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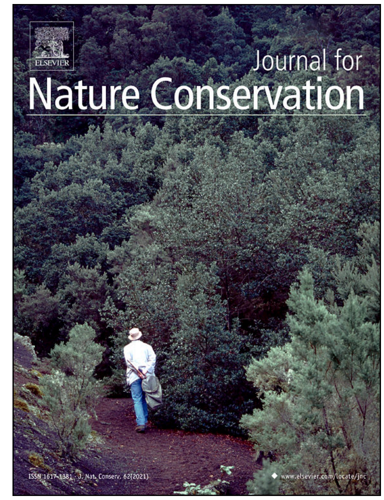

Ten years on from a predator removal experiment in the English uplands: Changes in numbers of ground-nesting birds and predators

David Baines

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Ten years on from a predator removal experiment in the English uplands: changes in numbers of ground-nesting birds and predators

David Baines

Game & Wildlife Conservation Trust, The Coach House, Eggleston, Barnard Castle, Co. Durham. DL12 0AG, UK.

Email: dbaines50@outlook.com

Abstract

There are growing concerns that increasing generalist predators in the UK over the last few decades have contributed to declines in ground-nesting birds. Crow, *Corvis corone* and *C. corvix* combined, and Red Fox *Vulpes vulpes* abundances are either the highest or among the highest in any European country. These high densities are linked with a landscape of intensive agriculture and non-native woodland into which large numbers of non-native gamebirds are annually released, and from which several species of apex predators, which may otherwise limit mesopredators and scavengers, have been extirpated. Ground-nesting birds are particularly susceptible to predation and experimental legal removal of predators in North Northumberland during the 2000s demonstrated a three-fold improvement in breeding success amongst ground-nesting birds, with subsequent increases in their abundance. Ten years after the experiment and cessation of predator control, the experimental plots were resurveyed to measure changes in numbers of four species of waders, three native wild gamebirds, two protected avian predators (Raven *C. corax* and Buzzard *Buteo buteo*) and two non-protected predators, Carrion Crow and Red Fox, whose abundances had been significantly reduced during the experiment. Carrion Crow abundance and a Red Fox index had increased by 78% and 127% respectively since the experiment, whilst Raven and Buzzard showed non-significant increases that paralleled UK trends for those species. Increases in non-protected and protected predators were associated with the local extinctions of Black Grouse *Lyrurus tetrix* and Grey Partridge *Perdix perdix*, together with significantly reduced Red Grouse *Lagopus lagopus scotica* (-71%), Golden Plover *Pluvialis apricaria* (-81%), Snipe *Gallinago gallinago* (-76%), Curlew *Numenius arquata* (-24%), and a non-significant reduction in Lapwing *Vanellus vanellus* (-49%). These bird declines occurred whilst most habitat measures showed no change. They mirror patterns of decline amongst the same species across the UK. Continued lethal control of predators at landscape scales may be essential to help prevent further declines in birds of conservation concern, pending longer-term restructuring of habitat compositions at landscape scales to render them less predator friendly.

Keywords: predator control, Black Grouse, breeding waders, heather, mesopredator, landscape scale

1. Introduction

Widespread bird population declines have occurred across Europe (Inger et al., 2015). Many are attributed to intensified agriculture or afforestation (Bowler et al., 2019; Rigal et al., 2023), but there are growing concerns that increased generalist predators may have contributed to declines (McMahon et al., 2020). Some common generalist predators have increased in the UK over the last few decades. Amongst avian predators recorded by Breeding Bird Surveys (BBS) from 1995, Buzzards *Buteo buteo* have increased by 89%, Ravens *Corvus corax* by 33% and Carrion Crows *Corvus corone* by 17% (Heywood et al., 2023). Similarly, indices of predators killed by gamekeepers as part of the National Gamebag Census (NGC) suggested 180% and 50% increases in Red Fox *Vulpes vulpes* and Stoat *Mustela erminea* respectively in the period 1966-2016, the former mostly in the first 25 years and the latter mostly in the last 25 years, and a 72% increase in Carrion Crows (Aebischer, 2019). Meanwhile, Badger *Meles meles*, an important predator of wader clutches (MacDonald & Bolton, 2008), have probably more than doubled in numbers in England and Wales since the 1980s (Judge et al., 2017).

