

Capercaillie breeding success in relation to forest habitat and predator abundance

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Summary

1. The capercaillie *Tetrao urogallus* is widely valued as a game bird and an indicator of forest ecosystem quality. In Scotland, its numbers have declined since the 1970s, due primarily to poor breeding success. We investigated whether differences in breeding success among forests are related to predator abundance or to aspects of forest structure, with a view to identifying beneficial management practices.
2. Capercaillie breeding success was estimated in 7–14 forest areas in Scotland each year during 1991–2001. Forest habitat, including ground vegetation, and indices of predator abundance were assessed in each of the 14 areas in 1995.
3. Capercaillie breeding success increased with increasing bilberry *Vaccinium myrtillus* ground cover, but did not improve further above 15–20% cover.
4. The main predators were carrion crow *Corvus corone*, fox *Vulpes vulpes* and raptors. Indices of their abundance were confounded such that their respective effects on capercaillie breeding success could not readily be distinguished. However, capercaillie breeding success was negatively related to a principal component score that represented the combined abundance of crows, foxes and, to a lesser extent, raptors.
5. A management trial in one forest showed that capercaillie bred better when most crows and some foxes were killed than when they were not.
6. An index of pine marten abundance was related neither to the other predator indices nor to capercaillie breeding success.
7. *Synthesis and applications.* Capercaillie reared more young in forests with more bilberry and fewer predators. Management to improve the breeding success of capercaillie should aim for at least 15–20% bilberry ground cover, and legal control of crows and foxes.

Key-words: bilberry, forest management, ground vegetation, predator killing.

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Introduction

The capercaillie *Tetrao urogallus* L. was re-established in Scotland in 1837–38 (Lever 1977). Several releases, associated with widespread reforestation and extensive killing of potential predators by gamekeepers, resulted in rapid recolonization of much of its former range. However, capercaillie in Scotland are again in severe decline and the possibility of extinction returns (Moss 2001). This latest decline began in the mid-1970s (Tapper 1992; Moss 1993) and forms part of a wider decline throughout much of the species' range (Cramp

& Simmons 1980; de Franceschi 1994; Menoni 1994; Beshkarev *et al.* 1995; Storch 2001). Population estimates from line transects surveyed in the winters of 1992–94 suggested that 2200 [95% confidence limit (CL) 1500–3200] birds remained in Scotland, and by 1998–99, using the same method, the population was estimated to have fallen to 1100 birds (95% CL 500–2000; Wilkinson *et al.* 2002).

The main demographic cause of the decline has been low breeding success (Moss *et al.* 2000) associated with climate change (Moss, Oswald & Baines 2001) and exacerbated by deaths of full-grown birds flying into forest fences (Catt *et al.* 1994; Baines & Summers 1997; Moss 2001). Other factors that might have contributed to the decline include habitat destruction through changed silvicultural practices, reductions in the quality

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of chick-rearing habitat through overbrowsing (Baines, Sage & Baines 1994) or underbrowsing of dwarf shrubs by red deer *Cervus elaphus*, increased predation and widespread pollution (Moss 1994). In this study, we first established that there were consistent differences in breeding success between different forests over several years. We then investigated whether differences in breeding success between forests were related to habitat structure or to the species and abundance of predators.

Methods

STUDY AREAS

The study was carried out in 14 areas of forest in Scotland (Fig. 1), including at least one within each of the main centres of capercaillie population (parts of Perthshire, Deeside, Strathspey and Morayshire; Catt *et al.* 1998). Choice of study areas ('forests') was constrained by the requirement to find a sample of 10 hens in each forest each year, so providing a reasonably reliable estimate of breeding success (Moss 1986). This was impracticable in many forests due to the generally low numbers of birds present, hence counts were made in forests where initial questionnaire surveys indicated moderate or high densities of capercaillie (Catt *et al.* 1998). Even so, due to the decline observed during the study, 10 or more hens were found in only six of the chosen study areas in 1991, 1992 and 1993, in four in 1994, 1995 and 2000, in two in 1996 and 1997 and in only one in 1998, 1999 and 2001.

