Nest site characteristics and nest success in red grouse Lagopus lagopus scoticus

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We assessed the influence of habitat characteristics on nest site selection and nest success of red grouse *Lagopus lagopus scoticus* in three populations on managed moorland in Scotland during 1998-1999. We measured habitat characteristics at the nests of 148 radio-tagged female grouse and compared them with similar measurements taken at fixed and random points within their home range. Red grouse nested in vegetation that was significantly taller and denser, and with greater canopy cover, than points adjacent to nests or to random points. They nested more in mature heather and less in grass-dominated vegetation than would be expected by chance. Red grouse nest success was high with 77% initial success rising to a minimum of 80% success once re-nesting had occurred. Nest success was weakly related to vegetation height in 1998, but no similar relationship was found in 1999. We suggest that the high nest success of red grouse and the relatively small influence of habitat characteristics on the outcome of nesting attempts is due to predator control on managed grouse moors in Scotland.

Key words: habitat characteristics, Lagopus lagopus scoticus, nesting success, nest sites, predator control, red grouse

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Many birds suffer high rates of nest loss, and ground-nesting species may be at greater risk than others since they are exposed to a wider range of predators (Ricklefs 1969, Martin 1995, Newton 1998). Studies on a variety of ground-nesting birds have shown that the vegetation immediately surrounding nests can differ from a random selection of vegetation and that vegetation attributes can influence nesting success, e.g. in mallard *Anas platyrhynchos* (Greenwood, Sargeant, Johnson, Cowardine & Schaffer 1995), lesser snow goose *Anser caerulescens* (Jackson, Hik & Rockwell 1988), greater prairie chicken *Tympanuchus cupido* (McKee, Ryan &

Mechlin 1998), lesser prairie chicken *Tympanuchus pallidicinctus* (Riley, Davis, Ortiz & Wisdom 1992), sage grouse *Centrocercus urophasianus* (Gregg, Crawford, Drut & DeLong 1994), northern bobwhite *Colinus virginianus* (Taylor, Church & Rusch 1999), and grey partridge *Perdix perdix* (Rands 1988). Nesting cover may be important in reducing the risk of nest detection by predators and, in addition, may shelter eggs from either chilling or overheating. The relative importance of nesting cover in reducing predation may depend on the type of predators that are present. Mammalian predators such as red fox *Vulpes vulpes* and stoat *Mustela erminea* rely mainly on olfactory cues whereas avian predators such as carrion crows *Corvus corone* use visual cues (Bergerud & Gratson 1988). There may also be complex fitness trade-offs involved in nest site selection. For example, dense cover may reduce the chances of incubating white-tailed ptarmigan *Lagopus lecurus* being detected by predators, but it may also hinder their attempts to escape if they are detected (Wiebe & Martin 1998). The presence of linear features such as tracks and fences or an interface with less densely structured vegetation may afford birds ease of access to a nest site. However, these same linear features may be used by predators thus increasing the risk of nest detection.

Red grouse *Lagopus lagopus scoticus* are medium-sized (400-600 g) gamebirds that inhabit moorland dominated by heather *Calluna vulgaris* in northern Britain. Grouse populations are maintained at high densities for shooting by intensive habitat management and predation control (Hudson 1992, Smith, Redpath, Campbell & Thirgood 2001). Despite 50 years' intensive research on red grouse there is little published information on nest site selection and its effect on nesting success. Jenkins, Watson & Millar (1963) noted that grouse nested in heather that was taller than expected by chance and that most nests tended to be overhung with vegetation but they did not relate this to nest success or predation rates. Picozzi (1975) found that dummy grouse eggs placed in open nest sites were more likely to be located by corvids than dummy eggs placed in closed sites. Corvid predation on dummy eggs was higher in a year when corvids were not killed compared to the following year when corvids were killed. The intensive predator control practised on grouse moors may reduce predator numbers and, as a result, nest failure and nesting habitat may be of less importance than in natural systems. A further reason for the reduced importance of nest failure in red grouse population dynamics is that initial nest failure may result in re-nesting, although there may be complex trade-offs involving the reduced survival of re-nesting females or chicks from second clutches. Bergerud (1970) reported that nest success in willow ptarmigan *Lagopus lagopus* rose from 75 to 91% once re-nesting had occurred whilst Jenkins et al. (1963) recorded re-nesting in red grouse but did not quantify its occurrence or importance in grouse population dynamics. In this paper we first assess the habitat characteristics of red grouse nests on managed grouse moors and determine whether grouse select specific nesting habitat. We then investigate the relationship between the nest habitat and nest success in red grouse.