A review of predation as a limiting factor on bird populations concluded that crow densities (Carrion and Hooded Crows *C. cornix* combined) in the UK were highest of all European countries, whereas those of Red Fox were third highest (Roos et al., 2018). Possible explanations for this include a landscape configuration of intensified agriculture, which may promote greater food availability for corvids (Barnett et al., 2004), and non-native woodlands, which provide predators with refuge and breeding places (Douglas et al., 2014). The annual release of 40-60 million Ring-necked Pheasants *Phasianus colchicus* and Red-legged Partridges *Alectoris rufa* for shooting in the UK (Aebischer, 2019; Madden, 2021) together with the associated provision of grain, live prey, and resultant carrion from roadkills represents a major food source that helps sustain predators and scavengers (Lees et al., 2013; Sanchez-Garcia et al., 2015; Madden & Perkins, 2017, Pringle et al., 2019). Most apex mammalian predators such as Wolf *Canis lupus* or Eurasian Lynx *Lynx lynx* were anthropogenically extirpated from the UK well before 1900 (Wilson, 2004; Manning et al., 2009). Similarly, most raptor species including Golden Eagle *Aquila chrysaetos*, White-tailed Eagle *Haliaetus albicilla* and Goshawk *Accipiter gentilis*, whose presence could help limit numbers of mesopredators and scavengers (Toyne, 1998; Whitfield et al. 2013) were heavily culled, leading to low densities or extinction by 1900. Since then, legislative changes have provided protection that, together with reintroductions, have aided the recovery of several predatory mammals (Sainsbury et al., 2019) and birds (Love & Ball, 1979). Illegal killing of raptors has diminished in most circumstances in the UK, but remains widespread for Hen Harrier *Circus cyaneous*, Peregrine *Falco peregrinus* and Golden Eagle on moors managed for Red Grouse *Lagopus lagopus scotica* shooting (Newton, 2019). Many raptors also underwent severe population declines in 1960s owing to organochlorine pesticides (Ratcliffe, 1970), with recoveries following legislative restrictions on their use.

Roos et al., (2018) summarised that predation can limit ground-nesting waders (Charadriiformes) and gamebirds. Two experimental studies in the UK that lethally removed generalist predators helped underpin this conclusion. The first at Salisbury Plain resulted in increased breeding success and population size of the Grey Partridge *Perdix perdix* (Tapper et al., 1996). The second, showed similar benefits for an assemblage of ground-nesting moorland birds in Northumberland (Fletcher et al., 2010). Here, lethal removal of a community of predators chiefly comprising Red Fox, Carrion Crow, Stoat, and Weasel *Mustela nivalis*, was conducted by two gamekeepers. Abundance of Red Fox was reduced by an estimated 43% and Carrion Crow by 78%. This was associated with a three-fold improvement in breeding success amongst Lapwing *Vanellus vanellus*, Golden Plover *Pluvialis apricaria*, Curlew *Numenius arquata*, Red Grouse, and Meadow Pipit *Anthus pratensis,* with subsequent increases in breeding numbers where predators were controlled and declines where they were not (Fletcher et al., 2010). When the experiment was completed in 2008, predator control ceased. Ten years later, we resurveyed the experimental plots in springs 2018 and 2019. Changes in bird abundance relative to the experimental period were measured for four species of waders, three gamebirds, two protected avian predators, and one avian and one mammalian predator that can still be legally controlled. This paper summarises the findings.