We categorized each study area, according to the predominant structure and species composition of its

trees and ground vegetation, into one of three types: (i) open-canopied forest with well-developed ericaceous ground layers typical of native pinewoods dominated by Scots pine *Pinus sylvestris*; (ii) mature Scots pine plantation with canopy sufficiently open for the development of ericaceous ground layer shrubs; and (iii) mixed species plantations, often of spruce *Picea* spp. and larch *Larix decidua*, with closed canopy and few ericaceous shrubs, often having clear-felled and restocked areas (Table 1).

COUNTS OF HENS AND CHICKS

Counts of hens and chicks were made using trained dogs to locate birds between mid-July and late August. We use 'hen' to include all full-grown hens but not female chicks. Some hens do not breed until their second or third year (Borchtchevski 1993; Moss *et al.* 2000) but we did not distinguish hens that had lost eggs or chicks from hens that had not attempted to breed. The mean area searched per forest was 3.0 km² (range 0.8–6.0 km²), and the total area searched over all forests each year ranged from 27 km² to 40 km². The areas of forest searched were not always representative of the forest as a whole, being biased towards parts where capercaillie were known to occur and biased against thicket stage plantations and wind-blow, where continued observation of the dogs proved impracticable. Three measurements of reproductive success were made in each area: the proportion of hens with at least one chick was 'broods per hen', the number of chicks per hen that had at least one chick was 'brood size', and the overall measure of breeding success was the number of 'chicks per hen'.

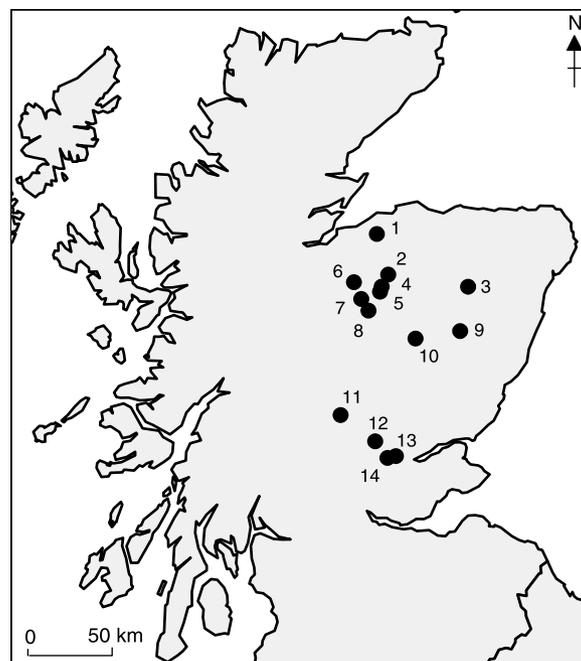


Fig. 1. Approximate locations of the forest areas searched for capercaillie broods. 1, Findhorn; 2, Grantown; 3, Alford; 4, Nethybridge; 5, Abernethy; 6, Carrbridge; 7, Aviemore; 8, Cairngorm; 9, Aboyne; 10, Ballater; 11, Aberfeldy; 12, Crieff; 13, Perth; 14, Auchterarder.

Table 1. Location and characteristics of the 14 forest study areas. Forest type: 1, open canopy, as in native pinewoods; 2, mature Scots pine plantation, canopy sufficiently open for some dwarf shrubs; 3, mixed species plantation with closed canopy, often with some clear-felled areas and restocked ground

Forest area	Region	Forest type	Count years	Count area (km ²)
Abernethy	Strathspey	1	1991–2001	5.5
Ballater	Deeside	1	1991–93, 2001	3.9–5.1
Grantown	Strathspey	1	1991–93	3.0–4.0
Aboyne	Deeside	1	1991–2001	2.7–3.2
Aviemore	Strathspey	1	1992–2001	1.4
Alford	Donside	1	1991–2001	0.8
Cairngorm	Strathspey	1	1991–2001	6.0
Nethybridge	Strathspey	2	1991–2001	1.0–2.0
Aberfeldy	Perthshire	2	1991–2001	2.3
Perth	Perthshire	2	1991–2001	4.0
Findhorn	Morayshire	2	1991–93, 2001	2.5
Auchterarder	Perthshire	3	1991–2001	3.0
Carrbridge	Strathspey	3	1992–2001	0.5
Crieff	Perthshire	3	1991–1993	0.7–2.0

FOREST STRUCTURE AND GROUND VEGETATION COMPOSITION

In April–July 1995, measurements of forest structure and ground vegetation were made at 20 plots evenly spread within each searched area, at the intersections of a 300-, 400- or 500-m grid, the size of the grid depending on the size of the area. Walking a random distance of ≤ 50 m in a random compass direction randomized the position of each plot.

