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In the United Kingdom, black grouse *Tetrao tetrix* are in severe decline with only 6,500 displaying males in 1995-1996 and a range retraction of 28% between 1972 and 1991. Recent declines have been greatest in central and southern Scotland and parts of Wales and contrast with relative stability in northern England. We compare the demography of black grouse in three regions: North Wales, northern England and the Scottish Highlands. Patterns in annual fecundity, measured as fledglings per breeding female, were correlated between regions, suggesting that annual weather patterns common across regions may be a key determinant of breeding success. Site related effects such as habitat quality or management were also significant in northern England and North Wales. Male population growth rates at leks were positively correlated with fecundity in the previous year. Fecundity was highest in North Wales and the Scottish Highlands at 1.7 chicks per female in August compared to 1.3 in northern England. Variations in the annual fecundity of radio-tagged females were linked to differences in brood survival rather than clutch survival, which did not differ among years. We found a non-significant trend for juvenile survival to be lower in North Wales (0.18) than in either northern England (0.65) or the Scottish Highlands (0.56). Similarly, annual adult survival also tended to be lower in North Wales (0.44) than in either northern England (0.70) or the Scottish Highlands (0.66). Predation was the main cause of death in all regions, with red fox *Vulpes vulpes* and raptors being the chief predators in North Wales and the Scottish Highlands and stoat *Mustela erminea* in northern England. The last 10 years have seen the implementation of a series of black grouse recovery projects in the UK. An understanding of the limiting demographic stage in each project area is critical before appropriate remedial management prescriptions can be implemented.

Key words: black grouse, fecundity, mortality, population dynamics, recovery, survival

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During the last century, the black grouse *Tetrao tetrix* has declined in numbers and range in most parts of western and central Europe, and in several countries it has become extinct (Storch 2000). Factors responsible vary throughout their range, but generally include loss, degradation and fragmentation of habitat, caused by changes in land use, chiefly agricultural intensification or changes in forest management (Cramp & Simmons 1980). In the United Kingdom, the decline, identified through shooting bag records, has been long-term (Baines & Hudson 1995), but has recently accelerated, with a retraction in range of 28% during 1972-1991 (Gibbons et al. 1993). The first UK population estimate based on counts in the early 1990s gave a mean of 25,000 displaying males, whereas a first systematic survey in 1995-1996 estimated only 6,500 males (Hancock et al. 1999). The most recent survey conducted in 2005 showed a further reduction to only 5,100 males (Sim et al. submitted). Concerns over declines in the UK culminated in black grouse being red-listed as a species of High Conservation Concern (Gregory et al. 2002) and as a priority species in the UK Biodiversity Action Plan (UK Biodiversity Group 2001).

Black grouse occupy a mosaic of habitats that includes heather moorland, herb-rich meadows and pastures and the edges of both native and commercial forests (Baines 1994). Over the last century there have been considerable changes in the landscape of the United Kingdom, including the loss or degradation of moorland fringe habitat, either to agricultural intensification, overgrazing by red deer *Cervus elaphus* (Baines et al. 1994) and sheep *Ovis aries* (Fuller & Gough 1999), or maturation of commercial forests (Cayford 1990, Pearce-Higgins et al. 2005). These activities have created a more homogenous landscape instead of the diversity of habitats and structures that black grouse prefer. As numbers have declined, other compounding factors have probably increased in their importance. These include increased mortality of full-grown birds to predators, such as red fox *Vulpes vulpes*, and raptors, such as peregrine *Falco peregrinus* and goshawk *Accipiter gentilis*, and clutches to corvids, all of which have increased their range and abundance over the last 40 years (Tapper 1992, Crick & Ratcliffe 1995, Stone et al. 1997). Furthermore, in the Scottish Highlands it is likely that collisions with deer fences may have become more important as bird numbers decrease (Baines & Summers 1997, Baines & Andrew 2002).

A review of studies of black grouse breeding success in Europe showed a 60% decrease in the number of young reared per female during 1950-1990 (Baines 1991), suggesting that this may be a demographic stage limiting population size on a wide geographical scale. Several factors are likely to be responsible for changes in either breeding success or survival of full-grown birds. In the UK, the relative importance of these probably vary between regions and habitats (Baines 1990, Warren & Baines 2002), thus complicating conservation action aimed at population recovery.

