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Source: Wildlife Biology, 2017(SP1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00246>

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Long-term trends in abundance and breeding success of red grouse and hen harriers in relation to changing management of a Scottish grouse moor

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Large areas of heather moorland in the British uplands are managed for shooting red grouse *Lagopus lagopus scotica*. However, there has been a long-standing conflict between grouse moor management and the conservation of raptors, particularly the hen harrier *Circus cyaneus*. Langholm Moor, a grouse moor in southwest Scotland, has hosted studies aiming to resolve this conflict for 24 years. Between 1992 and 1997, whilst managed as a grouse moor, hen harrier numbers increased from two to 20 breeding females, and raptor predation removed large proportions of both adult grouse and chicks. As driven shooting was no longer viable, grouse moor management ceased in 1999, and was not restored until 2008. This paper considers how cessation and subsequent restoration of grouse moor management, which involved heather management and legal control of generalist predators, affected the abundance and breeding success of red grouse and hen harrier, as well as the abundance of their perceived key predators; red fox *Vulpes vulpes* and carrion crow *Corvus corone*. Grouse moor management had a positive effect on abundance and breeding success of grouse and harriers, which were two- to three-fold higher when fox indices and crow abundance were reduced by 50–70%. Fox indices were negatively correlated with red grouse density and harrier breeding success, whereas crows were negatively correlated with grouse breeding success.

This study confirms that both grouse and harriers can benefit from grouse moor management, if harriers are not persecuted. However, restoration of grouse moor management, in combination with diversionary feeding of harriers, has not yet resulted in a sufficiently increased grouse density to allow driven shooting on Langholm Moor, and thus the management to be considered as economically viable.

Heather *Calluna vulgaris* moorland is an internationally important habitat of high conservation importance, and in Europe its distribution is largely restricted to Britain and Ireland (Thompson et al. 1995, Thirgood et al. 2000a). In the British uplands, large areas of heather moorland are privately owned and managed for red grouse *Lagopus lagopus scotica* shooting, which can provide both economic and ecological benefits (Sotherton et al. 2009). On grouse moors, open heather moorland is maintained by rotational burning and sheep grazing, whilst legal control of generalist predators (e.g. red fox *Vulpes vulpes* and carrion crow *Corvus corone*) can benefit other ground-nesting upland birds, e.g. curlew *Numenius arquata* and golden plover *Pluvialis apricaria* (Tharme et al. 2001, Baines et al. 2008, Fletcher et al. 2010, Douglas et al. 2014).

However, there has been a long-standing, contentious conflict between grouse moor management and the conservation

of raptors in Britain, and patterns of illegal persecution of raptors have been associated with the distribution of grouse moors (Green and Etheridge 1999, Whitfield et al. 2003, 2004, Amar et al. 2012). This conflict has focused particularly on the hen harrier *Circus cyaneus* (Thirgood and Redpath 1999, 2008). Despite legal protection since 1954, the abundance and distribution of harriers is still limited by illegal killing on grouse moors (Etheridge et al. 1997, Green and Etheridge 1999, Sim et al. 2007) due to their ability to limit grouse numbers and reduce shooting bags to an extent whereby shooting becomes unviable (Redpath and Thirgood 1997, 1999, Thirgood et al. 2000b). The abandonment of grouse shooting may not only lead to the cessation of predator control, and the benefit for other birds of conservation concern (Tharme et al. 2001, Fletcher et al. 2010, Douglas et al. 2014), but can also lead to the loss of heather moorland due to intensive sheep grazing or afforestation (Robertson et al. 2001).

Langholm Moor, a grouse moor in southwest Scotland, has hosted studies that aim to resolve raptor–grouse conflicts since 1992. Despite legal protection since 1954, it has been suggested that raptor persecution persisted on Langholm Moor until 1990 (Redpath and Thirgood 1999, Thirgood

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and Redpath 2000). The subsequent increase in harrier abundance on Langholm Moor contributed to increased raptor predation on grouse until shooting became unviable and ceased in 1996 (Redpath and Thirgood 1997). As raptor predation prevented the recovery of grouse densities (Thirgood et al. 2000b), active grouse moor management was abandoned in 1999. Grouse moor management was resumed in 2008 to test whether sustainable driven grouse shooting could be restored in the presence of a viable harrier population. In this study, we consider how changes in grouse moor management influenced the abundance and breeding success of grouse and harriers in relation to fox indices and carrion crow abundance.