The plot was sufficiently large to include 10 main canopy-forming trees. Four quadrats of size 4 m² were placed at random, one within each quadrant of the plot. Within each quadrat the separate vegetation layers (moss, brash, dwarf shrubs and scrub with young trees) were identified and the percentage species composition of each layer below 2 m in height was estimated by eye to the nearest 10%. The height of each vegetation layer was measured at five places evenly spaced within the quadrat. Using a key from Picozzi, Catt & Moss (1992), each plot was given a box number, which classified the stand according to its structural characteristics. Each box has two scores derived from a principal component analysis of 14 forest habitat variables. A high GRANNY score, typically good for capercaillie (Picozzi, Catt & Moss 1992), is typified by well-spaced ‘granny’ trees (Steven & Carlisle 1959), with an open canopy and a well-developed ericaceous shrub layer. A high PLANTATION score, often poor for capercaillie, is characterized by tall, closely spaced mature plantation trees, especially spruces, with little ground vegetation.

PREDATOR ABUNDANCE

Little is documented about predators of capercaillie in Scotland, but both fox *Vulpes vulpes* and pine marten *Martes martes* are known predators of capercaillie elsewhere (Marcstrom, Kenward & Engren 1988; Schroth 1991; Storch 2001) and our experience in Scotland

(D. Baines, R. Moss & D. Dugan, unpublished data) confirms this. Within each forest area, approximately 10 km of tracks were searched for mammal scats. Where practicable, vehicle tracks were used rather than footpaths. The route formed a circuit that passed through representative parts of the area that was searched for capercaillie hens and chicks. Scats were classified as ‘fox’, ‘pine marten’ and ‘others’.

The tracks were walked five times in spring 1995, initially in April to count and remove all scats, twice in May and twice in June. The number of scats found per kilometre on the initial clearance round in April in each forest (y) was correlated with the total number of scats (x) found per kilometre on the four subsequent rounds in May and June ($y = 0.71x + 5.15$, $r_{12} = 0.88$, $P < 0.001$). In six of the 14 forests scats were again counted in spring 1997. No significant differences were found between years ($\chi^2_1 = 0.02$, $P = 0.90$), showing that mammalian scat abundance did not change significantly within these forests between 1995 and 1997. In short, scat-based indices showed consistent differences between forests and we assumed that they reflected predator abundance.

A minimum of 5 km of the same circuit was also used as a transect along which raptors and crows *Corvus corone*, potential avian predators of capercaillie eggs and chicks (Cramp & Simmons 1980; Storch 2001), were counted. Transects were walked just after dawn, twice monthly in May and June, and sightings and calls of crows and raptors were recorded.

Some predators are routinely killed by gamekeepers. Hence the number of gamekeepers and deer-stalkers actively involved in killing predators, on either a full-time (one person) or part-time (half a person) basis, was expressed as a density (gamekeepers per 100 km²) for the estate or forest block as a whole, not for just the area of forest studied. In three forests there was either very little or no organized predator control and gamekeeper density was entered as zero. Data on the effort made by individual keepers and on the range and

number of each species killed on each estate were not collated.

DATA ANALYSIS

We analysed the three measures of capercaillie breeding success in two stages. First, we checked whether breeding success differed consistently between forests over years. Secondly, we investigated whether aspects of habitat or indices of predator abundance explained differences in breeding success between forests.

To assess the effects of explanatory variables on breeding success, we used generalized linear models (SAS Institute 1996; GENMOD procedure, release 8.02) in preliminary exploration of the data and generalized linear mixed models (SAS GLIMMIX macro; Littell *et al.* 1996) to enact the analyses presented here. The main difference between the two approaches was that the category year had to be entered as a fixed effect in generalized linear models, but could be treated as a random effect in generalized linear mixed models, so increasing the generality of the conclusions. We investigated variations in chicks per hen by setting the number of chicks seen in each forest each year as the dependent variable and forest descriptors as explanatory variables, in Poisson regressions (Poisson distribution, log link, adjusted for overdispersion; see Appendix 1) with the logarithm of the number of hens as an offset. We allowed for the fact that counts were repeated annually at the same forests by defining forest as a repeated measure. Brood size was analysed in the same way but excluding hens with no chicks and setting the logarithm of the number of broods as the offset. Broods per hen was modelled using logistic regression (binomial distribution, logit link), categorizing hens as successful if they had at least one chick, or as unsuccessful.