Restoration plans for black grouse have been written for the UK as a whole and for each of the nation countries England, Scotland and Wales, separately. Over the last 10 years, several regional recovery projects (e.g. Lindley et al. 2003, Warren & Baines 2004) have been established. However, knowledge of the underlying mechanisms for decline in terms of limiting demographic stages is imperative before adequate and efficient remedial management can be instigated. Our study compares the population dynamics of black grouse in three regions of the United Kingdom and relates these to management actions necessary to restore black grouse populations.

Methods

Study areas

Black grouse fecundity and survival were compared for three different parts of the United Kingdom: North Wales, the North Pennines (northern England) and Strathspey and Deeside (Scottish Highlands). The habitats occupied by black grouse differed markedly between the three regions. In the Scottish Highlands, birds were studied within the remaining fragments of Scots pine *Pinus sylvestris* forest with an ericaceous field layer dominated by bilberry *Vaccinium myrtillus* and heather *Calluna vulgaris*, where birds were associated with forest clearings and forest edge habitats. In stark contrast, birds in northern England occurred in habitats with few or no trees, where bilberry was largely absent, but where heather was found on blanket bog and moorland at altitudes of >500 m a.s.l. Here, black grouse occupied a mosaic of habitats that included acid grasslands, heather moorland and blanket bog managed for red grouse *Lagopus lagopus scoticus* shooting, and enclosed rough grazings and hay meadows managed by hill farmers for sheep and

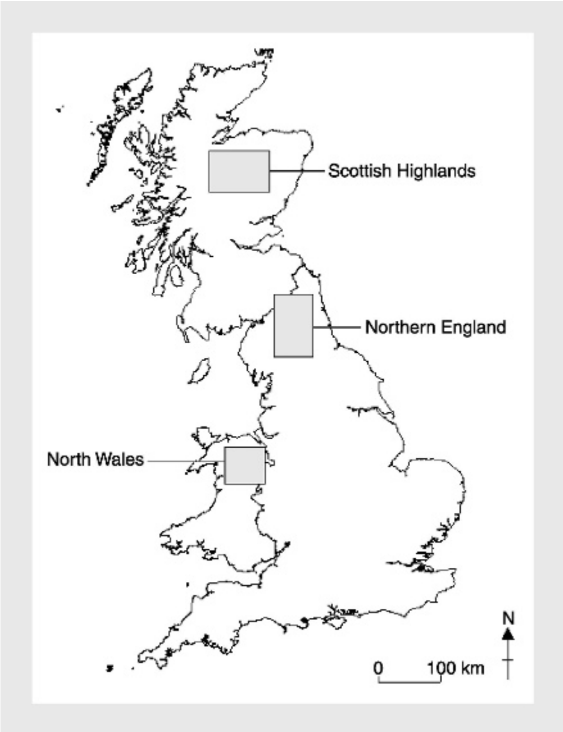

Figure 1. Location of the three regions enclosing our study sites.

cattle (Baines 1994). Habitats in North Wales were a mosaic of heather moorland and younger stands of commercial plantation forests. These forests, largely comprised of Sitka spruce *Picea sitchensis*, were planted from the 1920s onwards, often onto what had been moors managed for red grouse.

Data on black grouse fecundity, measured as fledglings per female, were obtained from annual counts conducted in late July or August during 1997-2002 using pointer dogs to locate females and their broods. Data were collected from 21 sites in northern England (Calladine et al. 2002), nine sites in the Scottish Highlands and seven sites in North Wales, six of which hosted more than 80% of the Welsh black grouse population (Williams 1996; Fig. 1). The size of each count area ranged within 1.0-7.4 km^2 (mean 2.6 km^2) in northern England and within 2.5-12.5 km^2 in the Scottish Highlands (mean 5.4 km^2). In North Wales, females were systematically counted within a 1.5 km radius of each of three leks at each site (Johnstone & Lindley 2003). In all instances, estimates were considered to be total counts.

Survival rates of radio-tagged juveniles and adults were estimated from 148 individuals at 15 sites in northern England during 1998-2004 (Warren & Baines 2002, Baines & Richardson 2007), from 28 birds at four sites in the Scottish Highlands during 2002-2004, and from 39 birds at one site in North Wales during 1999-2003 (Bowker et al. in press; Table 1). Annual fecundity was also measured at all of these sites. All birds in North Wales and the Scottish Highlands were caught in August when still in family groups and aged 8-10 weeks old. A large hand held net was dragged by two people over a pointing dog that indicated the position of the brood. The sample of 93 juveniles and six adult females caught by this technique in northern England was supplemented with a further 49 birds (44 females and five males) caught at night-time roosts in winter or early spring using a high powered lamp and a small hand held net. All birds were fitted with 17-g necklace radio transmitters.