Material and methods

Study area

The Langholm study area (120 km²) included most of the 76 km² Langholm–Newcastleton Hills hen harrier Special Protection Area (SPA, designated in 2001) and Site of Special Scientific Interest (SSSI, designated in 1985 for the upland breeding bird and habitat assemblage). The vegetation is dominated by heather moorland, blanket bog and acidic grasslands. Historically, Langholm was managed for ‘driven’ grouse shooting (see Sotherton et al. 2009 for a detailed description of shooting styles). Grouse bags at Langholm have followed quasi-cyclical fluctuations in numbers, which have been linked to both intrinsic and extrinsic mechanisms (reviewed by Martínez-Padilla et al. 2013), with on average 1815 (\pm 176 SE) birds shot per annum between 1950 and 1996, after which shooting ceased (Fig. 1). Before the Second World War grouse bags fluctuated on an even higher level, and the available bag records for one part of the moor showed a significant long-term decline of 1.7% per annum between 1913 and 1990 (Redpath and Thirgood 1997). Between 1950 and 1990, grouse bags for the whole moor showed a similar, but non-significant, decline of approximately 1.3% per annum (Redpath and Thirgood 1997). The loss of nearly half of the heather-dominated moorland to grass following overgrazing by sheep during the same period may have contributed to this long-term decline, whereas grouse bags between 1991 and 1996 were reduced by increasing raptor predation (Redpath and Thirgood 1997).

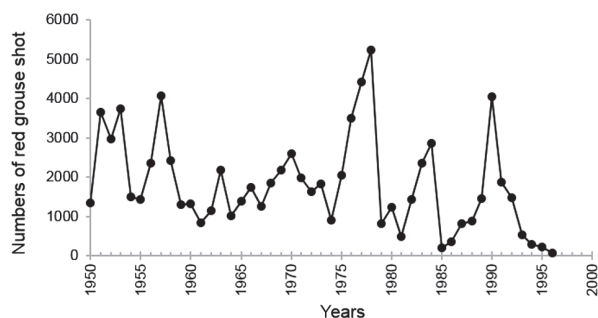


Figure 1. Grouse bags at Langholm Moor 1950–2000. No grouse were shot after 1996.

During the study period (1992–2015), the moor was subject to the cessation and subsequent restoration of grouse moor management. Up to 1999 and then from 2008–2015 the moor was managed by a team of five gamekeepers, who burned the heather to generate fresh heather growth for the benefit of grouse, and legally controlled generalist predators such as red fox, corvids (excluding raven *Corvus corvix* and chough *Pyrrhocorax pyrrhocorax*), stoat *Mustela erminea* and weasel *Mustela nivalis*, on the whole study area. In an attempt to reduce predation of grouse chicks by harriers, half of the harrier nests were supplied with diversionary food in 1998–1999 (Redpath et al. 2001), which was extended to all nests from 2008 onwards. In addition to heather burning, sheep grazing was reduced on 6600 ha from 2011 onwards, and heather was reseeded on a further 300 ha in 2009 and 2010. Between 2008 and 2013/14, the gamekeepers used medicated grit to help control the parasitic nematode *Trichostrongylus tenuis* in grouse and thus to prevent quasi-cyclical grouse population crashes (Hudson et al. 1998, Newborn and Foster 2002). In the intermediate years, 2000–2007, the moor was not managed for grouse shooting. Sheep grazing was the primary land-use and generalist predators were no longer routinely controlled, although some limited heather burning and legal predator control took place (Baines et al. 2008).

Monitoring

Red grouse were counted twice a year on ten 0.5 km² count areas, in March/early April to estimate pre-breeding densities (birds km⁻²) and in July/early August to estimate post-breeding densities (birds km⁻²) and breeding success (mean young per adult). Within each count area, the observer walked along parallel transects 150 m apart, whilst a pointing dog quartered the ground on either side of the transect. Spring counts were not conducted in 2001 due to foot and mouth disease in livestock, which prevented access to the moor.

Hen harrier nests were located in April–June by observing displaying birds, nest-building, prey transports and food-passes (Hardey et al. 2013). All nests were visited at least three times: during incubation to record clutch size, within a week after hatching to record the number of chicks hatched, and shortly before fledging to record the number of chicks reared. As hen harriers can be polygamous, i.e. one male can have more than one female, breeding success was calculated as young fledged per breeding female. We also determined the proportion of successful breeding attempts, i.e. those which fledged at least one chick.

Carrion crow abundance was estimated annually within 15 1 km² squares distributed across the study area. Within each square the observer walked two parallel 1 km transects, each 250 m from the side of the square and thus separated by 500 m, recording all birds seen or heard (Thirgood et al. 1995). Counts were conducted between mid-May and mid-June. From 2003 onwards, a second (early) visit between mid-April and mid-May was included to ensure compatibility with the Breeding Bird Survey (BBS) guidelines (Harris et al. 2015). However, as the annual crow indices between the two visits were highly correlated ($r_s = 0.798$, $p < 0.001$, $n = 13$), the abundance indices were calculated as the

number of crows encountered per km during the late visit throughout the whole study period.

From 2003 onwards, an index of red fox activity was estimated annually from surveys of scats along transects (2003–2007: three transects, 2008–2010: five transects, 2011–2015: six transects). Each transect was approximately 10 km long and surveyed four times, with a clear-up round in March and three repeat surveys in monthly intervals. From 2013 onwards, only one repeat survey was conducted in May. To adjust for variation in transect length and interval between consecutive surveys, the number of scats found during the repeat surveys, excluding those found on the clear-up round, was divided by total transect length and the exposure period in days (i.e. the time interval between the end of the clear-up round and the final visit). As there was a strong positive correlation between the scat indices from the three original transects only and from all six transects ($r_s = 0.989$, $p < 0.001$, $n = 13$), we used data from all six transects in years when they were available. The indices were presented as the average number of scats/km/10 days.