The statistical significance of the results was assessed in two ways. Sequential (SAS type 1) analyses estimated the significance of each of the fixed effects as they were entered one by one into the model. Partial (SAS type 3) analyses estimated the significance of each effect, after controlling for all other effects, giving the same result as if each effect was entered last in a sequential analysis. Partial analyses were appropriate for models with main effects only, not for models that included interactions between explanatory variables.

Ideally we should have made measurements of habitat and predator abundance throughout the study, but this was not done for financial reasons. We had planned to make these measurements in 1995 and to compare them with capercaillie data from 1995. However, again for financial reasons, we did not count capercaillie in all forests in 1995. Also, by 1995 numbers of capercaillie were generally low and in only four of the forests did we see the target of 10 hens, hence estimates of breeding success were unreliable. Therefore we increased sample size by continuing the study until 2001, used the 1995 measurements as continuous variables

that described each forest, and modelled year as a categorical effect.

The indices of predator abundance (fox scats day⁻¹ 10 km⁻¹, pine marten scats day⁻¹ 10 km⁻¹, carrion crows km⁻¹ and raptors km⁻¹, where 'day' is the number of days since the previous visit) were negatively skewed, with a few big measurements that would have disproportionately influenced the results. We therefore used the natural logarithm (+0.1) of each index, so approximately normalizing them.

At Abernethy forest, most crows and some foxes were killed in some years but not in others, as part of a management trial to discover whether the killing of these predators improved capercaillie breeding success. Full details of this trial will be given elsewhere (Summers *et al.* 2004). For present purposes we categorized data from Abernethy into years when crows and foxes were killed (1992–96 and 2000–01) or not killed (1991 and 1997–99). Data from other forests were arbitrarily categorized as 'killed' to indicate no experimental change in predator management.

There were too many habitat measurements to include them all in the results. We selected the most useful ones by plotting scatter diagrams of capercaillie breeding success against summary statistics of the measurements. These included scores from two principal component analyses (SAS Institute 1996; PRINCOMP procedure), one representing three-dimensional forest structure and one ground vegetation. The breeding success data were too sparse to give reliable estimates for each forest in each year (above) and so, for the scatter diagrams, we postdicted (predicted after the event) breeding success from a generalized linear mixed model that had forest as the sole fixed effect and year as a random effect.

The summary statistics investigated by scatter diagrams included the mean, the median and the upper and lower quartiles of each habitat measurement and principal component score. We analysed the data for simple correlations and for quadratic associations between the three measures of breeding success and each summary statistic. In the event, only mean values gave significant results.

Results

BREEDING SUCCESS: FOREST EFFECTS

The 114 capercaillie counts done between 1991 and 2001 involved 675 chicks and 816 sightings of hens, 279 of which had at least one chick, giving an average of 0.83 chicks hen⁻¹ year⁻¹ (95% CL 0.77–0.89). Annual samples of hens varied from 44 in eight forests (1998) to 121 in 14 forests (1992 and 1993).

Breeding success differed among forests. The postdicted values (Table 2) showed chicks per hen varying eightfold ($\chi^2_{13} = 30.2$, $P = 0.01$; see Appendix 1, last paragraph) and brood size threefold ($\chi^2_{13} = 32.8$, $P = 0.007$). Broods per hen varied fivefold but not significantly

Table 2. Mean breeding success of capercaillie (95% CL in parentheses) postdicted from generalized linear mixed models with forest as the sole fixed effect and year as a random effect. 'Years' is the number of years when at least one hen was found at each forest

