Survival Rates and Causes of Mortality in Black Grouse Tetrao Tetrix at Lake Vyrnwy, North Wales, UK

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Survival rates and causes of mortality in black grouse *Tetrao tetrix* at Lake Vyrnwy, North Wales, UK

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Rates of survival and reproductive success in black grouse *Tetrao tetrix* were assessed during a four-year study at Lake Vyrnwy in North Wales between 1999 and 2003. We used radio-tracking to assess survival rates of 33 individuals. The juvenile (September-February) survival rate was 0.18, compared with 0.66 over the same time interval for adults. Predation by raptors accounted for almost ⅔ of deaths. Broods were surveyed using pointer dogs in late August. Reproductive success was low, averaging 1.0 chicks/hen. Recruitment into the breeding population was insufficient to balance the observed mortality rates, resulting in a 67% decrease in breeding adults during the four-year study. This happened despite the likely immigration into the study area of dispersing juvenile females from adjacent areas with higher breeding success. An equivalent reduction in the abundance of red grouse *Lagopus lagopus scoticus* was observed, and this was also associated with years of low breeding success. Management methods that both reduce the impact of raptors on juvenile black grouse survival and improve breeding success are probably required to conserve black grouse in Wales.

Key words: black grouse, predation, radio telemetry, raptors, survival, Tetrao tetrix

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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 some places the species has become extinct (Storch 2000). Factors responsible vary throughout their range, but generally include habitat loss, degradation and fragmentation caused by changes in land use, chiefly agricultural intensification or changes in forest management (Cramp & Simmons 1980, Baines 1994). In the United Kingdom, the decline based on shooting bag records has been long-term (Baines & Hudson 1995), but has recently accelerated. The first UK population estimate based on counts in the early 1990s suggested a mean of 25,000 displaying males, whereas a more accurate systematic survey in 1995-1996 estimated 6,500 males (Hancock et al. 1999).

The Welsh population has been declining since the end of the 19th century, but had a temporary revival in the middle of the 20th century, when extensive afforestation of the Welsh uplands provided suitable habitat (Grove et al. 1988). Further declines in the mid 1980s prompted a national survey in 1986, which found 264 displaying males (Grove et al. 1988). Repeat surveys in the 1990s showed progressive declines, culminating in only 131 males in 1997 (Williams 1996, Lindley et al. 2003). These declines were linked to several interacting factors including the loss of younger stages of conifer plantations through tree maturation (Cayford 1990), agricultural intensification and increases in generalist predators of black grouse such as red fox *Vulpes vulpes* and corvids (Lovegrove et al. 1995).

Concern over the decline of black grouse in Wales, and in the UK as a whole, culminated in black grouse being red-listed as a species of High Conservation Concern (Gregory et al. 2002), and made a priority species in the UK Biodiversity Action Plan (UK Biodiversity Group 2001). Against this background, a black grouse conservation project was launched in 1999 to improve habitat management for black grouse at six key sites that collectively contained 80% of the Welsh population (Lindley et al. 2003). Whilst this project provided a much needed boost to habitat quality, it was not designed to provide detailed insight into the potential mechanisms responsible for national population decline. This complementary research project was established by Severn Trent Water at their Lake Vyrnwy National Nature Reserve in 2000 to consider the population dynamics of black grouse and to identify factors that may have brought about population decline.

Material and methods

Study area

The Lake Vyrnwy catchment encompasses an area of 9,400 hectares of moorland, forestry and farmland. The land is owned by the Severn Trent Water company and forms the largest nature reserve in Wales managed by the Royal Society for the Protection of Birds (RSPB). The 400-ha lake supplies drinking water to Liverpool. The area includes a 4,700 ha farm of mixed moorland and grassland managed by RSPB under agreement with Severn Trent Water and 2,000 ha of forestry managed by Forestry Commission Wales, also under agreement with Severn Trent Water. The farm is one of the largest organic units in Britain, with a flock of around 3,500 sheep and 30 Welsh black cattle.