The average number of foxes and crows killed each year in the study area by gamekeepers was recorded. Although some casual predator control was carried out during the unmanaged period, there were no records available.

Statistical analysis

We defined ‘period’ as a factor with three levels (1 = 1992–1999, managed; 2 = 2000–2007, unmanaged; 3 = 2008–2015, managed). For each period, we calculated the average abundance of hen harrier, red grouse and carrion crow, and fox for the last two periods. As red grouse spring counts in 2008 were conducted before predator control resumed, that count was assigned to the unmanaged period (‘period’: 2 = 2000–2008, 3 = 2009–2015). Changes in species abundance in relation to presence or absence of grouse moor management were tested using either general or generalised linear models (GLM) with abundance indices as dependent variables and ‘period’ as factor. Grouse density was analysed using a normal distribution with an identity link function, and for harriers and crows we used Poisson distribution with a log link function. To analyse fox indices, we used the number of scats found during the repeat surveys, offset by $\ln(\text{transect length} \times \text{exposure time})$, using a Poisson distribution with a log link function.

For each period, we estimated annual changes in grouse and harrier abundance by linear regression. Variation in breeding success of grouse and harriers was analysed using

linear regression with $\ln(\text{young/adult grouse})$ or $\ln(\text{young/female harrier})$ as the dependent variables using a normal distribution and an identity link function and ‘period’ as a factor. To test for correlation between grouse and harrier productivity we calculated Pearson’s correlation coefficient. To compare the proportion of successful harrier breeding attempts between managed and unmanaged periods we used logistic regression with ‘success’ as the dependent variable, using a binomial distribution and a logit link function, and ‘period’ as factor.

To estimate the impact of foxes and crows on abundance and productivity of grouse and harriers we used GLMs with fox and crow indices each in turn as co-variables. Grouse densities and breeding success of grouse and harrier were analysed using a normal distribution, and harrier abundance using a Poisson distribution with a log link. When assessing the impact of crows, we also included ‘period’ as a factor and interactions between ‘period’ and crow index, however, this was not possible for foxes as the sample size during the unmanaged period was too low to obtain meaningful results. The correlation between fox and crow indices was analysed using Spearman’s correlation coefficient as these variables were not normally distributed. Statistical analyses were conducted in GenStat 17.1 (VSN International 2014), and models were adjusted for over-dispersion when necessary.

Results

Predator abundance

When the moor was managed for red grouse and generalist predators were routinely controlled, gamekeepers removed on average 187 ± 20 foxes and 308 ± 18 carrion crows per annum between 1992 and 1999, and 189 ± 22 foxes and 260 ± 22 carrion crows per annum between 2008 and 2015, i.e. 1.6 ± 0.2 foxes km^{-2} and 2.2 ± 0.2 crows km^{-2} (2008–2015). Accordingly, crow abundance and the fox index were three times higher during the unmanaged period than in managed periods (Table 1), although crows showed a high level of annual fluctuation throughout the study period (Fig. 2). The high fox index in 2008 reflected that predator control was not resumed until March in that year, and when excluding 2008 from the second managed period the average fox index for 2009–2015 was reduced from 0.11 ± 0.05 to 0.06 ± 0.02 . Fox and crow indices were not correlated ($r_s = 0.345$, $p = 0.255$, $n = 13$).

Table 1. Mean grouse, harrier and predator indices (\pm SE) during periods when the moor was managed for grouse and when it was unmanaged. n = numbers of years in each period. Calculation of abundance indices varied between species: ¹ count data (grouse km^{-2}), ² breeding female harriers, ³ crows km^{-1} , ⁴ scat index (scats/km/10 days). Note that grouse spring density in 2008 was assigned to the unmanaged period.

Species	1992–1999 (n) Managed	2000–2007 (n) Unmanaged	2008–2015 (n) Managed	
Grouse spring ¹	(7) 28.40 ± 2.88	(8) 11.65 ± 1.03	(7) 25.60 ± 2.55	$F_{2,19} = 17.11$, $p < 0.001$
Grouse July ¹	(8) 58.65 ± 7.20	(8) 14.22 ± 1.92	(8) 48.60 ± 6.99	$F_{2,21} = 15.60$, $p < 0.001$
Hen harrier ²	(8) 11.25 ± 2.14	(8) 4.38 ± 0.94	(8) 3.88 ± 1.41	$F_{2,21} = 6.79$, $p = 0.005$
Carrion crow ³	(8) 0.09 ± 0.04	(8) 0.31 ± 0.07	(8) 0.15 ± 0.08	$F_{2,21} = 3.36$, $p = 0.054$
Red fox ⁴	N/A	(5) 0.31 ± 0.01	(8) 0.11 ± 0.05	$F_{1,11} = 14.73$, $p = 0.003$