2. Methods

2.1. Study sites

The experiment was based around the village of Otterburn in North Northumberland and conducted between 2000 and 2008, with a follow-up monitoring year in 2009. Generalist predators were controlled by two or more gamekeepers in a crossover experiment involving four plots of similar habitat composition, with plot size varying between 9.3 and 14.4 km^2, spatially separated by 6-7 km. Plots comprised a mosaic of heather-dominated heath and bog, together with unenclosed acid grassland and enclosed fields at altitudes of 220-470 m. The plots were grazed by sheep, with some cattle grazing, the latter especially within the fields (see Fletcher et al., 2010 for details). In 2000, all plots were monitored during a baseline year prior to treatments being allocated within a paired design. One pair of plots (A and B) were situated on the Ministry of Defence's Otterburn Training Area, which comprised 24,000 ha of the southern Cheviot Hills, forming 23% of the Northumberland National Park. They formed a crossover pair, where predator control was allocated at random to one plot (Plot A), with plot B having no predator control. Then in September 2004, predator control was switched to plot B, with plot A then receiving no predator control. The remaining pair of plots (C and D), both comprised former grouse moors together withadjacent marginal farmland, and had predator control assigned at random to one plot (Plot C), which was retained throughout the experiment, with Plot D having no predator control throughout. Predator control prior to and after the experiment was largely restricted to occasional shooting of foxes by farmers to protect lambing sheep and hunting foxes with dog packs, before it became illegal to do so in 2004.

2.2. Prey, predator, and habitat monitoring

Survey methods deployed during the experiment (see Fletcher et al., 2010 were repeated in springs 2018 (plots A and B) and 2019 (plots C and D)). Original surveyors were unavailable for the repeat surveys, but biases associated with using different surveyors were minimised through training and only using experienced surveyors familiar with the original surveys. Each of the four study plots were divided into blocks, typically of area 1.5 km^2, that could be surveyed during periods of peak wader activity (Reed et al., 1985). Four species of wader (Lapwing, Golden Plover, Curlew, and Snipe *Gallinago gallinago*) were monitored, together with three gamebirds (Red Grouse, Black Grouse *Lyrurus tetrix* and Grey Partridge), three avian predators (Buzzard, Raven, and Carrion Crow) and one mammalian predator (Red Fox). Birds were counted on two dawn survey visits between mid-April and late-May and their locations assigned 10-figure grid references using a hand-held GPS. Unlike during the experiment, the commonest passerines Meadow Pipit and Skylark *Alauda arvensis* were not included for logistical time constraint reasons. Bird registrations were combined from the two visits to estimate annual breeding numbers.

During the experiment, Red Grouse were surveyed using pointing dogs within the same blocks used for wader surveys in early spring, when grouse were in pairs, repeated in July and early August post-breeding to measure breeding success and autumn densities. For logistical reasons, red grouse were resurveyed only in a sub-set of those blocks in 2018-19 and surveys were split between those conducted in spring (Plots C & D in 2019) and those conducted in July (Plots A & B in 2018). Black Grouse and Grey Partridge were present only on Plots A & B (Otterburn Training Area), where Black Grouse were surveyed over the entire military training area by visiting known display sites at dawn. Black Grouse surveys were conducted annually from 2000-12, then in 2014, 2018 and 2019.

Fox scats were counted along set routes of 18 – 26 km on each plot. In 2018/19, a sub-sample of the full routes covered during the experimental years were surveyed. Unlike during the experiment, when fox scats were gathered monthly, we conducted only an initial clear-up round on each plot and compared those with the corresponding clear-up rounds during the experimental years.

The experiment manipulated predators only, whilst maintaining habitat composition and management at similar levels to those which existed prior to the experiment. To monitor potential changes, measures of habitat structure and composition were made annually in mid-summer during the experiment. The dominant plant species and their height were recorded with 25 x 25 cm quadrats every 20 m along 1-km transects (20 transects in plots A & B and 15 in C & D). No differences in dominant vegetation, Heather *Calluna vulgaris*, Purple Moor Grass *Molinia caerulea,* other species, or their heights were found between plots with and without predator control during the experiment (Fletcher et al., 2010). These measures were repeated in 2019 to assess possible change in subsequent years. In 2019, the number of transects was reduced to 15 on plot A owing to a wildfire and subsequent explosion risk from live ordnance. Most of the plot areas were within UK Government agri-environment schemes both during and after the experiment which helped restrict any habitat changes.