The major conservation interest of the area lies on the heather moorland, 5,300 hectares of which have been designated as a National Nature Reserve, Site of Special Scientific Interest, Special Protection Area and Special Area of Conservation. The moorland generally undulates between 300 and 500 m a.s.l., rising to 600 m a.s.l. at its highest altitude. The black grouse study area encompassed the whole of the moorland part of the Vyrnwy Estate, plus an adjacent 500 ha at Cerniau managed by the RSPB to the southwest of the estate. The RSPB has undertaken heather management on the study area since the early 1990s using a combination of burning and cutting. No control of red foxes or crows was carried out on the moorland by any of the parties, but there were occasional fox hunts in the forest organised by local gamekeepers and farmers. Shooting rights were divided between the Lake Vyrnwy Hotel and the RSPB, but were not exercised for either red grouse *Lagopus lagopus scoticus* or black grouse during the study period.

Grouse abundance and productivity estimates

The number of displaying male black grouse was estimated annually based on spring lek counts (Cayford & Walker 1991, Baines 1996). Dawn visits to known lek sites and to other places to look for new locations of lekking birds were made from March onwards. A collective count of all males present at all identified displaying areas was made in the second week of May and formed the official annual total (Gilbert et al. 1998). Observers were placed at each lek, with additional observers spaced between leks at a maximum distance of 700 m apart. All observers were in radio communication with each other to clarify observations and to avoid repeat counts of any individuals that moved between leks.

Surveys of females were completed between mid-April and the end of May using trained pointer dogs. The whole area was systematically searched. This survey of females was repeated in August to locate broods and estimate breeding success. All broods found were revisited in the last week of August to record brood size and to provide a final estimate of productivity prior to brood break-up in early September. Comparative data on the abundance and breeding success of red grouse were collected each year in late-July from six 100-ha sample blocks of representative moorland within the study area. The number of adults (males and females), together with the number of juveniles were recorded and summed across the six blocks.

Radio-tracking

Pointer dogs were used to locate broods in late-August when the chicks were between eight and 12 weeks old. Over the four years, 34 juveniles and five adults were caught in nets at this time and fitted with 17 g necklace mounted radio tags (Biotrack - TW3 tags), which at the time of capture represented 2-3% of the juvenile's body weights (Table 1). These birds included a brood of eight two-week old chicks that were reared in captivity following the death of the female and were returned to their natal range at the end of August 2001. On average, tagged birds were located and flushed every two weeks.

Causes of death were assigned to either raptor or mammal (i.e. red fox) by examining carcasses both externally and internally for puncture marks from claws (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. The time of death was recorded as the mid-date between the last flushing occasion and the date of corpse recovery. The dispersal distance was defined as the straight-line distance from the natal tagging location and the subsequent nest site for females, or the lek for males.

Survival rates were estimated by modelling individual survival histories from two weeks after capture, or in the case of the eight captive reared birds, two weeks after their release, to death, loss of radio signal or the end of the study, whichever occurred first. To avoid bias due to capture and handling any deaths within the first two weeks after capture were ignored. Accordingly, six birds (five juveniles and an adult) were excluded. This approach was consistent with that adopted in other studies of black grouse (Caizergues & Ellison 1997, Warren & Baines 2002), thus enabling a comparison of survival rates. Survival histories of 33 birds (29 juveniles upon entry and four adults) were modelled using a product of weekly survival rates for each week that a bird survived, and a weekly mortality rate (1- survival rate) if it died. This method permitted inclusion of birds tagged at different times of the year. The survival history of birds caught as juveniles could involve both juvenile and adult survival rates; five such birds were considered to be adults on 1 March in the year following capture (Warren & Baines 2002). Weekly survival rates were initially assumed to differ between sexes, between seasons, i.e. winter (September-February) and summer (March-August), between juvenile (September-February after hatching) and adult birds. Models were fitted using the programme SURVIV (White & Garrott 1990); estimated survival rates were compared using likelihood ratio tests. Juvenile (i.e. over the six months September-February) and the comparative adult survival probability were calculated by raising weekly survival rates to the power of 26, annual adult survival rates by raising the weekly rate to the power of 52. As an example of survival history modelled in this way, a juvenile caught on 1 September 2000 that died exactly two years later gave rise to a survival probability modelled on $(S_{\text{1st, winter 2000}})^{24}$ $(S_{\text{adult, summer 2001}})^{26}$ $(S_{\text{adult, winter 2001}})^{26}$ $(S_{\text{adult, summer 2002}})^{25}$ $(1-S_{\text{adult, summer 2002}})$, allowing 26 weeks per season and discounting the first two weeks after capture.