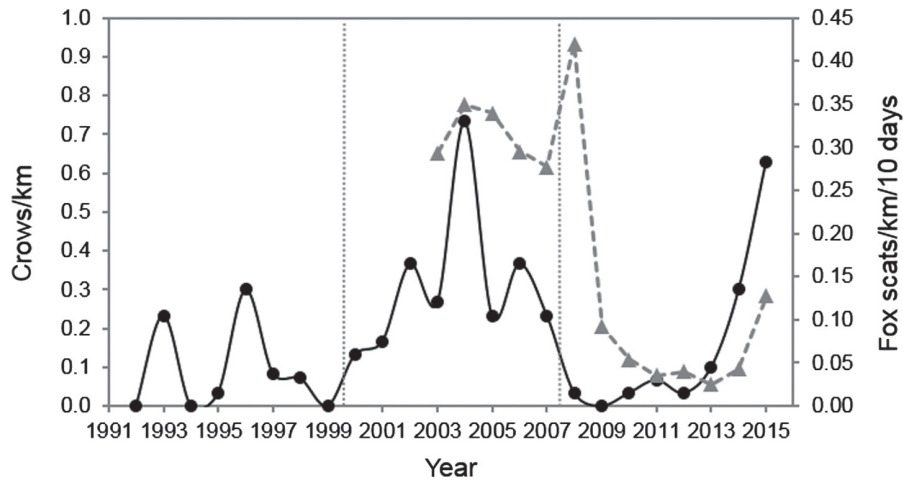


Figure 2. Annual variation in abundance of carrion crows (black solid line, left axis) and fox scat index (grey dashed line, right axis). The dotted vertical lines separate the three periods (managed – unmanaged – managed).

Grouse and harrier abundance

When the moor was not managed and abundance of crows and the fox index were both higher, grouse densities in spring and July were 60% and 76% lower, respectively, and the number of female harriers 61% lower than when the moor was managed (Table 1). After management was resumed in 2008, red grouse densities increased two- and three-fold, however, the average number of breeding hen harrier females remained low (Table 1).

Between 1992 and 1999 the number of breeding female harriers increased by $10 \pm 3\%$ per annum ($F_{1,6} = 12.36$, $p = 0.013$), peaking at 20 females in 1997 (Fig. 3a). Over the same period, grouse densities declined by $8 \pm 2\%$ per annum in spring ($F_{1,5} = 12.39$, $p = 0.017$, Fig. 3b) and by $9 \pm 1\%$ per annum in July ($F_{1,6} = 242.43$, $p < 0.001$). During the unmanaged period, the number of female harriers declined sharply from 2001 to 2002, then remained fairly stable for the remaining six years ($-8 \pm 4\%$ per annum, $F_{1,6} = 5.40$, $p = 0.059$), whereas grouse densities in spring and July remained low, but stable (spring: $-0.7 \pm 3\%$ per annum, $F_{1,5} = 0.05$, $p = 0.838$; July: $4 \pm 4\%$ per annum, $F_{1,6} = 0.84$, $p = 0.396$). When grouse moor management resumed in 2008, the number of female harriers remained low at one to three until 2014, when they increased to 12 (Fig. 3a). Grouse density in spring increased until 2014, then fell sharply in 2015, resulting in an overall population increase of $8 \pm 1\%$ per annum between 2008 and 2015 ($F_{1,6} = 39.17$, $p < 0.001$). Post-breeding density followed the same pattern but on a lower level (2008–2015: $6 \pm 3\%$, $F_{1,6} = 2.91$, $p = 0.139$).

Grouse and harrier breeding success

Grouse and harrier breeding success (Fig. 4) was two- to three-fold higher when the moor was managed (Table 2), irrespective of which management period (grouse: $t = -0.79$, $p = 0.439$; harrier: $t = 1.96$, $p = 0.064$). When managed, 80% and 78% of harrier breeding attempts fledged chicks, compared to only 39% when unmanaged (Table 2).

Associations between generalist predators and red grouse and hen harrier performance

Grouse densities in both spring and July were negatively associated with the fox index (Table 3, Fig. 5). However, grouse breeding success was negatively associated with crow abundance, rather than the fox index (Table 3). Fox index and crow abundance were unrelated to numbers of female