2.3. Statistical analyses

The baseline data against which post-experimental changes in bird abundance were considered were those years for which predator control treatment was consistent on a given plot. Fletcher et al., (2010) found that bird abundance each year was related to treatment in the previous year. Accordingly, bird abundance data from the first year of treatment were not included. For the crossover plots (A & B), the plot-means of 2006-09 were used and for the fixed plots (C & D), the plot-means of 2003-09 were used. These plot-means were compared against the mean of the first and second counts for each plot in either 2018 or 2019 within a Generalised Linear Model with a Poisson error and log link function, sum of first and second counts per plot-year as the response variable, ln(2) as an offset, and period (1 = 2003-09, 2 = 2018/19) and plot as explanatory factors. The same model framework was used for fox scats, with the difference being that the response variable was the number of scats, and the offset was the $\log_e$ total transect length within the plot.

To consider changes in vegetation composition and height between the experimental period and the resurvey, annual plot-means during for the years 2002-08 were compared with plot-means from 2019 in a GLM with a normal error distribution and identity link function. Each vegetation measure in turn was the response variable and plot and period (1 = 2002-08, 2 = 2019) as explanatory factors.

3. Results

3.1 Prey and predators

When comparing bird abundance during the experimental years with the resurvey, all four wader species were fewer in each plot during the resurvey, resulting in significant decreases for Golden Plover, Snipe, and Curlew of 81%, 76% and 24% respectively, with a non-significant decline of 54% for Lapwing (Table 1). Of the gamebirds, Red Grouse were fewer across all plots by an average of -74%, whilst Grey Partridge and Black Grouse had both become locally extinct between the experimental years and the resurvey. Grey Partridge became extinct at the level of the plots (A & B), whilst Black Grouse declined from a high of 69 displaying males in 2003 across the whole military training area to zero in 2014 and subsequent survey years.

The mean number of sightings of protected avian predators (Buzzard and Raven) showed non-significant increases of 48% and 110% respectively, a change consistent across all plots and both species (Table 2). Carrion Crow abundance and fox scat indices had significantly increased across all plots by an average of 78% and 127% respectively.

3.2. Vegetation composition and height

Of the four vegetation measures considered, there was no difference in the proportion of quadrats dominated by either Heather or Purple Moor Grass between 2002-2008 (period 1) and 2019 (period 2), with the respective proportions averaging 0.24 in each period for Heather and 0.34 and 0.40 for Purple Moor Grass (Table 3). Where Heather was present, its height did not differ between years, averaging 32.2 cm in period 1 and 31.0 in period 2. Non-ericaceous vegetation, typically Purple Moor Grass, but also Soft Rush *Juncus effusus* and Jointed Rush *J. articulatus* was 35% taller in period 2 at 33.8 cm than in period 1, when it was 25.0 cm. This difference may merely represent an earlier or better growing season for grasses and deciduous perennials such as Jointed Rush in the latter year (2019).

4. Discussion

Dramatic changes in numbers of some ground-nesting birds and their potential predators had occurred since the end of the experiment in spring 2009. Most notable were the local extinctions of Black Grouse and Grey Partridge. Significant decreases in abundance occurred in Golden Plover (-81%), Snipe (-76%), Curlew (-24%), and Red Grouse (-74%), with a non-significant change of -49% for Lapwing. These changes were broadly consistent with UK-wide declines since 1995 from BBS, with significant declines in Grey Partridge (-63%), Lapwing (-49%), and Curlew (-49%), now red-listed as being birds of conservation concern in the UK, with non-significant declines in Snipe, Red Grouse (amber listed) and Golden Plover green listed (Stanbury et al., 2021; Heywood et al., 2023). The consistency of bird trends between the study and the wider UK suggests that reductions in predator management, habitat changes, or a combination of both are widespread in the uplands of several UK regions following loss of heather moorland to sheep grazing and their replacement by either forestry or re-wilding schemes (Robertson et al., 2017; Ludwig et al., 2020a).