Data analysis

Regional differences in fecundity were analysed in relation to region and year by two-way ANOVA. Data used in the analysis were annual site means of the number of chicks reared per female, weighted by the number of females in the sample. This corresponded to 34 site years in the Scottish Highlands, 99 in northern England and 32 in Wales.

Correlations in both the mean annual fecundity between regions and the relationship between fecundity in year 't' and male population growth rates at leks between year 't' and year 't+1' were considered for longer time series in northern England (1989-2004) and the Scottish Highlands (1990-2002). Within these longer time series, annual estimates of fecundity were based on a mean of 63 females per year at 4-21 sites per annum in northern

Table 1. The age and sex of black grouse caught and radio-tagged in three regions of the United Kingdom during 1998-2004.

		Adult		Juvenile		
Region	Period	Males	Females	Males	Females	Unknown
Scottish Highlands	2002-2004	0	0	10	18	0
Northern England	1998-2000	3	19	20	28	0
Northern England	2002-2004	2	30	14	31	0
North Wales	1999-2003	0	5	20	13	1

England, and a mean of 49 females per year at 3-7 sites per annum in the Scottish Highlands. No long term data were available for North Wales. These long time series were also used to consider variations in fecundity within each region in relation to 'site' and 'year'.

Additional data on fecundity were obtained from radio-tagged females in northern England during 1999-2004, excluding 2001 when access to birds was severely restricted due to an outbreak of foot and mouth disease. A total of 101 breeding attempts were monitored through incubation to fledging, allowing a breakdown of breeding success into clutch and brood survival. Differences in clutch and brood survival among years were analysed by logistic regression (1 = clutch or brood survived, 0 = failed). Small sample sizes prevented such an analysis in both North Wales and the Scottish Highlands.

Survival rates were estimated by modelling individual survival histories from two weeks after capture to death, loss of radio signal or the end of the study, whichever occurred first. To avoid bias due to capture and handling, the first two weeks after capture were ignored. Therefore, five juveniles and one adult were excluded from the Welsh sample, four juveniles from the Scottish sample and three juveniles from northern England, because these were not resighted two weeks after capture. This approach was consistent with that adopted in other studies of black grouse (e.g. Caizergues & Ellison 1997, Warren & Baines 2002), thus enabling a comparison of survival rates among studies. Survival histories were modelled using a product of weekly survival rates for each week that a bird survived, and of a weekly mortality rate (1-survival rate) if it died. Weekly survival rates were initially assumed to differ between sexes and between juvenile (September-February after hatching) and adult birds. The survival history of birds caught as juveniles could involve both juvenile and adult survival rates. Such birds were considered to be adults on 1 March in the year following capture (Warren & Baines 2002). This method permitted inclusion of birds tagged at different times of the year. Models were fitted using the program SURVIV (White & Garrott 1990), and estimated survival rates were compared using likelihood ratio tests. Juvenile survival probability (i.e. over the six months September-February) was calculated by raising weekly survival rates to the power of 26, and annual adult survival probability by raising the weekly rate to the power of 52. The northern England data set was split into two periods, 1998-2000 (73 birds) and 2002-2004 (74 birds), to overcome the problems of a maximum entry level of 75 birds in the programme. Potential differences in adult survival rates between winter (September-February) and summer (March-August) and between males and females were considered for the northern England sample, but no significant differences were found. Hence, data from males and females were combined. Small sample sizes of adults in North Wales and the Scottish Highlands prevented such analyses in these regions.

Causes of death were assigned to either predation by mammal (red fox or stoat *Mustela erminea*), predation by raptor, disease or accident. Accidents were further categorised as collisions with either wires or fences, or as shot. The type of predator was identified by examining carcasses both externally and internally for puncture marks from talons and notches on the sternum (raptor) or teeth (mammal). Feathers were examined to assess whether they had been plucked clean from the body (raptor) or chewed (mammal). Other field signs such as trails of feathers, suggestive of an attack by a raptor, or fox scats present in the vicinity of the corpse were considered. Birds killed by stoats were distinguished from those killed by foxes by the size of the teeth puncture marks and their position, with stoats typically biting their prey on the neck. Stoat-killed birds were confined to northern England, where pine martens *Martes martes* are absent, thus avoiding potential confusion between these two predators. Data on causes of death in the Scottish Highlands were supplemented by 10 records from birds radio-tagged during 1993-1996 at one of the our study areas and at an additional site. Differences in causes of death were analysed by χ^2-test, with cause assigned to one of four categories: predation by fox, by stoat, by raptor and cause other than predation.