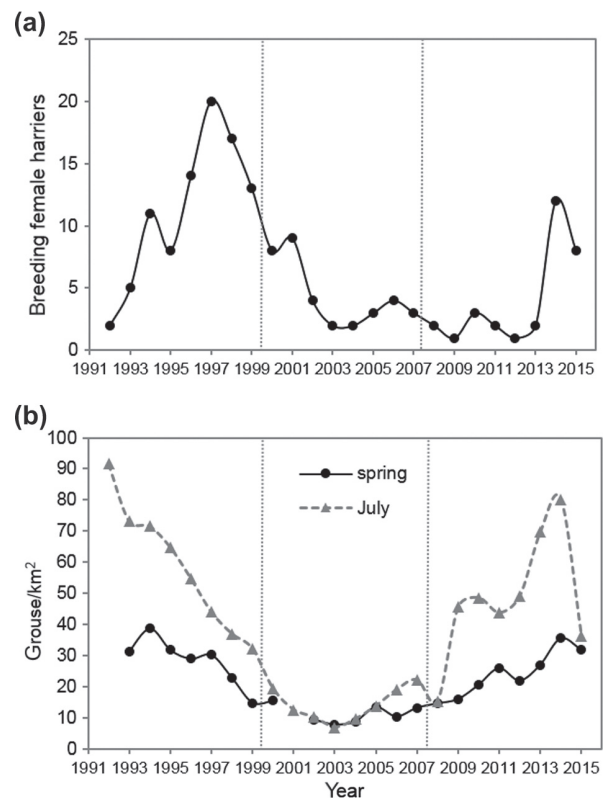


Figure 3. Annual variation in (a) the number of female hen harriers and (b) red grouse densities in spring (black solid line) and July (grey dashed line). The dotted vertical lines separate the three periods (managed – unmanaged – managed).

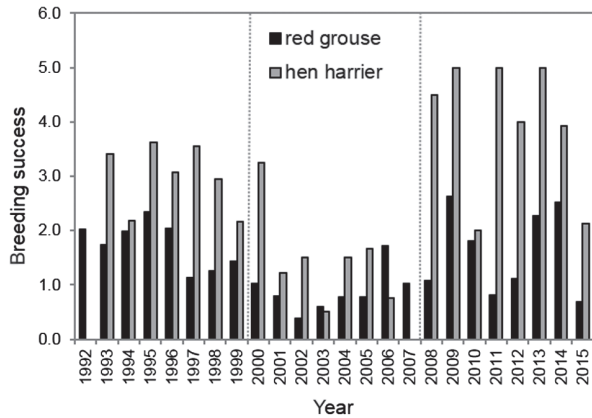


Figure 4. Annual variation in breeding success of red grouse (young/adult) and hen harrier (young/female). The dotted vertical lines separate the three periods (managed – unmanaged – managed).

harriers, but harrier breeding success tended to be lower in years with higher fox indices (Table 3). There were no significant ‘period × crow’ interactions for any variable.

Discussion

This study considers a 24-year time-series of grouse and harrier abundance and breeding success in relation to changes in grouse moor management, i.e. principally the control of generalist predators. Grouse moor management was associated with higher grouse densities and breeding success and with lower fox indices and crow abundance, as has been experimentally shown by Fletcher et al. (2010). Foxes, who predate not only eggs and chicks, but also adult grouse (Watson and Moss 2008), were negatively linked to grouse densities, whereas crows, which are mainly predators of eggs and young chicks (Watson and Moss 2008), were negatively associated with grouse breeding success, which is likely to contribute to lower post-breeding densities. This study was not experimental and simultaneous to changes in predator control there were changes in heather management, particularly burning, but also levels of sheep grazing. Furthermore, in 1998–1999 and from 2008 onwards breeding harriers were provided with diversionary food. Hence, given the design of this study it is not possible to disentangle the relative contribution of individual managements to the patterns described. It is likely that factors other than the control of foxes and crows will further explain changes in grouse breeding success and hence densities. These may include other predators such as stoat (Park et al. 2002) or raptors (Redpath and Thirgood 1999, Thirgood et al. 2000b), arthropods (Erikstad 1985, Park et al. 2001),

weather (Erikstad et al. 1982, Erikstad 1985) and parasites (Newborn and Foster 2002). The low productivity and steep reduction in the post-breeding density of grouse in 2015 coincided not only with increased fox and crow indices, but also with a cold and wet spring and the discontinuation of parasite worm control in grouse.

Baines and Richardson (2013) found that cessation of grouse moor management at Langholm was associated with lower abundance and breeding success of hen harriers. Our subsequent data show that once grouse moor management was restored, harrier breeding success was restored, with on average 3.9 young fledged per female, a rate more than double the 1.8 young recorded throughout Scotland over the same period (Challis et al. 2015). Harrier breeding success at Langholm was negatively associated with fox indices, and since grouse moor management was re-established in 2008, no harrier nests have failed due to fox predation, whereas during the unmanaged period 33% of the failed breeding attempts ($n = 24$) showed signs of fox predation (Baines and Richardson 2013). Predation by foxes was also the main cause for harrier nest failure on the Isle of Skye (McMillan 2014). However, Green and Etheridge (1999) did not find any beneficial effect of fox control on harrier breeding success, probably because fox control in many places coincided with human interference (i.e. killing and nest destruction) with hen harriers during the breeding season.