Forest	Years	Chicks per hen	Broods per hen	Brood size
Abernethy	11	0.8 (0.5–1.2)	0.29 (0.18–0.42)	2.8 (2.4–3.4)
Ballater	4	1.2 (0.6–2.3)	0.54 (0.28–0.78)	2.4 (1.8–3.3)
Grantown	3	0.6 (0.1–3.4)	0.22 (0.02–0.77)	2.9 (1.3–6.7)
Aboyne	11	0.5 (0.3–0.9)	0.28 (0.17–0.43)	2.0 (1.5–2.5)
Aviemore	9	1.1 (0.5–2.4)	0.38 (0.15–0.67)	3.0 (2.1–4.4)
Alford	10	0.3 (0.1–0.9)	0.17 (0.06–0.41)	1.5 (0.8–2.7)
Cairngorm	11	1.1 (0.7–1.9)	0.42 (0.24–0.61)	2.8 (2.2–3.5)
Nethybridge	11	0.9 (0.6–1.5)	0.46 (0.31–0.62)	2.1 (1.7–2.6)
Aberfeldy	11	0.4 (0.2–0.8)	0.24 (0.12–0.44)	1.5 (1.0–2.2)
Perth	10	0.6 (0.3–1.2)	0.30 (0.15–0.49)	2.2 (1.6–3.0)
Findhorn	4	1.0 (0.5–2.2)	0.35 (0.15–0.63)	3.1 (2.2–4.4)
Auchterarder	8	0.2 (0.0–0.8)	0.11 (0.03–0.35)	1.6 (0.8–3.3)
Carrbridge	8	1.7 (1.0–3.1)	0.56 (0.30–0.79)	3.3 (2.5–4.3)
Crieff	3	0.2 (0.0–1.8)	0.17 (0.03–0.58)	1.0 (0.3–3.2)

Table 3. Indices of predator abundance from forest transects walked between April and June 1995, and gamekeeper densities (keepers 100 km⁻²), in the 14 forest areas where capercaillie brood counts were done. Values for foxes and pine martens are mean scats 10 km⁻¹ day⁻¹ 10³ and exclude the clearance round. Those for crows and raptors are mean observations 10 km⁻¹ visit⁻¹

Forest	Fox	Pine marten	Crow	Raptor*	Keepers
Abernethy	9.3	7.0	0.9	0	2.0
Ballater	5.1	0	0.4	0.3	3.5
Grantown	0	0	2.5	2.8	3.9
Aboyne	4.9	0	0.7	0.2	3.4
Aviemore	11.1	25.9	0	0.5	3.9
Alford	19.8	0	1.3	0.2	5.0
Cairngorm	8.1	0	1.3	0.2	2.0
Nethybridge	13.4	4.5	1.2	0.7	5.6
Aberfeldy	9.0	47.8	0.9	0.4	0
Perth	1.8	3.5	0.8	2.1	5.3
Findhorn	8.7	36.0	1.4	0.2	0.7
Auchterarder	60.5	1.8	5.4	1.1	0
Carrbridge	11.0	26.5	0.3	0	3.9
Crieff	125.1	0	5.7	0.9	0

*Raptor sightings comprised 31 buzzard, seven sparrowhawk, two golden eagle *Aquila chrysaetos*, two kestrel *Falco tinnunculus* and one goshawk *Accipiter gentilis*.

($\chi^2_{13} = 20.3$, $P = 0.11$) until the predator management trial at Abernethy was included as a second explanatory category (partial $\chi^2_{13} = 23.9$, $P = 0.049$).

GAMEKEEPERS AND PREDATORS

Indices of predator abundance varied considerably among forests (Table 3). We expected predators to be less abundant where gamekeeper densities were higher, but the only correlation that approached significance was with the fox index (Table 4), while the correlation between keepers and martens was positive.

We investigated whether variations in the three measures of breeding success among forests could be explained by generalized linear mixed models with explanatory variables in the following order: the density of keepers, the four indices of predator abundance, the years (1991 and 1997–99) when foxes and crows were not killed during the management trial at Abernethy (categorical), and forest habitat structure (see below).

Table 4. Correlations between predator indices ($\log_e(\text{index} + 0.1)$) and keeper densities (keepers 100 km⁻²). Simple correlations, top right; partial correlations (keeping all other variables constant), bottom left. Partial correlations between predator indices, excluding keepers, were almost identical to those shown

Partial	Simple				
	Crow	Fox	Raptor	Marten	Keepers
Crow		0.77**	0.42	-0.37	-0.35
Fox	0.76**		0.12	-0.22	-0.48
Raptor	0.46	-0.32		-0.33	-0.07
Marten	-0.20	0.08	-0.18		0.20
Keepers	0.06	-0.34	-0.01	0.12	