Results

Breeding success

Fecundity varied significantly among the three regions ($F_{2,157} = 3.52$, $P = 0.03$) and also between years ($F_{5,157} = 5.13$, $P < 0.001$), being lowest in northern England with 1.26 ($\pm$0.22 SE) chicks per female and highest in the Scottish Highlands (1.65 $\pm$ 0.25) and North Wales (1.73 $\pm$ 0.25). Patterns of annual fecundity were positively correlated between northern England and North Wales ($r_5 = 0.80$, $P <$

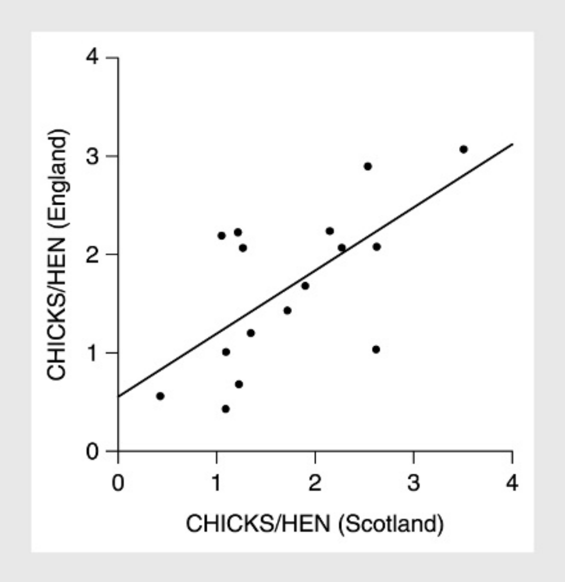

Figure 2. Annual fecundity (chicks fledged per female) of black grouse in the Scottish Highlands and northern England. N = 16 years.

0.05) and between northern England and the Scottish Highlands, the latter involving a longer time series collected during 1989-2004 ($r_{15} = 0.64$, $P < 0.01$; Fig. 2), but not between the Scottish Highlands and North Wales ($r_5 = 0.08$, $P = 0.88$). The trend for similar spatial patterns of annual fecundity among different regions was supported by analysis of variations in fecundity within regions in relation to the explanatory variables 'site' and 'year'. 'Year' related effects were significant in the Scottish Highlands and northern England and explained 45 and 33% of the variation, respectively, confirming the likely overall importance of weather on breeding success. However, no significant 'year related' effects were found in North Wales (Table 2). Probably in response to variations in factors such as habitat quality and management within regions, differences in fecundity among sites were significant in both northern England (13% of the variation explained) and North Wales (46% of the variation explained).

Male population growth rates at leks were positively correlated with fecundity the previous year in the Scottish Highlands ($y = 2.77x + 1.81$, $r^2 = 0.70$, $F_{1,11} = 25.88$, $P < 0.001$), but not in northern England ($r^2 = 0.14$, $F_{1,14} = 2.29$, $P = 0.15$). Combining data for the Scottish Highlands and northern England, breeding success explained 36% of the variation in the population growth rate of males ($y = 2.36x + 1.75$, $F_{1,27} = 15.14$, $P = 0.001$; Fig. 3).

Table 2. ANOVA of the effects of year and site on the fecundity (log chicks reared per female, weighted by the number of females in each sample) of black grouse in three regions of the United Kingdom. N = the number of site-years.

	ANOVA				
Region	df	Mean square	F-ratio	P	R^2
Scottish Highlands (N = 83)					
Site	9	12.56	1.71	0.109	0.14
Year	15	28.18	3.82	0.000	0.45
Error	58	7.37			
Northern England (N = 177)					
Site	20	8.12	1.75	0.033	0.13
Year	16	25.57	5.50	0.000	0.33
Error	140	4.65			
North Wales (N = 37)					
Site	6	36.95	4.60	0.004	0.46
Year	9	10.37	1.29	0.299	0.19
Error	21	8.04			

A total of 101 breeding attempts by radio-tagged females were monitored in northern England permitting a breakdown of fecundity into clutch and brood survival. The proportion of breeding attempts that fledged ≥ 1 chicks varied significantly between years from 0.06 to 0.42 ($\chi^2 = 4.24$, df = 1, $P = 0.039$), in response to significant annual variations in the proportion of broods where ≥ 1 chicks survived ranging within 0.10-0.73 ($\chi^2 = 6.10$, df = 1, $P = 0.013$; Table 3). Neither clutch size (mean 8.2 eggs ± 0.2 SE) nor hatching success (the proportion