Provision of diversionary food might have also contributed to high breeding success at Langholm (González et al. 2006, Byholm and Kekkonen 2008, Rooney et al. 2015), and was associated with harriers fledging on average one chick more than during the earlier managed period, when broods were largely unfed. However, this tendency contrasts with the experiment by Redpath et al. (2001), who found no benefit of feeding to breeding success. Despite high breeding success, numbers of female harriers only started to recover six years after grouse moor management was resumed in 2008. As hen harriers show only low rates of philopatry (Watson 1977, Picozzi 1978, Etheridge et al. 1997), changes in their breeding abundance are perhaps unlikely to be determined by local breeding success, but more by external recruitment, which is influenced by the abundance of voles *Microtus agrestis* and meadow pipits *Anthus pratensis*, their preferred prey (Redpath and Thirgood 1999, New et al. 2011). Thus, the delay in population recovery at Langholm may have been associated with large-scale variation in the abundance of these prey species, or with high persecution rates elsewhere (Etheridge et al. 1997, Green and Etheridge 1999), which reduces potential recruits. Nevertheless, the increase in the number of breeding females at Langholm in 2014 is in contrast to lack of change in home ranges occupied between 2008 and 2014 for Scotland as a whole ($1 \pm 2\%$, $F_{1,5} = 0.46$, $p = 0.529$) (data in Challis et al.

Table 2. Average breeding success (\pm SE) for red grouse (young/adult in July) and hen harrier (fledged young/female, % successful breeding attempts) in managed and unmanaged periods.

Species	1992–1999	2000–2007	2008–2015	
	Managed (n = 8)	Unmanaged (n = 8)	Managed (n = 8)	
Red grouse	1.74 \pm 0.15	0.88 \pm 0.14	1.61 \pm 0.28	$F_{2,21} = 6.55$, $p = 0.006$
Hen harrier (young/female)	2.50 \pm 0.41	1.21 \pm 0.28	3.94 \pm 0.44	$F_{2,21} = 8.71$, $p = 0.002$
Hen harrier (% successful)	80% (n = 93)	39% (n = 32)	78% (n = 32)	$F_{1,162} = 10.48$, $p < 0.001$

Table 3. Relationships between fox and crow indices and abundance and productivity of red grouse and hen harrier. Values are parameter estimates \pm SE, n = number of years.

	Fox index (n = 13)	Crow index (n = 24)
Red grouse		
Spring density	-46.8 ± 10.7 , $F_{1,11} = 18.99$, $p = 0.001$	-10.1 ± 10.4 , $F_{1,20} = 0.94$, $p = 0.343$
July density	-132.9 ± 22.8 , $F_{1,11} = 33.96$, $p < 0.001$	-49.4 ± 25.2 , $F_{1,22} = 3.84$, $p = 0.063$
Productivity	-1.7 ± 0.9 , $F_{1,11} = 3.44$, $p = 0.091$	-1.2 ± 0.5 , $F_{1,22} = 5.61$, $p = 0.027$
Hen harrier		
Breeding females	-1.6 ± 1.6 , $F_{1,11} = 1.06$, $p = 0.326$	-0.4 ± 0.9 , $F_{1,22} = 0.18$, $p = 0.674$
Productivity	-2.2 ± 1.0 , $F_{1,11} = 4.59$, $p = 0.055$	-0.7 ± 0.5 , $F_{1,22} = 1.71$, $p = 0.205$

2015). Our results support the hypothesis of Baines and Richardson (2013) that legal control of generalist predators on grouse moors can benefit breeding hen harriers, if they are left undisturbed, although on a larger scale this positive effect might still be out-weighted by the negative effects of persecution (Green and Etheridge 1999).

Predation of grouse by hen harriers can limit grouse populations (Thirgood and Redpath 2000), hence mitigation methods are needed to resolve the existing conflict (Thirgood et al. 2000b). Provision of diversionary food has been used at Langholm alongside predator control and habitat restoration since 2008. Despite this, the observed recovery rate of grouse has been low, especially when compared with rates at other studies, but where raptor indices were lower than at Langholm (Fletcher et al. 2010). Apart from hen harriers, Langholm Moor is used by a whole suite of other raptors, including the “avian specialists” peregrine *Falco peregrinus* and goshawk *Accipiter nisus*, which have a high proportion of gamebirds in their diet (Valkama et al. 2005). In addition, Langholm Moor has a population of 12–15 common buzzard *Buteo buteo* pairs, which also have gamebirds as part of their diet, albeit to a lower extent than hen harriers, peregrines and goshawks (Valkama et al. 2005, Park et al. 2008). 69% of grouse carcasses found on Langholm Moor from 2008 onwards showed signs of raptor predation, but as it is difficult to separate signs of the different species (Thirgood et al. 1998) the relative importance of individual raptor species as well as the proportion of depredated and scavenged red grouse is unknown.

Between 2008 and 2015, approximately £225 000 (ca €290 000) per year were invested into moorland management at Langholm, although this figure does not include additional costs for fencing, new tracks or heather reseeded. However, the current degree of predator control and habitat

restoration, in combination with diversionary feeding of hen harriers, has to-date not resulted in a sufficiently high grouse density to recommence driven shooting (Elston et al. 2014) and thus the management to become economically viable. Therefore, an adequate solution to resolve the existing conservation conflict still remains to be found, and on-going analyses will consider which factors were most important in preventing full grouse recovery.