Methods

Study areas

Our study was conducted during 1998-1999 on two grouse moors: Langholm in southern Scotland and Crubenmore in northern Scotland. A third moor, Ralia, adjacent to Crubenmore, was studied in 1999. Descriptions of these moors are given by Hudson, Newborn & Robertson (1997) and Thirgood, Redpath, Rothery & Aebischer (2000). Mammalian and avian predators were killed by gamekeepers on all moors. Predator bags for a 100 km^2 encompassing Langholm and the surrounding farmland and forest during 1980-1996 averaged 150 foxes, 25 stoats and 200 crows per year (Redpath & Thirgood 1997). Comparable data for Crubenmore and Ralia were not available, but in 1999 a total of four foxes, 72 stoats and 40 crows were killed on a 30 km^2 area encompassing the two moors.

Nest and habitat data

A total of 148 female grouse were caught in March 1998 and 1999 and fitted with 15-g necklace radio-tags. Thirgood, Redpath, Hudson, Hurley & Aebischer (1995) found no significant effect of these radio-tags on survival or breeding success. Of the females from Crubenmore and Ralia, 20 were used in clutch manipulations in 1999 and were excluded from analysis of nest success, but as nest selection occurred prior to intervention these birds were included in the nest selection analysis. Data were collected from 86 nests in 1998 and 71 nests in 1999, and more nests were located on Crubenmore (74) and Langholm (66) than on Ralia (17). All tagged grouse were located every second day prior to nesting, and later visits were made to determine clutch size and hatching success. A successful nest was defined as one in which at least one egg hatched indicated by the condition of the empty shells or by the presence of chicks with the female, whilst unsuccessful nests were indicated by a deserted clutch or a missing clutch during the incubation period.

Habitat measurements were taken by the same observer (SC) when nest success had been established. The dominant vegetation type was recorded at the species level for more common species with some less common species being grouped. These data were subsequently rationalised into five dominant vegetation categories: grasses and sedges, *Erica tetralix*, mature heather, rank heather and 'other species'. Vegetation height was measured within 10 cm of the nest centre by recording the maximum height of the vegetation touching a cane marked in 1-cm intervals. Vegetation density between ground level and 40 cm was measured using a stick marked with 1-cm bands placed vertically in the centre of the nest. The proportion of bands obscured by vegetation when viewed from the four cardinal points from a distance and height of 1 m was recorded. Canopy cover was estimated using an identically marked 20-cm stick that was placed across the nest at ground level and the proportion of bands obscured by vegetation recorded when viewed from 1-m height. The distance in metres to the nearest habitat edge or linear feature (fence or ditch) was recorded. These measurements were repeated at four points located 4 m from the nest in random directions, and again at four points at a random distance between 5 and 32 m from the nest in a random direction. The 32-m distance is 50% of the radius of a typical grouse home range calculated using the bivariate normal ellipse method from radio-tracking data collected at Crubenmore during 1997-1998 (A. Smith, unpubl. data). The use of this distance ensured that sampling was random within the grouse home range.

Statistical analysis

Differences between habitat characteristics at nests and at 4-m and random sites were analysed using ANOVA, paired t-tests and logistic regression. The mean of the four samples taken at each 4-m and random site was used in all analyses. All proportional data underwent angular transformation prior to analysis. Habitat data were initially tested for year and site effects on the difference between the nest and the 4-m and random points using ANOVA with a Bonferroni correction where P = 0.0125 thus removing the need to put interaction terms into the other analyses. Habitat data from the 4-m and random samples could not be considered independent of the nest habitat, therefore paired t-tests were conducted for each variable on the differences between nest and 4-m samples and nest and random samples, respectively. Logistic regression with forward stepwise entry (P = 0.05 to enter) was used to test the importance of the habitat variables in predicting two binary variables (nest-4 m and nest-random) each coded nest or non-nest. The lack of independence of the habitat data collected at nests and at 4-m and random sites was addressed by forcing a categorical coding variable identifying the pairs of data for nest-4 m and nest-random into each regression model at the first step. Wilcoxon rank sum tests were used to test for differences in the distribution of nests and 4-m and random sites into grass-dominated and heather-dominated habitat. The effect of habitat characteristics on nesting success was initially tested by comparing the habitat variables of successful and unsuccessful nests by t-test with data transformation as described above. Logistic regression with forward stepwise entry (P = 0.05 to enter) was then used to predict nest success as a binary variable from the habitat variables, and the categorical variables moor and year were forced into the model. All statistical analyses were conducted in SYSTAT 7.0.

Results

Nest habitat

There was no significant effect of site and year on the habitat characteristics measured at nests and at the 4-m and random points; therefore data were pooled for further analysis ($F_{4,152} > 1.77$, $P > 0.14$). Vegetation height, density and canopy cover were significantly greater at nest sites than at the 4-m and random points (Table 1). There were no differences in the distance to habitat edge between nest sites and the 4-m and random points (see Table 1). Logistic regression with forward stepwise entry found vegetation height to be the only significant

Table 1. Habitat characteristics of red grouse nests and habitat 4 m from the nest and at random points around the nest. Values given are arithmetic means and standard deviations (in parentheses). T-test values with degrees of freedom are given for differences between the nest and 4-m points and the nest and random points, respectively.