Insufficient BBS encounters occurred to establish a UK Black Grouse trend but repeat UK surveys have illustrated the steepness of their decline from an estimated 25,000 (95%CL: 13,800 – 36,700) displaying males in 1991-93 (Baines & Hudson, 1995) to 6,500 in 1995/96 (Hancock et al., 1999) and 5,100 in 2005 (Sim et al., 2008). The decline has been most severe in South Scotland, whilst in northern England the population recovered from 773 males in 1998 to 1,437 in 2014 (Warren et al., 2015). However, trends differed markedly between English regions, with a doubling and trebling in the North Pennines and Yorkshire Dales associated with the proximity of grouse moors (and predator control) in both regions (Warren & Baines, 2004), a dedicated Black Grouse Recovery Project, and trial translocation of birds into the Yorkshire Dales (Warren et al., 2017; 2018).

By contrast in North Northumberland, where managed grouse moors were few and most birds were on the Otterburn Training Area, numbers of Black Grouse crashed from 101 males in 2002 (68 at Otterburn) to only two in 2014 (0 at Otterburn) (Warren et al., 2015). Habitat loss, degradation, and fragmentation leading to small, isolated populations, together with increasing predators, are cited as causes of decline in Europe (Storch, 2000). At Otterburn, a previously stable population became extinct in just over a decade. During this time, our measures of habitat extent and quality had not changed, but numbers of Goshawk, a protected predator which can specialise on tetraonid grouse, had risen to 32 occupied territories by 2011 in Kielder Forest, the largest man-made forest in England covering 650 km^2, part of which is adjacent to and surrounds the UPE plots (Hoy et al., 2015). In the boreal forests of Scandinavia, Goshawks removed 15-25% of the grouse population during the breeding season (Linden & Wikman, 1983), with estimates for Black Grouse removal in Sweden being 25% of females and 14% of males (Widen, 1987,) and 35% of Black Grouse, sexes combined, in northern Finland (Tornberg, 2001). The crash in Black Grouse numbers at Otterburn is thus spatially and temporally linked with local increases in Goshawk, but evidence is lacking to state cause and effect. Moreover, predation by Red Foxes and Carrion Crows may also have contributed.

Predatory species previously removed during the experiment had recovered to pre-management levels (Carrion Crow and Red Fox). The small size of the experimental plots relative to the surrounding large areas where predators were unmanaged facilitated rapid immigration, often by the next spring (see Fig. 2. Fletcher et al., 2010). Numbers of protected species (Buzzard and Raven) had doubled since the experiment finished, consistent with UK-wide trends (Heywood et al., 2023).

5. Conclusions

Rapid declines in abundance amongst a community of ground-nesting birds, involving several species of highest conservation concern in the UK, together with extinctions of Grey Partridge and Black Grouse, were strongly associated with both the recovery of legally controllable predators following cessation of their removal, and increased abundance of protected predators. This resurvey adds weight to the experimental findings reported in Fletcher et al., (2010), which are further supported by evidence that waders at Langholm Moor in SW Scotland increased following restoration of predator control by gamekeepers (Ludwig et al., 2019). Furthermore, increases in the ground-nesting raptors Hen Harrier and Merlin *Falco columbarius* occurred during periods of grouse-moor management, when a higher proportion of nesting attempts were successful following reduced predation (Baines & Richardson, 2008; Ludwig et al., 2020b).Likewise, retrospective modelling within an adaptive management framework found that changes in Red Grouse abundance were best explained by the combined effects of protected and unprotected predators (Powell et al., 2022).

