. If present, any adverse effects of tag deployment are most likely to present as an excess of natural mortality in first-year males.

4.2. Role of illegal killing

The most likely cause of low Hen Harrier survival is illegal killing. We have direct, incontrovertible evidence that several harriers tagged during this project were illegally killed. Post-mortem examinations confirmed that three individuals were victims of shooting with shotguns, one was snared in a spring trap, and one was poisoned with a banned

pesticide, carbofuran. A further post-mortem examination indicated a Hen Harrier that died of natural causes contained shot gun pellets from a previous persecution attempt (RSPB, 2017).

Powerful circumstantial evidence of widespread illegal killing also comes from the 43 harriers whose previously well-performing satellite tags suddenly stopped transmitting, with these birds never recovered, despite intensive searches. Beyond illegal killing, there are few other plausible explanations to account for such a large cohort of tracked individuals disappearing. A few disappearances could be attributable to incidents where a transmitter suffered catastrophic damage or where a naturally predated harrier was taken to an underground burrow, thus obscuring the tag from the view of satellites, but we have no evidence of this from our cohort of tracked birds. Signal transmission from grounded Argos tags can be compromised when a tagged bird dies on its back, but this would probably have been a rare occurrence as many tags continue to transmit at a lower rate in this position (Gordon, 2020). Tag failure is also unlikely to underpin the abrupt cessation of these tags. Whitfield and Fielding (2017) documented that failure rates of satellite tags fitted to Golden and Bald Eagles in America, Norway and Scotland were around 2 % (Whitfield and Fielding, 2017), close to the 3 % of tagged individuals in our Tag Failure fate class. Higher failure rates have been recorded in other studies (e.g. Klaassen et al., 2014; Sergio et al., 2019b), but this tends to occur in non-persecuted species where long deployments bring tags close to or over their expected operating lifespans. For tag failure to account for many of the Stop No Malfunction classifications, there would need to have been a failure rate of 32 %, much greater than previously documented and highly implausible. Furthermore, sensitivity analysis suggested that key results documented by this study were robust to high levels of tag failure misspecification (Supplementary Materials 4). Illegal killing, and disabling of satellite tags to evade detection, remains the most plausible explanation to account for the loss of so many Hen Harriers.

The distribution of final satellite tracking locations of Hen Harriers known or likely to have been illegally killed corresponded closely with areas managed for grouse shooting. Our results showed that weekly
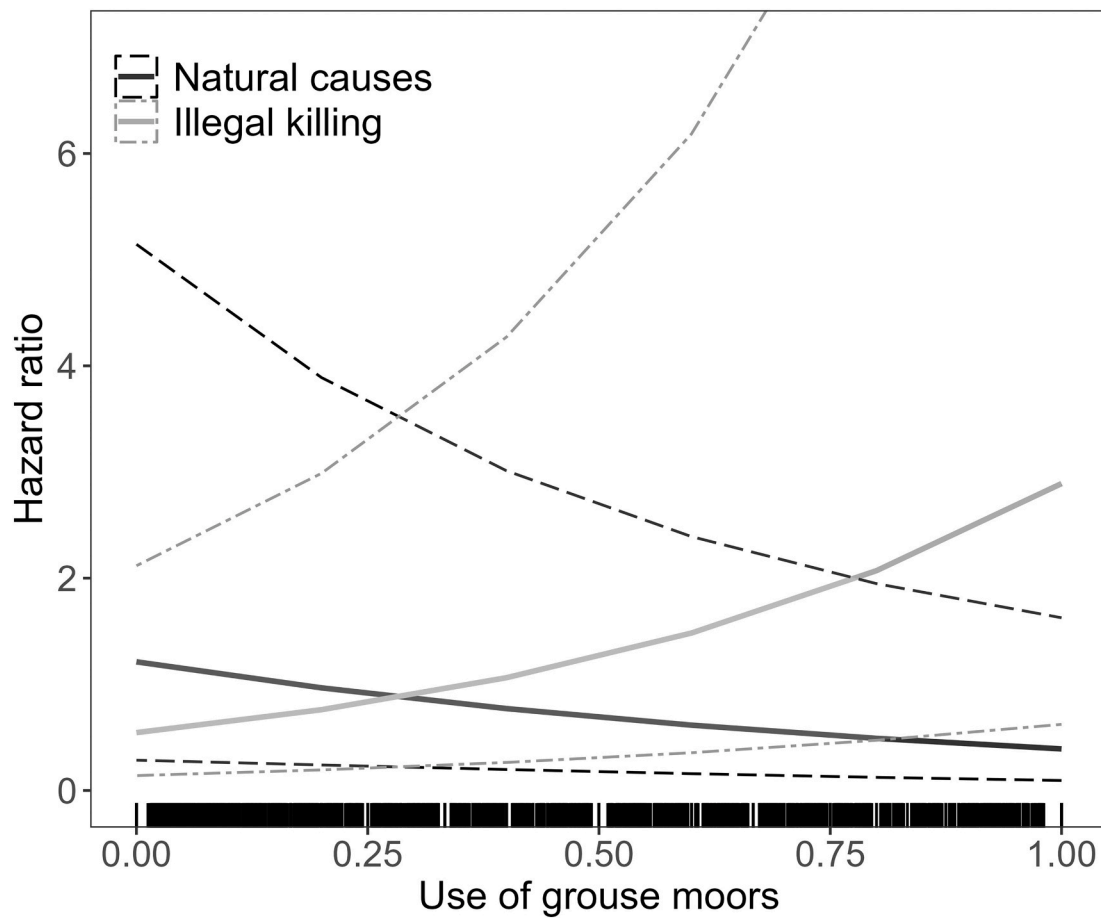
Fig. 5. Predicted relationships between Hen Harrier survival (as measured by hazard ratios) and grouse moor use, showing contrasting risks of Hen Harriers dying due to natural causes and illegal killing with increasing use of grouse moor habitats. Dashed lines denote the 95 % confidence intervals of predictions.