Managing conservation conflicts is often hindered by disagreement over objectives, and needs to integrate not only conservation but also social and economic aspects (Redpath et al. 2013). Some stakeholders are in favour of less intensive grouse management (Thompson et al. 2009). However, this may render commercial shooting at the current levels observed in Britain uneconomic as well as have impacts on some bird species positively associated with grouse moors (Tharme et al. 2001, Baines et al. 2008, Fletcher et al. 2010) and local economies (Sotherton et al. 2009). Other stakeholders favour a more interventional management of protected raptors, which may not only increase densities of gamebirds but may also benefit other bird species. However, any solution to resolve the conflict between raptor conservation and shooting interests is likely to include some compromise.

Acknowledgements – We thank Buccleuch Estates for access and support throughout the study period, and Steve Redpath for supporting our use of the data collected between 1992 and 1999. We are also grateful to the members of the local branches of the Scottish Raptor Study Group and the many field assistants, volunteers and students who were involved with this long-term study. Olav Hjeljord provided helpful comments to improve this manuscript.

Funding – This study was conducted as part of the Langholm Moor Demonstration Project (2008–2015), funded by the Game & Wildlife Conservation Trust, Scottish Natural Heritage (SNH), Buccleuch Estates, Royal Society for the Protection of Birds (RSPB) and Natural England. The first phase of fieldwork (1992–1999) was funded by The Game Conservancy Trust (GCT), The Game Conservancy Scottish Research Trust, Centre for Hydrology and Ecology, SNH, RSPB and the Joint Nature Conservation Committee. Monitoring from 2000–2007 was funded by GCT and SNH.

References

Amar, A. et al. 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.

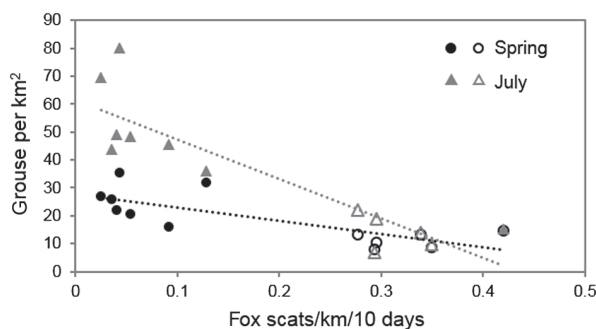


Figure 5. Relationship between red grouse densities and fox scat index. Filled symbols indicate the managed period, open symbols the unmanaged period.