	Nest	4 m			Random		
	Mean (SD)	Mean (SD)	T_{156}	P	Mean (SD)	T_{156}	P
Height (cm)	38.7 (7.9)	25.0 (8.3)	21.08	<0.001	23.3 (7.5)	24.48	<0.001
Density (%)	40.7 (11.4)	36.1 (8.9)	4.65	<0.001	35.2 (7.1)	5.79	<0.001
Cover (%)	69.1 (15.5)	55.6 (12.8)	8.84	<0.001	55.6 (13.1)	9.57	<0.001
Edge (m)	14.0 (15.1)	14.1 (15.0)	-0.38	0.7	14.5 (13.3)	-0.98	0.33

Table 2. Logistic regression models of habitat variables predicting the binary variables nest-4 m and nest-random. The standard error of the slope estimate is given in parentheses. The model likelihood ratio statistic is chi-squared to test the hypothesis that the coefficients = 0. Rho^2 is analogous to r^2 in linear regression.

Dependant variable	Explanatory variable	Slope estimate	Model χ^2	df	P	Rho^2
Nest - 4 m	Height	0.90 (0.13)	373.6	156	<0.001	0.86
Nest - random	Height	1.20 (0.25)	396.4	156	<0.001	0.92

predictor of nest occurrence when compared with data collected at 4-m and random points (Table 2). Only 3% of nests occurred in grass-dominated areas as opposed to 18% of 4-m and 21% of random points. There were significantly fewer nests found in grass-dominated sites than would be expected by chance (Wilcoxon rank-sum: nest vs 4 m: Z = 6.30, N = 147, P < 0.001; nest vs random: Z = 7.49, N = 147, P < 0.001; Fig.1).

Nest success

Initial nest success was high in all sites and years (1998: 78% successful (N = 86); 1999: 77% successful (N = 62)). There were no differences in initial nest success between study sites in either year (1998: $\chi^2 = 0.20$, df = 1, P > 0.5; 1999: $\chi^2 = 1.45$, df = 2, P > 0.5). In 1998 females were not monitored after the first nesting attempt and therefore overall nest success was unknown. During 1999 the breeding attempts of all females were monitored at Langholm until August to quantify the extent of re-nesting. Second nesting attempts were made by 9/29 females and one female re-nested twice. At Crubenmore and Ralia, re-nesting did not occur during 1999 as all nest failures were due to adult female mortality. When second clutches at Langholm were included a minimum of 80% of female grouse nested successfully during 1999.

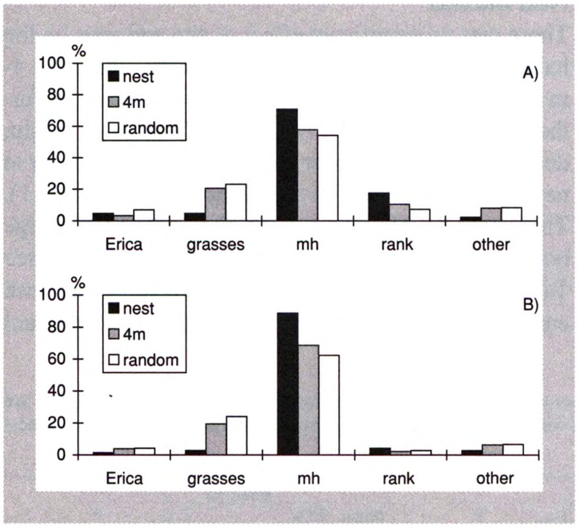

Figure 1. Percentage of grouse nests, 4-m points and random points occurring in the five different vegetation categories in 1998 (A) and 1999 (B). The vegetation categories included were Erica = *Erica cineria*; grasses; mh = mature heather; rank = rank heather; other = 'other species'.

Nest habitat and nest success

Vegetation height was significantly greater at successful nests than at unsuccessful nests in 1998 but not in 1999 (1998: t = 2.49, df = 84, P = 0.02; 1999: t = -0.72, df = 60, P = 0.48; Fig. 2). The other habitat variables did not differ significantly between successful and unsuccessful nests in either year. Logistic regression was used to predict nest success from the habitat variables with the categorical variables moor and year forced to enter the model. No habitat variables entered the model as significant predictors of nesting success (Model likelihood ratio (LR): 1.29, df = 3, P = 0.73).