mortality rates of illegally killed Hen Harriers, but not those dying of natural causes, increased with greater use of grouse moors. There was also a strong spatial correspondence between the distribution of final-week fixes of illegally killed harriers and the prevalence of areas managed for grouse shooting in 20 km squares. The most parsimonious explanation for this is that satellite-tagged Hen Harriers were killed on grouse moors. Together with Murgatroyd et al. (2019), our findings suggest that illegal killing on grouse moors continues to severely reduce the survival of Hen Harriers across the British uplands, more than 25 years after these impacts were first quantified by Etheridge et al. (1997) and almost 70 years since this species was first afforded legal protection under the Protection of Birds Act, 1954.

Mortality due to illegal killing was apparently higher in first-year female harriers than males. Different sex-specific behaviors may render females more vulnerable to illegal killing. Whereas male harriers typically move to coastal and lowland areas during winter, females tend to remain in upland areas, including on grouse moors where they may be exposed to illegal persecution for a greater proportion of the annual cycle than males (Etheridge and Summers, 2006). During the breeding season, females spend more time at the nest site than males, which likely makes them more susceptible to illegal killing where nesting birds are targeted (Newton et al., 2016).

Murgatroyd et al. (2019) identified that the intensity of illegal killing of Hen Harriers in northern England was higher in protected areas with more grouse moors compared to those with little grouse moor. We examined the relative magnitude of illegal killing within the protected area network by superimposing protected area boundaries on top of spatial maps of the proportion of final-week fixes in 20 km squares (Fig. S3a & S3b). This showed hotspots of harrier mortality due to illegal

killing within the same areas highlighted by Murgatroyd et al. (2019) (Fig. S3a). Our data collected over a wider geographic area also enabled us to identify additional mortality hotspots, most notably in the central and eastern Highlands of Scotland, centred on the Cairngorms National Park (Fig. S3b). Whitfield and Fielding (2017) found clusters of mortality in similar areas of the central and eastern Highlands for satellite-tagged Golden Eagles known or suspected to have been killed illegally.

Seasonal patterns of mortality also lend support to illegal killing of Hen Harriers being associated with grouse moor management. Models identified two equally plausible seasonal patterns of harrier mortality due to illegal killing. The first distinguished no seasonal peaks, whereas the second identified two mortality peaks. The first protracted peak coincided with the grouse moor shooting season from August to November, when first-year birds are dispersing from their natal sites (Etheridge and Summers, 2006) and may travel into areas of increased risk. This is also the point in the year when harriers are targeted at communal winter roosts (RSPB, 2019). The shorter mortality peak identified in March/April coincides with territory establishment and may reflect illegal killing to prevent breeding attempts being initiated on grouse moors.