- Baines, D. and Richardson, M. 2013. Hen harriers on a Scottish grouse moor: multiple factors predict breeding density and productivity. – *J. Appl. Ecol.* 50: 1397–1405.
- Baines, D. et al. 2008. The direct and indirect effects of predation by hen harriers *Circus cyaneus* on trends in breeding birds on a Scottish grouse moor. – *Ibis* 150: 27–36.
- Byholm, P. and Kekkonen, M. 2008. Food regulates reproduction differently in different habitats: experimental evidence in the goshawk. – *Ecology* 89: 1696–1702.
- Challis, A. et al. 2015. Scottish raptor monitoring scheme. Report 2014. – BTO Scotland.
- Douglas, D. J. T. et al. 2014. Upland land use predicts population decline in a globally near-threatened wader. – *J. Appl. Ecol.* 51: 194–203.
- Elston, D. A. et al. 2014. Working with stakeholders to reduce conflict – modelling the impact of varying hen harrier *Circus cyaneus* densities on red grouse *Lagopus lagopus* populations. – *J. Appl. Ecol.* 51: 1236–1245.
- Erikstad, K. E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. – *Ornis Scand.* 16: 181–190.
- Erikstad, K. E. et al. 1982. The influence of weather on food intake, insect prey selection and feeding behaviour in willow grouse chicks in northern Norway. – *Ornis Scand.* 13: 176–182.
- Etheridge, B. et al. 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.
- Fletcher, K. et al. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. – *J. Appl. Ecol.* 47: 263–272.
- González, L. M. et al. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). – *Biol. Conserv.* 129: 477–486.
- Green, R. E. and Etheridge, B. 1999. Breeding success of the hen harrier *Circus cyaneus* in relation to the distribution of grouse moors and the red fox *Vulpes vulpes*. – *J. Appl. Ecol.* 36: 472–483.
- Hardey, J. et al. 2013. Raptors. A field guide for surveys and monitoring, 3rd edn. – The Stationery Office.
- Harris, S. J. et al. 2015. The Breeding Bird Survey 2014. BTO Research Report 673. – British Trust for Ornithology, Thetford.
- Hudson, P. J. et al. 1998. Prevention of population cycles by parasite removal. – *Science* 282: 2256–2258.
- Martínez-Padilla, J. et al. 2013. Insights into population ecology from long-term studies of red grouse *Lagopus lagopus scoticus*. – *J. Anim. Ecol.* 83: 85–98.
- McMillan, R. L. 2014. Hen harriers on Skye, 2000–12: nest failures and predation. – *Scottish Birds* 34: 30–39.
- New, L. F. et al. 2011. Hen harrier management: insights from demographic models fitted to population data. – *J. Appl. Ecol.* 48: 1187–1194.
- Newborn, D. and Foster, R. 2002. Control of parasite burdens in wild red grouse *Lagopus lagopus scoticus* through the indirect application of anthelmintics. – *J. Appl. Ecol.* 39: 909–914.
- Park, K. J. et al. 2001. The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. – *J. Zool.* 254: 137–145.
- Park, K. J. et al. 2002. Breeding losses of red grouse in Glen Esk (NE Scotland): comparative studies, 30 years on. – *Ann. Zool. Fenn.* 39: 21–28.
- Park, K. J. et al. 2008. Impacts of birds of prey on gamebirds in the UK: a review. – *Ibis* 150: 9–26.
- Picozzi, N. 1978. Dispersion, breeding and prey of hen harriers *Circus cyaneus* in Glen Dye, Kincardineshire. – *Ibis* 120: 498–509.
- Redpath, S. M. and Thirgood, S. J. 1997. Birds of prey and red grouse. – Stationery Office.
- Redpath, S. M. and Thirgood, S. J. 1999. Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. – *J. Anim. Ecol.* 68: 879–892.
- Redpath, S. M. et al. 2001. Does supplementary feeding reduce predation of red grouse? – *J. Appl. Ecol.* 38: 1157–1168.
- Redpath, S. M. et al. 2013. Understanding and managing conservation conflicts. – *Trends Ecol. Evol.* 28: 100–109.
- Robertson, P. A. et al. 2001. Loss of heather *Calluna vulgaris* moorland in the Scottish uplands: the role of red grouse *Lagopus lagopus scoticus* management. – *Wildl. Biol.* 7: 37–42.
- Rooney, E. et al. 2015. Supplementary feeding increases common buzzard *Buteo buteo* productivity but only in poor-quality habitat. – *Ibis* 157: 181–185.
- Sim, I. M. W. et al. 2007. Status of the hen harrier *Circus cyaneus* in the UK and Isle of Man in 2004, and a comparison with the 1988/89 and 1998 surveys. – *Bird Study* 54: 256–267.
- Sotherton, N. et al. 2009. Hen harriers and red grouse: economic aspects of red grouse shooting and the implications for moorland conservation. – *J. Appl. Ecol.* 46: 955–960.
- Tharme, A. P. et al. 2001. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. – *J. Anim. Ecol.* 38: 439–457.
- Thirgood, S. J. and Redpath, S. M. 1999. Raptors and grouse: a conflict in the uplands? – In: *Proc. 22 Int. Ornithol. Congr. Bird Life South Africa*, pp. 2125–2129.
- Thirgood, S. J. and Redpath, S. M. 2000. Can raptor predation limit red grouse populations? – In: Chancellor, R. D. and Meyburg, B.-U. (eds), *Raptors at risk*. WWGBP, Hancock House, pp 527–534.
- Thirgood, S. and Redpath, S. 2008. Hen harriers and red grouse: science, politics and human–wildlife conflict. – *J. Appl. Ecol.* 45: 1550–1554.
- Thirgood, S. J. et al. 1995. Diurnal and seasonal variation in line transect counts of moorland passerines. – *Bird Study* 42: 257–259.
- Thirgood, S. J. et al. 1998. Estimating the cause and rate of mortality in red grouse *Lagopus lagopus scoticus*. – *Wildl. Biol.* 4: 65–71.
- Thirgood, S. J. et al. 2000a. Raptors and grouse: conservation conflicts and management solutions. – *Conserv. Biol.* 14: 95–104.
- Thirgood, S. J. et al. 2000b. Raptor predation and population limitation in red grouse. – *J. Anim. Ecol.* 69: 504–516.
- Thompson, D. B. A. et al. 1995. Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. – *Biol. Conserv.* 71: 163–178.
- Thompson, P. A. et al. 2009. Resolving the conflict between driven-grouse shooting and conservation of hen harriers. – *J. Appl. Ecol.* 46: 950–954.
- Valkama, J. et al. 2005. Birds of prey as limiting factors of gamebird populations in Europe: a review. – *Biol. Rev.* 80: 171–203.
- VSN International. 2014. GenStat for Windows, 17th edn. – VSN International, Hemel Hempstead, UK.
- Watson, A. and Moss, R. 2008. Grouse. – Collins.
- Watson, D. 1977. The hen harrier. – T. & A. D. Poyser.
- Whitfield, D. P. et al. 2003. The association of grouse moor in Scotland with the illegal use of poisons to control predators. – *Biol. Conserv.* 114: 157–163.
- Whitfield, D. P. et al. 2004. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. – *Biol. Conserv.* 118: 249–259.