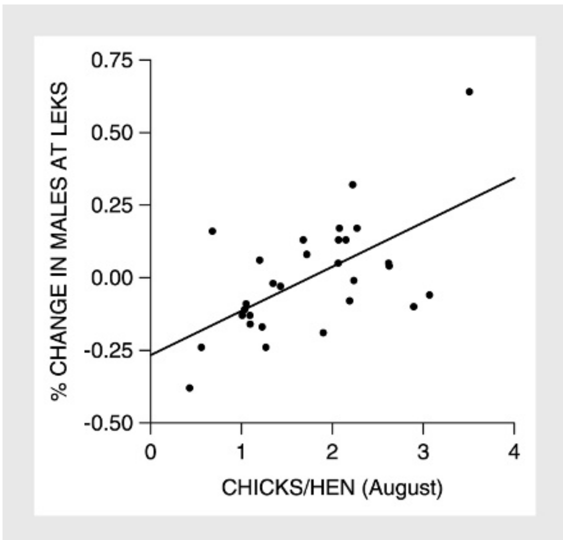

Figure 3. The relationship between black grouse fecundity (chicks fledged per female) and male population growth rates at leks the following year. N = 29 years (16 years for northern England and 13 years for the Scottish Highlands). Slopes did not differ significantly between regions and data have therefore been combined.

Table 3. Clutch survival (the proportion of clutches that hatched ≥1 eggs), brood survival (the proportion of broods that fledged ≥1 chicks) and overall breeding success (the proportion of clutches from which ≥1 chick fledged) for 101 breeding attempts by radio-tagged female black grouse in northern England during 1999-2004 . Foot and Mouth disease in 2001 severely restricted access to sites for data collection, and this year was therefore excluded from our analysis.

	Clutch survival		Brood survival		Breeding success	
Year	N	Hatched	N	Survived	N	Fledged
1999	8	0.50	4	0.25	8	0.13
2000	15	0.80	9	0.22	12	0.17
2002	17	0.59	10	0.10	17	0.06
2003	31	0.65	15	0.73	26	0.42
2004	30	0.60	18	0.56	30	0.33

of clutches from which ≥1 eggs hatched; mean 0.63 ± 0.05) differed among years.

Of the 101 clutches, 37 failed to hatch, and the cause of failure could be identified for 32 of these clutches. Predation was the main cause of clutch failure with 28 (88%) of clutches being predated. Mammalian predators were responsible for 75% of the predation (57% by stoat, 14% by either fox or badger *Meles meles*, and 4% (one predation event) by a domestic dog). Corvids were responsible for the remaining 25%. No information was gathered on the causes of chick losses.

Survival rates and causes of death

There was no overall significant difference in survival rates among regions ($\chi^2 = 4.53$, df = 9, NS; Table 4). Despite this, there was a non-significant trend for lower survival rates of juveniles in North Wales, with a survival probability of only 0.18 per six months (N = 28) compared to 0.56 in the Scottish Highlands (N = 24) and a mean of 0.65 over the two periods of study in northern England (N = 90). Similarly, survival of adults in winter tended to be lowest in North Wales, but again this was not significant. Within regions, six month survival probabilities were significantly higher in adults than in juveniles in both northern England (first period of study only), with 0.54 for juveniles and 0.89 for adults (winter; $\chi^2 = 11.59$, df = 1, $P < 0.001$) and in North Wales, with 0.18 and 0.66 for juveniles and adults, respectively ($\chi^2 = 13.96$, df = 1, $P < 0.001$).

Table 5. Causes of death in full-grown black grouse in three regions of the UK. Causes were categorised as predation, disease, collisions with fences or wires, or as shot.

	Northern England		Scottish Highlands		North Wales	
Cause	N	%	N	%	N	%
Predation						
Fox	5	11	12	48	12	33
Stoat	18	41	0	0	0	0
Raptor	13	30	10	40	22	61
Disease	3	7	0	0	0	0
Fences/ Wires	4	10	3	12	0	0
Shot	1	2	0	0	2	6

Cause of death differed among regions ($\chi^2 = 40.57$, df = 6, $P < 0.001$), with poor survival at the Welsh site being associated with a high proportion of birds being killed by raptors (61%) and by red fox (33%; Table 5). This situation was similar to the Scottish Highlands where 48% of birds were killed by red fox and 40% by raptors. In contrast, despite predation being important in all regions, the key predators differed in northern England with 41% of black grouse being predated by stoats and only 30 and 11% by raptors and red fox, respectively.