4.3. Role of natural sources of mortality

Among first-year birds, males were apparently more susceptible than females to natural mortality, thus contributing to the lower survival of tagged males. Although tagging effects are a possible explanation, other studies have documented lower survival rates of male than female harriers (Picozzi, 1984; Rothery, 1985; Whitfield and Fielding, 2009), so these patterns may be natural. For example, the fact that polygyny has

Table 2

Results from (a) competing-risks Cox proportional hazards models examining associations between use of grouse moor habitats and weekly mortality risk of tracked Hen Harriers and (b) beta-binomial GLMs exploring the spatial overlap in the distribution of the proportion of final-week fixes and intensity of grouse moor management in 20 km squares in Britain. For both analyses, we compare differences in the relationship with grouse moor between fate classes, age classes and sexes. Statistical significance was assessed based on *p*-values from Wald's or likelihood ratio tests. Results from both fully specified (containing all fitted main effects and interaction terms) and reduced (simplified via backwards deletion) models are presented.

Model term	(a) Competing-risks Cox proportional hazard model								(b) Beta-binomial GLM							
	Fully-specified model				Reduced model				Fully-specified model				Reduced model			
	est	s.e.	χ^2	*p*	est	s.e.	χ^2	*p*	est.	s.e.	χ^2	*p*	est	s.e.	χ^2	*p*
Main effects																
Intercept	na[1]				na[1]				−3.80	0.17	487.92	<0.001	−3.72	0.16	487.91	<0.001
Grouse moor	−0.97	0.61	2.55	0.111	−1.13	0.48	5.60	0.018	3.50	0.61	27.27	<0.001	2.93	0.55	22.84	<0.001
Fate class [N]	na[2]				na[2]				−0.18	0.24	0.59	0.442	−0.28	0.23	1.53	0.215
Sex [M]	0.43	0.22	3.83	0.050	–	–	–	–	−0.99	0.30	12.41	<0.001	−0.99	0.28	14.12	<0.001
Age class [Ad]	na[2]				na[2]				−0.55	0.34	2.77	0.096	−0.93	0.25	16.13	<0.001
Year	–	–	16.30	0.023	–	–	16.61	0.020	na[3]				na[3]			
Tagging date	0.36	0.08	19.47	<0.001	0.34	0.08	17.79	<0.001	na[3]				na[3]			
Interaction terms																
Grouse moor:fate class	3.00	0.67	20.00	<0.001	2.80	0.58	23.27	<0.001	−2.45	1.09	5.50	0.019	−1.83	1.04	3.36	0.067
Grouse moor:sex	−0.31	0.94	0.11	0.744	–	–	–	–	1.21	0.95	1.61	0.204	1.50	0.92	2.64	0.104
Grouse moor:age class	na[2]				na[2]				−2.44	1.25	4.34	0.037	–	–	–	–
Fate class:sex	na[2]				na[2]				1.60	0.38	18.73	<0.001	1.63	0.37	21.10	<0.001
Fate class:age class	na[2]				na[2]				−2.05	0.91	6.92	0.008	−1.13	0.53	5.38	0.020
Grouse moor:fate class:sex	−0.81	0.99	0.66	0.417	–	–	–	–	−3.35	1.67	4.11	0.043	−3.56	1.64	4.75	0.029
Grouse moor: fate class: age class	na[2]				na[2]				3.35	2.66	1.34	0.246	–	–	–	–
Fate class:age class:sex	na[2]				na[2]				–	–	1.01	0.604	–	–	–	–

[1] Intercepts are incorporated into the baseline hazard and are not reported by Cox proportional hazard models.

[2] These covariates did not conform to the proportional hazards assumption and were either used as stratification variables (main effects) or excluded from the model (interactions).

[3] These covariates could not be incorporated in this model due to its specification.

been widely reported in Hen Harriers (Balfour and Cadbury, 1979; Picozzi, 1984) and related species (e.g., Simmons et al., 1986), more so than other raptors (Newton, 1979), is consistent with natural differences in survival between the sexes leading to biased sex ratios in the adult breeding population (Picozzi, 1984). Smaller males may be more susceptible to mortality during periods of food scarcity or adverse environmental conditions as they are less able to compete with larger females and older males for high quality wintering ranges (e.g. Temeles, 1986) or may experience elevated mortality during longer migratory journeys to wintering grounds (Etheridge and Summers, 2006).