Table 1. Age and sex composition of black grouse radio-tagged during and immediately prior to the study at Lake Vyrnwy. The sample included four male and four female captive-reared juveniles released in autumn 2001.

	Year				
	1999	2000	2001	2002	Total
Adult					
females	1	1	0	1	3
males	1	1	0	0	2
Juvenile					
females	1	3	5	4	13
males	0	9	9	2	20
unknown	0	0	0	1	1
Total	3	14	14	8	39

Results

Grouse abundance and breeding success

During the four years of our study, the average number of chicks reared per female black grouse in late August ranged within 0.7-1.5, with a mean of 1.0 (Table 2). The proportion of females with chicks in late August averaged 0.58. Numbers of black grouse males and females in spring decreased by 67% during the study ($F_{1,5} = 23.21$, $P = 0.005$). There was no difference in rates of decrease between

Table 2. Estimates of grouse abundance and breeding success at Lake Vyrnwy during 1999-2003. Mean number of chicks per female is calculated from the number of juveniles (excluding the released birds) divided by the number of females in August (black grouse) or late-July (red grouse).

	Year				
	1999	2000	2001	2002	2003
Black grouse					
Number of females in spring	-	19	15	9	4
Number of females in August	-	15	9	6	4
Mean Number of chicks per female	-	0.8	1.1	0.7	1.5
Proportion of females with broods	-	0.67	0.56	0.50	-
Red grouse					
Number of males in July	18	18	-	6	2
Number of females in July	16	14	-	4	3
Mean Number of chicks per female	2.1	2.3	-	0.8	0.3
Proportion of females with broods	0.50	0.64	-	0.25	0.33

sexes ($F_{1,5}$ = 1.43, P = 0.29), with displaying males halving from 14 in 2000 to only seven in 2003, and females from 19 to only four at an average rate across sexes of -21.9% per annum (± 1.2 (SE); Fig. 1). The difference in the number of females in the spring count and the August count was used as an index of adult survival. An average of the four years of counts gave a survival rate of 0.77, which translated to an annual survival rate of 0.39, assuming no seasonal differences in survival.

The abundance of red grouse males and females decreased from 34 to five over the four years ($F_{1,5}$ = 85.3, P < 0.001), representing a similar rate of decrease (-23.5 ± 3.3% (SE) per annum) to that observed in black grouse. Again, decrease rates were consistent between sexes ($F_{1,5}$ = 1.63, P = 0.26).

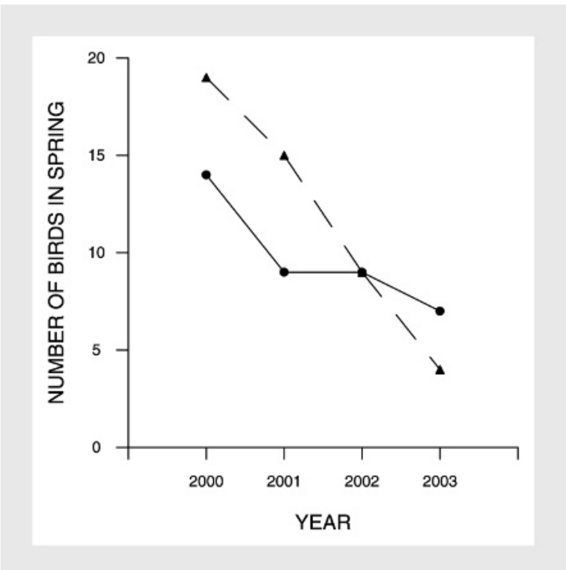

Figure 1. Annual counts of displaying male (—) and pre-breeding female black grouse (- - -) at Lake Vyrnwy.