** $P < 0.01$, otherwise $P > 0.05$.

Variables that had no useful explanatory value were dropped, as follows. In the model for chicks per hen, the effect of keeper density was insignificant (sequential $\chi^2_1 = 0.31$, $P = 0.58$; partial $\chi^2_1 = 0.40$, $P = 0.53$) and

Table 5. Capercaillie breeding success (chicks per hen) in relation to indices of predator abundance, the predator management trial at Abernethy (two categories: years with and without predator killing) and bilberry cover (quadratic, bilberry² is bilberry cover squared). Results are from two models: 1, predator indices considered separately; 2, predator indices combined in principal component score PRED1. Significance levels from sequential and partial χ^2 tests are shown. Total deviance is for models with no explanatory variable, other deviance values for models with explanatory variables on the same line plus any above them

	Parameter estimates SE		Deviance		χ^2 (sequential)		χ^2 (partial)	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Total	–	–	559.9	559.9	–	–	–	–
Crow	–0.50 ± 0.34	–	514.9	–	8.7**	–	2.2	–
Fox	–1.61 ± 1.29	–	514.5	–	0.08	–	1.6	–
Raptor	–0.43 ± 0.29	–	507.9	–	5.4*	–	2.2	–
Marten	0.35 ± 0.70	–	508.3	–	0.20	–	0.25	–
PRED1	–	–0.47 ± 0.12	–	507.6	–	14.3***	–	15.0***
Predator trial	3.21 ± 0.93	3.21 ± 0.92	429.9	430.5	10.4**	10.3**	11.9***	12.2***
Bilberry	0.15 ± 0.06	0.15 ± 0.05	373.8	388.8	12.2***	9.4**	–	–
Bilberry ²	–0.008 ± 0.002	–0.008 ± 0.002	334.1	334.7	11.0**	14.1***	–	–

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, otherwise not significant; –, row heading not applicable to this column.

Table 6. Principal component analysis of fox, crow and raptor indices ($\log_2(\text{index} + 0.1)$) from 14 forest areas in spring 1995

	Component		
	PRED1	PRED2	PRED3
Eigenvalue	1.93	0.90	0.17
Proportion variation explained	0.64	0.30	0.06
Eigenvector			
Fox	0.62	–0.47	0.63
Crow	0.68	–0.08	–0.72
Raptor	0.39	0.88	0.28

so keeper density was dropped from subsequent models (Table 5; see Appendix 2). The resultant model (Table 5; model 1) had negative parameter estimates for fox, crow and raptor abundance. The parameter estimate for marten abundance, however, was positive and insignificant and so it was dropped from further analysis.

The crow and raptor effects were significant in the sequential analysis but not significant in the partial analysis (Table 5). Also, when entered first into the model, the fox effect approached significance in a sequential analysis ($\chi^2 = 3.71$, $P = 0.057$) but not in the partial one (Table 5). Evidently, fox, crow and raptor indices were confounded (Table 4). We investigated this problem via a principal component analysis on crow, fox and raptor indices, using principal component scores to represent their combined abundance (Table 6). Weightings (eigenvectors) in the principal component analysis for PRED1 represented a situation with many crows and foxes and some raptors (mostly buzzards *Buteo buteo* and sparrow hawks *Accipiter nisus*; Table 3), PRED2 reflected a situation with more raptors but few foxes, and PRED3 a situation with more foxes but fewer crows. PRED1 explained 64% of the variation in the data and was the only component that had a significant explanatory value, and so we use PRED1 scores as an index of predator (excluding marten) abundance in model 2 (Table 5).

PRED1 was negatively related to all three measures of breeding success (Table 5 and Fig. 2; see Appendix 2). In addition, the killing of most breeding crows and some foxes at Abernethy was associated with higher breeding success, although the effect on brood size was not significant (see Appendix 2). Mean postdictions for chicks per hen at Abernethy, from model 2 (Table 5), were 0.1 (95% CL 0.0–0.3) in years without predator control and 1.4 (1.0–1.9) in years with it.

FOREST HABITAT EFFECTS

Ericaceous species dominated the ground vegetation (cover collectively > 50%) in the seven native pinewoods (Table 7). The four mature Scots pine plantations had 25–50% ericaceous ground cover, whilst three mixed species plantations had < 25%.