Temporal peaks in mortality due to natural causes of death differed from those attributable to illegal killing. We identified three seasonal peaks in natural mortality during August, October and January–March, which respectively correspond approximately to the post-fledging dependence period, the period of dispersal from the natal territory and settlement at wintering sites and the winter period (Jan-Mar), all points when juvenile birds may be particularly susceptible to predation, starvation or the impacts of inclement weather (McFadzen and Marzluff, 1996; Sergio et al., 2019b). The timing of fledging was also an important determinant of subsequent survival, with late-fledged Hen Harriers surviving poorly relative to earlier-fledged counterparts. Similar patterns have been reported for passerines (e.g., White et al., 2021), but such findings for raptors are rare. Early-hatched individuals may have more time to gain condition or improve hunting proficiency before independence due to longer periods of post-fledging parental care (e.g. Arroyo et al., 2002), or earlier departure from their natal territory may mean that they can locate, establish and monopolise high quality wintering territories (e.g. Akresh et al., 2021).

Natural mortality declined with greater use of grouse moors. This may indicate a partially compensatory relationship between illegal killing and natural mortality, perhaps resulting from density-dependent mechanisms reducing natural mortality in areas with high rates of illegal killing (e.g., Murray et al., 2010). However, should this be the case, compensatory processes are unlikely to fully offset mortality due to illegal killing (Fig. 5). On grouse moors, legal killing of mammalian mesopredators such as Red Fox *Vulpes vulpes* is widespread as part of grouse management. These mammalian predators are potential predators of incubating females, and it is possible that harriers on grouse moors benefit from this control. Illegal killing of apex avian predators such as Golden Eagle and Goshawk *Accipiter gentilis* may also reduce levels of intraguild predation on harriers (Fielding et al., 2003). Furthermore, harrier hunting success can be higher on grouse moors compared to other land uses (Redpath et al., 2002). Thus, where harriers escape illegal killing, lower natural predation pressure and higher prey capture rates may positively impact survival (Fig. 6).

5. Conclusions

Survival of Hen Harriers in this study was abnormally low and mortality hazards due to illegal killing were higher for individuals using upland areas managed for grouse shooting. The magnitude of mortality due to illegal persecution, which accounted for between 27 and 75 % of annual mortality depending on age class and sex, has undoubtedly contributed to the decline of Hen Harriers in the UK (Wotton et al., 2018) and the species' ongoing absence from large areas of the uplands, particularly grouse moors (Fielding et al., 2011). Our results, together with those of previous studies of Hen Harriers (Etheridge et al., 1997; Whitfield et al., 2008b; Fielding et al., 2011; Murgatroyd et al., 2019) and other raptors (Whitfield et al., 2003, Whitfield et al., 2004a, Whitfield et al., 2008a, Amar et al., 2012, Northeast Scotland Raptor Study
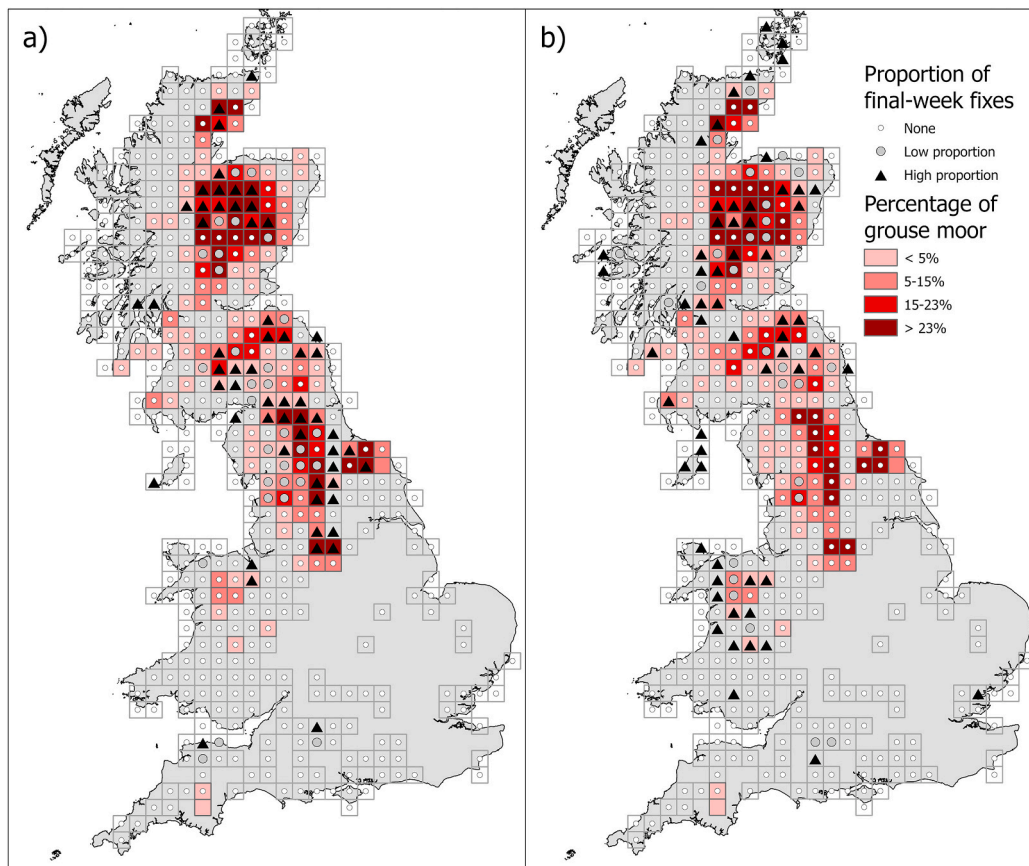
Fig. 6. Proportion of final-week fixes from tracked Hen Harriers in each 20 km square across Britain in relation to the extent of grouse moor management in each square, calculated separately for harriers that have died of (a) illegal killing and (b) natural causes. White circles indicate that no final-week fixes were recorded in 20 km squares, grey circles depict a below average proportion of final-week fixes and black triangles represent an above average proportion of final-week fixes. No Hen Harriers were recorded using squares lacking symbols. The increasing intensity of red colouration in squares indicates the extent of grouse moor management using the same gradation scale as Murgatroyd et al. (2019). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Group, 2015, Whitfield and Fielding, 2017, Melling et al., 2018), demonstrate the deeply ingrained and widespread illegal killing of raptors across UK grouse moors (Newton, 2021).