The growing body of evidence reviewed by Roos et al., (2018) suggests that crows and Red Fox have increased in the UK in recent decades, and that predation by them may limit population sizes of gamebirds and waders, through reducing their breeding success. They found that, amongst 11 studies involving experimental predator removal to benefit gamebirds, 81% resulted in population increases, whilst the equivalent value from 29 studies involving waders was 45% (Roos et al., 2018). Whilst such findings are increasingly accepted, division persists over what to do about it. The UK has a culture of intensive wild and reared gamebird management, which is dependent on lethal predator control which is considered an essential component of conservation management (Reynolds & Tapper, 1996). Lethal control is however costly and needs to be long-term. To be successful, it may require levels of removal that are impractical outside of intensive gamebird shoots (Douglas et al., 2023), and ethically questionable to many sectors of the public (Messmer et al., 1999).

Others consider lethal control to be a last resort once other options have been considered (Doherty & Ritchie, 2017). Alternative options include reconfiguration of landscapes such as removal of non-native forests, which whilst attractive to predators tend to be avoided by some gamebirds and waders (Hancock et al., 2009; Douglas et al., 2014). Tighter regulations over gamebird releases may reduce food availability to predators through fewer gamebird carcasses to scavenge (Lees et al., 2013) and less supplied grain for corvids and Brown Rats *Rattus norvegicus*, especially in winter when natural food sources are depleted (Sanchez-Garcia et al., 2015). Given the historic loss of apex predators from the UK, there may be opportunities for reintroductions and range expansions through translocation (Wilson & Campera, 2024). Some apex predators such as the White-tailed Eagle have already been reestablished (Love & Ball, 1979), other programmes are ongoing, e.g., Golden Eagle translocation into Southern Scotland (Barlow 2022), or are being considered, e.g., Lynx into Kielder Forest or elsewhere in Scotland (Ovenden et al., 2019; Bavin et al., 2023). If successfully established, these and other apex predators may reduce the abundance of mesopredators by directly killing them, or by instilling fear that modifies their behaviour and limits their distribution and abundance through spatial avoidance (Ritchie & Johnson, 2009). Thus, apex predator reintroduction may form a management tool, with subsequent benefits for prey species, thus helping to sustain biodiversity (Sergio & Hirlaldo, 2008).

Multiple approaches to biodiversity conservation and restoration need to be adopted and all the above recommended actions should be attempted. Lethal predator control, either as part of grouse moor management or publicly funded has already been shown to benefit groups of ground-nesting birds. It should be continued where it does not compromise potentially competing land-use options involving landscape diversification including re-wilding and sympathetic reafforestation to help address the climate change emergency (Crowle et al., 2022). Meanwhile, landscape-scale reconfiguration, tighter restrictions on gamebird releases, and reintroduction of apex predators should be trialled and their benefits to prey species of conservation concern assessed.

Declaration of competing interests

The author declares that he has no known competing financial interests or personal relationships that could have influenced the work reported in this paper. All procedures were performed in compliance with relevant law and institutional guidelines.

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Table 1. Predicted mean (se) abundance of four species of wader (curlew, golden plover, lapwing, and snipe) and three species of gamebirds (red grouse, black grouse (males at leks), and grey partridge (pairs)) within four plots during the experiment (Period 1) and 10-years after the experiment (Period 2). Values are from a GLM with plot and period as explanatory variables.

		No birds per plot				
Species	**Plot**	**Period 1**	**Period 2**	**Change**	$F_{1,19}$	**P**
Curlew	A	31.5 (2.9)	23.9 (3.5)			
	B	9.0 (1.5)	6.9 (1.4)			
	C	47.8 (2.8)	36.2 (4.9)			
	D	5.4 (0.9)	4.1 (0.9)			
	period means	**24.1 (1.1)**	**18.3 (2.4)**	**-24%**	**4.38**	**0.049**
Golden plover	A	18.1 (2.5)	3.4 (1.5)			
	B	2.4 (0.9)	0.5 (0.3)			
	C	14.5 (1.7)	2.8 (1.2)			
	D	7.1 (1.2)	1.3 (0.6)			
	period means	**10.6 (0.8)**	**2.0 (0.8)**	**-81%**	**26.10**	**<0.001**
Lapwing	A	10.8 (3.4)	4.6 (2.5)			