Discussion

The first important result of our study was that despite the apparently homogenous structure of heather moorland, female red grouse selected nest sites in vegetation that was taller, denser and with more cover than at random points within their home range. Vegetation

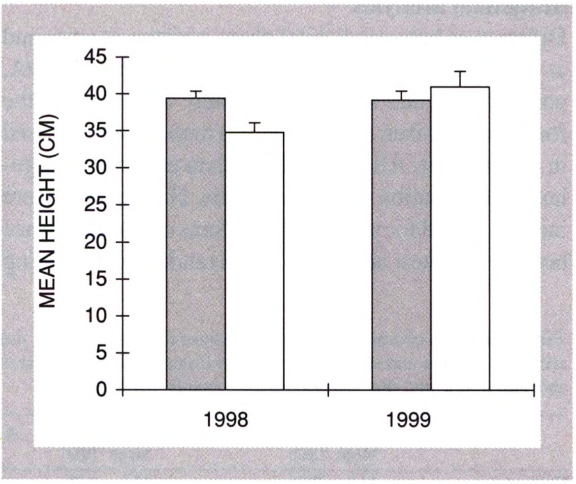

Figure 2. Mean vegetation height (in cm) of successful (▨) and unsuccessful (☐) grouse nests on the three moors during 1998 and 1999. Error bars represent standard error of mean.

height averaged 39 cm at nests compared to 25 cm at random points and canopy cover averaged 69% at nests compared to 56% at random points. Grouse nests occurred more often in mature heather and less often in grass than expected by chance, as had earlier been noted by Jenkins et al. (1963). The height of vegetation at nests and at random points was greater in our study than that recorded in northeastern Scotland in the early 1960s by Jenkins et al. (39 and 25 cm vs 27 and 17 cm). It is possible that this difference reflects a reduction in the frequency of muirburn over this time resulting in longer vegetation (Hester & Sydes 1992, Thompson, MacDonald, Marsden & Galbraith 1995). While it is clear that grouse select nest sites that exhibit certain structural criteria, our results suggest that only height can explain an appreciable amount of variation between nests and random points. Other factors that may be important in determining nest site location may include the wetness of the ground, topography and disturbance from human activity or livestock. It is also possible that the favoured nesting habitat occurs frequently enough on managed moorland for it to have little effect in determining grouse density.

The second important result was that nest success of red grouse in our study was high with 77% of initial nesting attempts succeeding and re-nesting increasing this to a minimum of 80%. The proportion of successful nests in red grouse is high in comparison to other wild gamebirds (e.g. Buhnerkempe, Edwards, Vance & Westemeier 1984, Storaas & Wegge 1987, Riley et al. 1992, Gregg et al. 1994, Lutz, Lawrence & Nova 1994, McKee et al. 1998, Taylor et al. 1999). Studies on willow ptarmigan in Norway and Canada have found an initial nesting success of 20-30% (Myrberget 1988, Hannon, Martin & Shieck 1988, O'Reilly & Hannon 1989) and Wiebe & Martin (1998) found that 67% of nesting attempts in white-tailed ptarmigan in Colorado failed due to predation. It is notable that one of the few studies to report high nesting success (initial success of 75% rising to 91% with re-nesting) is of willow ptarmigan on Newfoundland which also shows similarities to Scotland in having an impoverished predator fauna when compared to continental areas (Bergerud 1970). We did not have estimates of mammalian predator abundance on our study sites but it appears likely that the intense predator control conducted there and on other grouse moors in the UK reduced the abundance of avian and mammalian predators and thus reduced nest predation rates (Reynolds & Tapper 1996). Experimental control of nest predators has a large effect on nesting success in other gamebirds and wildfowl (Balser & Nelson 1968, Chesness, Nelson & Longley 1968, Duebbert & Lokemoen 1974, Marcström, Engren & Kenward 1988, Tapper, Potts & Brockless 1996).

Given the low rates of nest predation observed in our study it is perhaps not surprising that we failed to find a strong relationship between the vegetation characteristics of red grouse nests and their subsequent success. There was a weak relationship between vegetation height and nesting success in one year, and the habitat variables could not explain the difference between successful and unsuccessful red grouse nests. This finding contrasts markedly with studies on other gamebirds and wildfowl that have consistently found strong effects of vegetation height and density on nest success (Keppie & Herzog 1978, Hines & Mitchell 1983, Riley et al. 1992, Gregg et al. 1994, McKee et al. 1998, Taylor et al. 1999). As described above, the most plausible explanation for this result is the relatively low rate of nest predation that occurs in red grouse populations due to intensive predator control. Most of the other studies have taken place on the European or American continents where there is a greater diversity and density of nest predators and little or no predator control (Reynolds & Tapper 1996). The most likely role that habitat characteristics play in influencing nest success is to reduce detection by predators, and in situations of low predator density the effects of habitat may be diluted. If control of nest predators were reduced on grouse moors it is quite possible that nest habitat would have a greater influence on nest success. There is clearly scope to test this hypothesis through comparative studies and field experiments.

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