Red grouse breeding success was four times higher in the first two years of the study (2.2 chicks reared per female) than in the last two years (0.55 chicks).

Causes of mortality

Of the 39 black grouse that were radio-tagged, only one was alive at the end of the study. Excluding the six birds that died within two weeks of capture, one bird was lost (presumed radio failure) and one died from an unknown cause, leaving 31 birds whose cause of death was known (Table 3).With the exception of two birds which had been shot, all remaining 29 birds had been predated. Of the black grouse predated, 64% were considered to have been killed by raptors, probably either goshawk *Accipiter gentilis* or peregrine *Falco peregrinus,* and 36% by red fox.

Survival rates

Survival rates were calculated from 33 radio-tagged black grouse. Survival rates did not differ between sexes (χ^2_1 = 0.13, n.s.). The survival rate of the juveniles that had been reared in captivity did not differ following their release from other juveniles for the six-month period September-February (χ^2_1 = 1.21, n.s.). Accordingly, all juveniles were combined

Table 3. Fate of 33 adult and juvenile radio-tagged black grouse at Lake Vyrnwy during 2000-2003.

Fate	Number	%
Predation		
Raptor	18	55
Fox	10	30
Shot	2	6
Radio failed	1	3
Unknown	1	3
Survive	1	3

to give a weekly survival rate of 0.9365 (± 0.0743 (SE)); equivalent to a six-monthly survival rate of 0.18. This rate was approximately four times lower than the rate of adults: 0.9842 (± 0.0203 (SE)), equivalent to a six-month survival rate of 0.66 or annual survival rate of 0.44 (χ^2_1 = 13.96, P < 0.001). This difference remained if released juveniles were excluded from the analysis (χ^2_1 = 9.36, P = 0.002).

Dispersal

The high rates of mortality encountered, particularly amongst juvenile black grouse, greatly restricted the number of surviving birds from which estimates of dispersal distances could be made. Of four juvenile males that survived to recruit into leks the following spring, the maximum distance that each travelled from their hatch point in their first winter was a mean of 9.7 km (range: 4.0-14.5 km). However, all males finally recruited into leks nearer to their hatch position, resulting in an average breeding dispersal distance of only 1.5 km (range: 0.5-3.0 km). Two males recruited into the lek nearest to their hatch position. Dispersal distances were recorded from four females, and averaged 10.7 km (range: 8.6-17.0 km).

Discussion

The data on survival rates and fecundity were from one site only, were obtained over only four years, and the survival rate estimates had wide standard errors. Accordingly, the data may not necessarily be representative of the Welsh black grouse population as a whole. There is, however, a general lack of equivalent data on vital rates from other Welsh sites, and as far as we are aware, ours are the only estimates of survival rates and causes of mortality for black grouse in Wales.

The annual survival rate of 0.44 for adults from the sample of radio-tagged birds broadly agrees with the index of survival of 0.39 derived from the counts. When compared with other parts of the UK and Europe, the annual survival rate of 0.44 for adults and six-monthly survival rate of 0.18 for juveniles (September-February) are low. Equivalent values in the North Pennines, England, where raptor abundance is low (Calladine et al. 2002), were 0.72 and 0.54, respectively (Warren & Baines 2002), and 0.51 for adult females in northeast Scotland (Picozzi & Hepburn 1985). Comparative data from Scandinavia give estimates of 0.53 in Finland (Lindén 1981) and 0.54 in Sweden (Angelstam 1984), whilst estimates from the French Alps varied annually from 0.56 to 0.84 (Caizergues & Ellison 1997). Common to findings from our study, predation by raptors was the most frequent cause of death (Angelstam 1984, Picozzi & Hepburn 1985, Willebrand 1988, Caizergues & Ellison 1997, Spidsø et al.1997, Warren & Baines 2002).