Little sustained action has been taken by consecutive devolved and national governments to address the issue of illegal raptor killing. For a long time, those committing these wildlife crimes have been able to do so largely with impunity, with low detection and conviction rates and inadequate penalties from the courts (RSPB, 2021). The Scottish Government has published a new Wildlife Management and Muirburn Bill (Scottish Government, 2023), which outlines plans to introduce a licensing scheme for grouse moors, with individual licences potentially revoked where criminal activity is detected. In England, the DEFRA-led Hen Harrier Action Plan outlines three (of six) actions – diversionary feeding, a southern reintroduction, and trialling a brood management scheme – designed to reduce conflict between harriers and grouse shooting interests (DEFRA, 2016). As satellite tagging is the main method that provides insights into the magnitude of illegal killing, continued investment in tracking will be crucial to monitor the success of these contrasting approaches in resolving the longstanding conflict between Hen Harriers and grouse moor management in Britain.

CRediT authorship contribution statement

Steven R. Ewing: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Cathleen E. Thomas:** Conceptualization, Project administration, Funding acquisition, Data curation, Investigation, Methodology, Resources, Supervision, Writing - review & editing. **Nigel Butcher:** Conceptualization, Methodology, Data curation, Resources, Writing – review & editing. **David J.T. Douglas:** Writing – review & editing. **David I.K. Anderson:** Methodology, Investigation. **Guy Q.A. Anderson:** Methodology, Investigation. **James Bray:** Methodology, Investigation, Writing – review & editing. **Steve Downing:** Methodology, Investigation. **Ronan Dugan:** Project administration, Funding acquisition, Data curation, Investigation. **Brian Etheridge:** Methodology, Investigation. **Will Hayward:** Methodology, Investigation, Writing – review & editing. **Fiona Howie:** Methodology, Investigation, Resources, Data curation, Writing – original draft. **Staffan Roos:** Conceptualization, Methodology, Writing – review & editing. **Mark Thomas:** Project administration, Funding acquisition, Supervision. **Jenny Weston:** Methodology, Investigation. **Jennifer Smart:** Writing – review & editing, Supervision. **Jeremy D. Wilson:** Writing – review & editing, Supervision.

Declaration of competing interest

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110072.

References

Akresh, M.E., King, D.I., Marra, P.P., 2021. Hatching date influences winter habitat occupancy: examining seasonal interactions across the full annual cycle in a migratory songbird. Ecol. Evol. 11, 9241–9253.