	B	12.2 (3.6)	5.2 (2.8)			
	C	21.8 (3.8)	9.3 (4.7)			
	D	2.2 (1.2)	0.9 (0.7)			
	period means	**11.8 (1.5)**	**5.0 (2.4)**	**-49%**	**3.67**	**0.069**
Snipe	A	32.6 (5.2)	7.8 (2.8)			
	B	26.2 (4.6)	6.3 (2.3)			
	C	55.3 (5.2)	13.3 (4.5)			
	D	15.3 (2.7)	3.7 (1.4)			
	period means	**33.0 (2.3)**	**7.9 (2.6)**	**-76%**	**27.78**	**<0.001**
Red grouse (July)	A	43.8 (14.8)	11.4 (5.2)			
	B	92.9 (21.7)	24.2 (9.2)			
Red grouse (spring)	C	214.9 (19.8)	55.9 (19.1)			
	D	15.3 (2.7)	3.7 (1.4)			
	period means	**108.6 (8.6)**	**28.2 (9.4)**	**-74%**	**22.93**	**<0.001**
Black grouse	Otter-burn	**33.6 (6.1)**	**0**	**-100%**	**21.26**	**0.002**

Grey partridge	A	6.0 (0.7)	0	-100		
	B	2.8 (0.5)	0	-100		
	period means	**4.8 (0.6)**	**0**	**-100***	**46.46**	**<0.001**

Table 2.

Predicted mean (se) abundance of two legally protected predators (Buzzard and Raven) and two predators that can be controlled (Carrion crow and Red fox (scat index)) within four plots during the experiment (Period 1) and 10-years after the experiment (Period 2). Values are from a GLM involving plot and period as explanatory variables.

		No birds per plot				
Species	**Plot**	**Period 1**	**Period 2**	**Change**	**$F_{1,19}$**	**P**
Buzzard	A	1.3 (0.5)	1.9 (0.9)			
	B	4.0 (1.0)	5.9 (2.0)			
	C	3.1 (0.7)	4.5 (1.5)			
	D	1.2 (0.4)	1.7 (0.8)			
	period means	**2.3 (0.4)**	**3.4 (1.0)**	**48%**	**1.26**	**0.27**
Raven	A	0.4 (0.3)	0.8 (0.6)			

	B	1.2 (0.5)	2.3 (0.8)			
	C	0.6 (0.3)	1.3 (0.7)			
	D	1.7 (0.5)	3.5 (1.6)			
	period means	**1.0 (0.2)**	**2.1 (0.8)**	**110%**	**2.11**	**0.16**
Carrion crow	A	18.0 (3.0)	32.0 (6.6)			
	B	11.3 (2.3)	20.0 (4.8)			
	C	18.2 (2.4)	32.4 (6.4)			
	D	7.6 (1.5)	13.6 (3.4)			
	period means	**13.6 (1.3)**	**24.2 (4.0)**	**78%**	**8.34**	**0.009**
Fox scats/km	A	1.4 (0.4)	3.0 (1.1)			
	B	2.0 (0.4)	4.4 (1.4)			
	C	2.1 (0.6)	4.6 (1.5)			
	D	0.8 (0.3)	1.7 (0.7)			
	period means	**1.5 (0.2)**	**3.4 (0.9)**	**127%**	**4.57**	**0.044**

Table 3.

The proportion of quadrats in which *Calluna vulgaris* or *Molinia caerula* dominated and their heights in replicated transects across the four study plots during the experiment (2002-08, Period 1) again in 2019 (Period 2). Values are predicted means (SE) from a GLM with plot and period as explanatory factors.

	Period 1	Period 2	$F_{1,26}$	P
Calluna vulgaris dominant	0.24 (0.01)	0.24 (0.02)	0.05	0.83
Calluna vulgaris height (cms)	32.2 (0.6)	31.0 (1.7)	0.45	0.51
Molinia caerula dominant	0.34 (0.01)	0.40 (0.03)	3.85	0.06
Other species height (cms)	25.0 (0.6)	33.8 (1.6)	27.55	<0.001