The average reproductive rate of 1.0 chick reared per female during our study was also low compared to estimates from 10 previous studies in six European countries summarised by Baines (1990), which varied from 1.2 to 3.0, with a mean of 1.9 chicks, but was similar to that of 1.1 chicks per female in the North Pennines (Calladine et al. 2002). There are no estimates of black grouse breeding success at Vyrnwy prior to our study, so we cannot consider whether there has been any temporal trend in breeding success, but estimates from six other sites in Wales for the period 1997-2000 provide a higher average of 1.7 chicks per female (Warren & Baines 2002).

The annual adult survival rate for both sexes combined was 0.44, so 0.56 recruit per adult was required to enter the adult population on 1 September to maintain a constant population size. Assuming an even sex ratio, the required number of recruits would be 1.12 in year 't' per female seen in brood counts the previous year 't-1'. Winter (September-February) juvenile survival was 0.18, and juveniles were assumed adult on 1 March. Hence, taking these mean values for the study period as a whole, the number of juveniles on 1 September required to produce 1.12 recruits was $1.12/(0.18 \times 0.66) = 9.4$. Even if one used an annual adult survival of 0.84, the highest in the literature cited, then 2.0 juveniles would be required on 1 September, which is twice as much as found in our study.

Accordingly, without immigration, the observed reduction in spring black grouse abundance was to be expected, given both the high rates of mortality and the low rates of breeding success recorded. This pattern in black grouse was consistent with an equally dramatic decrease in red grouse in the same study area, again associated with years of low breeding success. This situation, however, contrasted that at Pale Moor, a moor of similar habitat composition and quality some 6-8 km away, but where foxes and crows were controlled to increase red grouse numbers for sport shooting between 1996 and 2000. At Pale Moor, in those years, black grouse bred well, averaging 3.6 chicks per female, and numbers of both grouse species increased (Game Conservancy Trust 2001). Our limited data on dispersal distances, backed up by those of Warren & Baines (2002), clearly show that Pale Moor could act as a source population, with juvenile females recruiting from there into Vyrnwy. However, when red grouse management ceased on Pale Moor in 2000, the abundance and breeding success of black grouse abruptly declined, thus reducing the likelihood of continued recruitment into Vyrnwy from this source.

Low survival of juvenile birds, largely due to predation by raptors, and poor reproduction appear to have caused the observed decrease in black grouse at Vyrnwy. Since their full legal protection in the United Kingdom in 1954, goshawk and peregrine, the principal raptor predators of black grouse in this study, have significantly increased in abundance. The goshawk, since its introduction in the early 1960s (Marquis 1981), has increased by approximately 16% per annum to 400-450 pairs in the UK (Stone et al. 1997), whilst the peregrine population is at 145% of its pre-1940 level following recovery from the effects of organo-chloride insecticides in the 1950s (Crick & Ratcliffe 1995). Increases of this magnitude, together with overgrazing by sheep reducing heather habitat quality (Fuller & Gough 1999) and afforestation reducing habitat extent (Robertson et al. 2001), have probably resulted in increased raptor predation on grouse (e.g. Redpath & Thirgood 1999).

Notably, however, the general pattern of black grouse decline in Wales over the last 20 years (Grove et al. 1988, Williams 1996) has recently been reversed at six sites (Lindley et al. 2003). At these sites, investment provided by European funding for habitat management has been associated with either stabilisation of numbers, or at one site where habitat management has been combined with marked increases in predator control to supply gamebirds for shooting, a substantial increase in lekking males. Given the apparent importance of predation by raptors on black grouse at Vyrnwy, and on gamebirds generally elsewhere (Valkama et al. 2005), controlled experiments are needed to evaluate effects of predator control and habitat management on vital rates.

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