Allen, K.A., Denelle, P., Ruiz, F.M.S., Santana, V.M., Marrs, R.H., 2016. Prescribed moorland burning meets good practice guidelines: a monitoring case study using aerial photography in the Peak District, UK. Ecol. Indic. 62, 76–85.

Amar, A., Court, I.R., Davison, M., Downing, S., Grimshaw, T., Pickford, T., Raw, D., 2012. Linking nest histories, remotely sensed land use data and wildlife crime records to explore the impact of grouse moor management on peregrine falcon populations. Biol. Conserv. 145, 86–94.

Anderson, D., Arkumarev, V., Bildstein, K., Botha, A., Bowden, C.G.R., Davies, M., Duriez, O., Forbes, N.A., Godino, A., Green, R.E., Krüger, S., Lambertucci, S.A., Orr-Ewing, D., Parish, C.N., Parry-Jones, J., Weston, E., 2020. In: A Practical Guide to Methods for Attaching Research Devices to Vultures and Condors, Vulture News 78a. IUCN Species Survival Commission Vulture Specialist Group Technical Publication No.1, pp. 1–72.

Arroyo, B.E., De Cornulier, T.H., Bretagnolle, V., 2002. Parental investment and parent–offspring conflicts during the postfledging period in Montagu's harriers. Anim. Behav. 63, 235–244.

Balfour, E., Cadbury, C.J., 1979. Polygyny, spacing and sex ratio among hen harriers Circus cyaneus in Orkney, Scotland. Ornis Scand. 10, 133–141.

Bodey, T.W., Cleasby, I.R., Bell, F., Parr, N., Schultz, A., Votier, S.C., Bearhop, S., 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. Methods Ecol. Evol. 9, 946–955.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. R J. 9, 378–400.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: Model Selection and Multimodel Inference. Springer, Cham.

Chapman, D.S., Bonn, A., Kunin, W.E., Cornell, S.J., 2010. Random Forest characterization of upland vegetation and management burning from aerial imagery. J. Biogeogr. 37, 37–46.

Costa, D.P., Robinson, P.W., Arnould, J.P., Harrison, A.L., Simmons, S.E., Hassrick, J.L., Hoskins, A.J., Kirkman, S.P., Oosthuizen, H., Villegas-Amtmann, S., Crocker, D.E., 2010. Accuracy of ARGOS locations of pinnipeds at-sea estimated using fastloc GPS. PloS one 5, e8677.

Cummings, C.R., Lea, M.A., Lyle, J.M., 2019. Fur seals and fisheries in Tasmania: an integrated case study of human-wildlife conflict and coexistence. Biol. Conserv. 236, 532–542.

De Knegt, H.J., Eikelboom, J.A., van Langevelde, F., Spruyt, W.F., Prins, H.H., 2021. Timely poacher detection and localization using sentinel animal movement. Sci. Rep. 11, 1–11.

DEFRA, 2016. Joint Action Plan to Increase the English Hen Harrier Population.Uplands Stakeholder Forum, Hen Harrier Sub-group.

Douglas, D.J., Buchanan, G.M., Thompson, P., Amar, A., Fielding, D.A., Redpath, S.M., Wilson, J.D., 2015. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. Biol. Conserv. 191, 243–250.

Etheridge, B., Summers, R.W., 2006. Movements of british hen harriers Circus cyaneus outside the breeding season. Ringing Migr. 23, 6–14.

Etheridge, B., Summers, R.W., Green, R.E., 1997. The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier Circus cyaneus in Scotland. J. Appl. Ecol. 34, 1081–1105.

Fieberg, J., DelGiudice, G.D., 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology 90, 1687–1697.

Fielding, A.H., Morgan, D., Haworth, P.F., Whitfield, D.P., Thompson, D.B.A., 2003. The impact of Golden Eagles on other raptors. In: D.B.A. Thompson S. Redpath A.H. Fielding M. Marquiss C. Galbraith (eds) Birds of Prey in a Changing Environment (pp. 221-244). The Stationary Office, Edinburgh.

Fielding, A., Haworth, P., Whitfield, D.P., McLeod, D., Riley, H., 2011. A conservation framework for Hen Harriers in the UK. In: JNCC Report.

Gordon, C., 2020. Influence of Environmental Factors on the Performance of Argos Satellite Telemetry in Scotland. University of Stirling. Unpublished BSc thesis.