In all forests, heather *Calluna vulgaris* was the most common ericaceous species, forming 10–55% of the ground vegetation. Bilberry *Vaccinium myrtillus* was subdominant to heather, forming more than 10% of the sward in 10 areas and more than 20% at Alford and Aberfeldy. In only four forests was bilberry cover < 10%: Perth, Auchterarder, Carrbridge and Crieff, the latter three sites all being mixed species plantations. Except for one forest (Auchterarder) with particularly short ground vegetation (8 cm), mean vegetation height was 15–41 cm.

Forest structure and ground vegetation differed significantly between forest types. GRANNY scores (ANOVA, $P < 0.001$), heather cover ($P < 0.001$), *Vaccinium* cover (bilberry and cowberry *Vaccinium vitis-idaea* grouped) ($P < 0.01$) and ground vegetation height ($P < 0.001$) were all higher in native pinewoods than in Scots pine plantations, which in turn had higher values than mixed species plantations. Conversely, plantation forests had significantly higher PLANTATION scores than native pinewoods ($P < 0.02$).

Preliminary scatter diagrams and analyses showed that neither the crude classification in Table 1, nor any

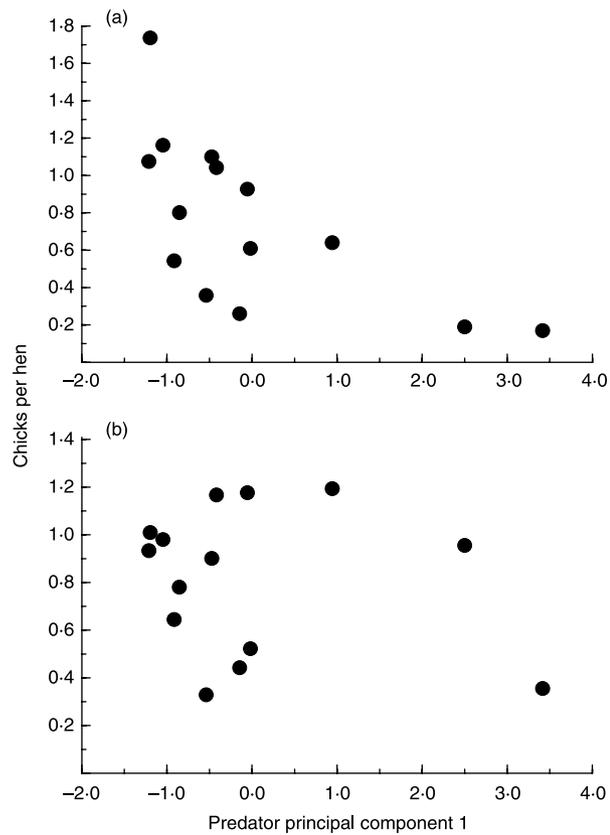


Fig. 2. Capercaillie breeding success and predator abundance in 14 forest areas. Predator abundance is represented by the principal component score PRED1, which incorporates indices of crow, fox and raptor abundance (Table 6). (a) Breeding success, postdicted from forest and year effects (Table 2). (b) A partial plot that controls for the effects of bilberry cover and the predator-killing trial at Abernethy. A partial plot that took no account of the Abernethy trial was almost identical. These illustrative plots give each forest equal weight although the number of hen sightings varied from seven (Grantown) to 175 (Abernethy).

Table 7. Forest structure and ground vegetation cover at the 14 forest areas. Values are mean \pm SE from 20 sample plots. GRANNY (GRAN) and PLANTATION (PLAN) scores are as in Picozzi, Catt & Moss (1992). High GRAN indicates a forest with a structure typical of native pinewoods, high PLAN a closed canopy plantation forest, typically of spruce. CV, *Calluna vulgaris*; VM, *Vaccinium myrtillus*; VV, *Vaccinium vitis-idaea*. The ANOVAS contrast the three forest types (Table 1)