Discussion

In this study, we synthesised data from different regions of the UK to compare the demography of three populations of black grouse. Patterns of fecundity were spatially correlated across regions, probably in response to weather patterns in June after chicks have hatched (Moss 1985, Loneux 2000), with 'year' related effects being significant predictors of fecundity in the Scottish Highlands and northern England. Fecundity also differed significantly among regions, with the lowest value found in northern England. Here, and also in North Wales, fecundity varied significantly among sites. In northern England, differences among sites were

Table 4. Mean weekly survival rates (± SE) for black grouse in three regions of the United Kingdom. Winter: September-February and Summer: March-August. Juveniles were consided to be adults on 1 March.

Region	Juvenile (Winter)	Adult (Winter)	Adult (Summer)
Scottish Highlands (N = 24)	0.9783 ± 0.0147	1.000 ± 0.0951	0.9841 ± 0.0436
North England 1998-2000 (N = 70)	0.9767 ± 0.0095	0.9956 ± 0.0051	0.9880 ± 0.0137
North England 2002-2004 (N = 74)	0.9896 ± 0.0057	0.9914 ± 0.0082	0.9966 ± 0.0047
Lake Vyrnwy, North Wales (N = 33)	0.9365 ± 0.0743	0.9793 ± 0.0254	0.9907 ± 0.1325

related to differences in habitat quality determined by levels of sheep grazing (Calladine et al. 2002), whereas in North Wales, high fecundity was associated with sites where predators were routinely controlled by gamekeepers (Game Conservancy Trust 2001).

Fecundity in northern England at 1.3 chicks per female was lower than elsewhere in the UK and lower than the mean of 1.9 chicks per female (range 1.2-3.0) found in a review of 10 studies in six European countries (Baines 1990). In northern England, fecundity was limited by stoat predation of clutches and by brood survival. Therefore, management actions both to reduce clutch predation rates and to increase brood survival are probably necessary to restore black grouse numbers in northern England. This has in-part been demonstrated by a black grouse recovery project in northern England, which reduced sheep grazing in brood rearing habitats to increase the abundance of insects preferred by chicks. This resulted in a breeding success which was 42% higher than in areas with no changes in grazing and a 5% per annum increase in numbers of lekking males (Calladine et al. 2002). Wider adoption of such grazing reductions by farmers in northern England, aided through Government agri-environment grants, has been the key factor associated with an increase in the English population from 777 lekking males in 1998 to 895 in 2002 (Warren & Baines 2004), and to >1,000 males in 2006 (P. Warren, unpubl. data). Further improvements may prove possible through targeting the control of stoats in order to reduce clutch predation rates.

In contrast to the situation in northern England, we found that fecundity in North Wales and the Scottish Highlands was high, but there was a non-significant tendency for juvenile survival to be three to four-fold lower in North Wales than in either northern England or the Scottish Highlands. Similarly, adult annual survival at 0.44 was also low in North Wales compared to the rest of the UK (mean 0.68) and other parts of Europe. Comparative data from Scandinavia gave survival estimates of 0.53 in Finland (Linden 1981) and 0.54 in Sweden (Angelstam 1984), whilst survival estimates from the French Alps varied annually between 0.56 and 0.84 (Caizergues & Ellison 1997). In North Wales almost two-thirds of deaths of full-grown birds were due to predation by raptors, probably goshawk or peregrine, with predation by red fox accounting for the remaining third. Predation by raptors was also the most frequent cause of death of black grouse in other European studies (Angelstam 1984, Willebrand 1988, Caizergues & Ellison 1997, Spidsø et al.1997, Warren & Baines 2002). Management to improve the survival of full-grown birds, particularly juveniles, through reducing the impact of predators such as raptors and red fox may be important in maintaining population viability in North Wales. Whilst the red fox can be legally killed, raptors are protected by law in the UK and cannot. Efforts to restore black grouse numbers that depend upon increasing survival rates of full-grown birds may consequently be difficult to achieve. In the absence of raptor removal, black grouse conservation efforts need to concentrate on reducing raptor impacts through increasing protective vegetation cover, or by reducing numbers of other predators, such as red fox (e.g. Marcstrom et al. 1988).

Knowledge of potentially limiting demographic stages gained through studies of population dynamics can form an important guide when planning black grouse recovery projects allowing targeting of scarce resources towards appropriate manipulations of key stages in the life cycle. Research into the population dynamics of black grouse should whenever possible be a precursor of any recovery programme.

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