Gurarie, E., Thompson, P.R., Kelly, A.P., Larter, N.C., Fagan, W.F., Joly, K., 2020. For everything there is a season: analysing periodic mortality patterns with the cyclomort R package. Methods Ecol. Evol. 11, 129–138.

Gusset, M., Swarner, M.J., Mponwane, L., Keletile, K., McNutt, J.W., 2009. Human–wildlife conflict in northern Botswana: livestock predation by endangered african wild dog Lycaon pictus and other carnivores. Oryx 43, 67–72.

Hardey, J., Crick, H.Q.P., Wernham, C.V., Riley, H.T., Etheridge, B., Thompson, D.B.A., 2009. Raptors: A Field Guide to Survey and Monitoring. The Stationary Office, Edinburgh.

Klaassen, R.H., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.M., Bairlein, F., Alerstam, T., 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J. Anim. Ecol. 83, 176–184.

Knight Frank, 2014. The Rural Report, Summer 2014. Knight Frank LLP, London.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B Biol. Sci. 279, 910–915.

Lunn, M., McNeil, D., 1995. Applying cox regression to competing risks. Biometrics 51, 524–532.

McMillan, R.L., 2011. Raptor persecution on a large Perthshire estate: a historical study. Scottish Birds 31, 195–205.

Melling, T., Thomas, M., Price, M., Roos, S., 2018. Raptor persecution in the Peak District National Park. British Birds 111, 275–290.

McFadzen, M.E., Marzluff, J.M., 1996. Mortality of prairie falcons during the fledging-dependence period. Condor 98, 791–800.

Murgatroyd, M., Redpath, S.M., Murphy, S.G., Douglas, D.J., Saunders, R., Amar, A., 2019. Patterns of satellite tagged Hen Harrier disappearances suggest widespread illegal killing on British grouse moors. Nat. Commun. 10, 1–8.

Murray, D.L., Bastille-Rousseau, G., 2020. Estimating survival and cause-specific mortality from continuous time observations. In: Murray, D.L., Sandercock, B.K. (Eds.), Population Ecology in Practice. Wiley Blackwell, Oxford, pp. 123–156.

Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J., Boyd, D., Jiminez, M., Niemeyer, C., Meier, T.J., Stahler, D., 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biol. Conserv. 143, 2514–2524.

Mustin, K., Arroyo, B., Beja, P., Newey, S., Irivine, R.J., Kestler, J., Redpath, S.M., 2018. Consequences of game bird management for non-game species in Europe. J. Appl. Ecol. 55, 2285–2295.

Newton, I., McGrady, M.J., Oli, M.K., 2016. A review of survival estimates for raptors and owls. Ibis 158, 227–248.

Newton, I., 1979. Population Ecology of Raptors. T &AD Poyser, Berkhamsted.

Newton, I., 2021. Killing of raptors on grouse moors: evidence and effects. Ibis 163, 1–19.

Northeast Scotland Raptor Study Group, 2015. Peregrines in Northeast Scotland in 2014 – further decline in the uplands. Scottish Birds 35, 202–206.

Picozzi, N., 1981. Weight, wing length and iris colour of hen harriers in Orkney. Bird Study 28, 159–161.

Picozzi, N., 1984. Sex ratio, survival and territorial behaviour of polygynous hen harriers Circus c. Cyaneus in Orkney. Ibis 126, 356–365.

R Core Team, 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Redpath, S., Amar, A., Madders, M., Leckie, F., Thirgood, S., 2002. Hen harrier foraging success in relation to land use in Scotland. Anim. Conserv. 5, 113–118.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D., Watt, A., Gutierrez, R.J., 2013. Understanding and managing conservation conflicts. Trends Ecol. Evol. 28, 100–109.

Rothery, P., 1985. Estimation of age-specific survival of hen harriers (Circus c. cyaneus) in Orkney. In: Statistics in Ornithology. Springer, New York, pp. 341–354.

RSPB, 2017. Carroll – a Northmberland bird to the very end [Blog]. Available at: https://community.rspb.org.uk/ourwork/skydancer/b/skydancer/posts/carroll-a-northumberland-bird-to-the-very-end.

RSPB, 2019. Man seen with gun at Hen Harrier roost site [Blog]. Available at. https://community.rspb.org.uk/ourwork/b/investigations/posts/man-seen-with-gun-at-hen-harrier-roost-site.

RSPB, 2021. Birdcrime 2020. Royal Society for the Protection of Birds, Sandy, UK.

Scharf, W.C., Balfour, E., 1971. Growth and development of nestling hen harriers. Ibis 113, 323–329.

Scottish Government, 2023. Wildlife management and Muirburn (Scotland) Bill. Available at: https://www.parliament.scot/bills-and-laws/bills/wildlife-management-and-muirburn-scotland-bill.

Sergio, F., Tanferna, A., Blas, J., Blanco, G., Hiraldo, F., 2019a. Reliable methods for identifying animal deaths in GPS-and satellite-tracking data: review, testing, and calibration. J. Appl. Ecol. 56, 562–572.

Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G., Hiraldo, F., 2019b. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. Sci. Rep. 9, 1–8.

Simmons, R., Barnard, P., MacWhirter, B., Hansen, G.L., 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding northern harriers: a 5-year study. Can. J. Zool. 64, 2447–2456.

Singmann, H., 2022. Monet: Interface for Testing Model Terms Via Nested Models. R Package Version 0.1.1.

Smart, J., Amar, A., Sim, I.M., Etheridge, B., Cameron, D., Christie, G., Wilson, J.D., 2010. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern–the red kite Milvus milvus. Biol. Conserv. 143, 1278–1286.

Temeles, E.J., 1986. Reversed sexual size dimorphism: effect on resource defense and foraging behaviors of nonbreeding northern harriers. Auk 103, 70–78.

Therneau, T., 2022. A Package for Survival Analysis in R. R Package Version 3.3-1.

Thirgood, S., Redpath, S., Newton, I., Hudson, P., 2000. Raptors and red grouse: conservation conflicts and management solutions. Conserv. Biol. 14, 95–104.

Thompson, P.S., Douglas, D.J., Hoccom, D.G., Knott, J., Roos, S., Wilson, J.D., 2016. Environmental impacts of high-output driven shooting of red grouse Lagopus lagopus scotica. Ibis 158, 446–452.

Weimerskirch, H., Collet, J., Corbeau, A., Pajot, A., Hoarau, F., Marteau, C., Filippi, D., Patrick, S.C., 2020. Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of nondeclared fishing. Proc. Natl. Acad. Sci. 117, 3006–3014.

Whitfield, D.P., Fielding, A.H., McLeod, D.R., Haworth, P.F., 2008. A conservation framework for golden eagles: implications for their conservation and management in Scotland. In: Scottish Natural Heritage Commissioned Report No 193.Scottish Natural Heritage, Edinburgh.

Whitfield, D.P., Fielding, A.H., 2009. Hen Harrier population studies in Wales. In: Report to Countryside Council of Wales, Contract Science No. 879. CCW, Bangor.

Whitfield, D.P., Fielding, A., 2017. Analyses of the fates of satellite tracked golden eagles in Scotland. In: Scottish Natural Heritage Commissioned Report no 982.Scottish Natural Heritage, Edinburgh.

Whitfield, D.P., Fielding, A.H., McLeod, D.R.A., Haworth, P.F., 2004a. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. Biol. Conserv. 118, 249–259.

Whitfield, D.P., Fielding, A.H., McLeod, D.R.A., Haworth, P.F., 2004b. Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. Biol. Conserv. 119, 319–333.

Whitfield, D.P., Fielding, A.H., Whitehead, S., 2008. Long-term increase in the fecundity of hen harriers in Wales is explained by reduced human interference and warmer weather. Anim. Conserv. 11, 144–152.

Whitfield, D.P., McLeod, D.R., Watson, J., Fielding, A.H., Haworth, P.F., 2003. The association of grouse moor in Scotland with the illegal use of poisons to control predators. Biol. Conserv. 114, 157–163.

White, E.M., Perlut, N.G., Travis, S.E., Strong, A.M., 2021. Diverse demographic factors influence apparent juvenile survival in a migratory songbird. Ecosphere 12, e03761.

Wipple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. The impact of human-wildlife conflict on natural systems. In: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), People and Wildlife, Conflict or Co-existence? Cambridge University Press, Cambridge.

Wotton, S.R., Bladwell, S., Mattingley, W., Morris, N.G., Raw, D., Ruddock, M., Stevenson, A., Eaton, M.A., 2018. Status of the hen harrier Circus cyaneus in the UK and Isle of Man in 2016. Bird Study 65, 145–160.