Forest	Forest structure			Ground vegetation			Height (cm)
	Type	GRAN	PLAN	%CV	%VM	%VV	
Abernethy	1	7.6 \pm 0.3	2.4 \pm 0.1	55 \pm 4	12 \pm 3	8 \pm 2	35 \pm 3
Ballater	1	7.8 \pm 0.3	2.5 \pm 0.2	44 \pm 4	16 \pm 4	10 \pm 3	35 \pm 3
Grantown	1	6.5 \pm 0.6	3.7 \pm 0.2	29 \pm 5	11 \pm 3	13 \pm 3	28 \pm 3
Aboyne	1	7.0 \pm 0.4	2.5 \pm 0.2	44 \pm 4	20 \pm 3	6 \pm 1	41 \pm 3
Aviemore	1	6.6 \pm 0.7	2.9 \pm 0.2	26 \pm 6	17 \pm 3	15 \pm 3	21 \pm 2
Alford	1	5.5 \pm 0.4	2.6 \pm 0.2	32 \pm 6	22 \pm 2	2 \pm 1	27 \pm 2
Cairngorm	1	5.8 \pm 0.4	2.5 \pm 0.2	36 \pm 5	17 \pm 3	9 \pm 2	24 \pm 2
Nethybridge	2	4.1 \pm 0.4	3.9 \pm 0.3	25 \pm 5	13 \pm 3	11 \pm 3	23 \pm 2
Aberfeldy	2	5.0 \pm 0.5	3.2 \pm 0.4	21 \pm 5	24 \pm 5	4 \pm 1	15 \pm 2
Perth	2	6.0 \pm 0.6	3.9 \pm 0.3	24 \pm 5	2 \pm 1	0	16 \pm 2
Findhorn	2	4.9 \pm 0.6	5.0 \pm 0.4	15 \pm 5	13 \pm 5	0	17 \pm 3
Auchterarder	3	3.8 \pm 0.5	5.2 \pm 0.3	10 \pm 4	7 \pm 3	0	8 \pm 2
Carrbridge	3	2.1 \pm 0.5	3.3 \pm 0.3	10 \pm 5	8 \pm 3	3 \pm 1	16 \pm 3
Crieff	3	2.1 \pm 0.3	3.6 \pm 0.5	14 \pm 5	0	0	16 \pm 3
ANOVA: $F_{2,11}$		23.3***	6.37*	13.5***	3.80	5.38*	12.9***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

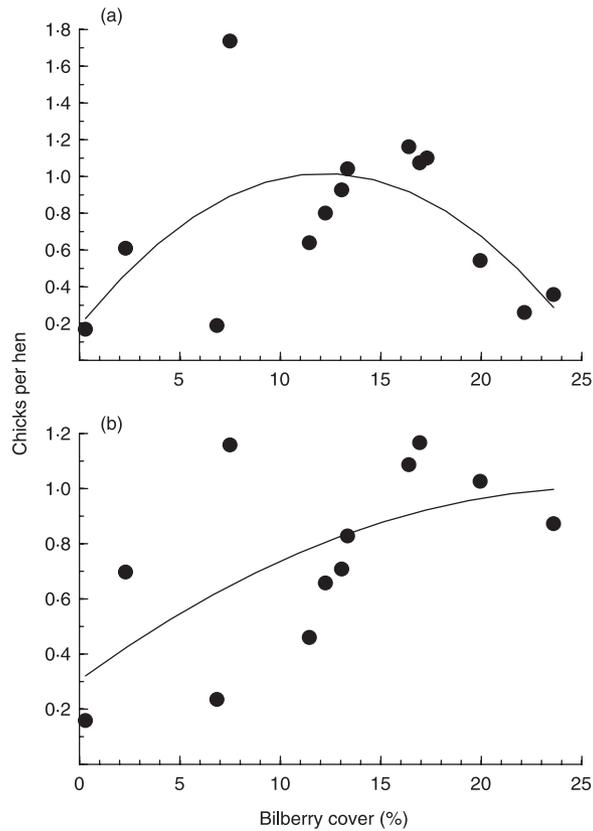


Fig. 3. Capercaillie breeding success and mean bilberry cover in 14 areas of forest. (a) Mean breeding success, postdicted from forest and year effects (Table 2). (b) A partial plot that controls for the effects of predator abundance (PRED1) and the predator-killing trial at Abernethy. A partial plot that took no account of the Abernethy trial was almost identical. The quadratic curves are fitted to the points shown, giving each equal weight although the number of hen sightings varied from seven (Grantown) to 175 (Abernethy).

other measure of forest structure, bore any significant relationship to capercaillie breeding success, except the proportion of bilberry on the ground. This, therefore, was the only habitat variable included in the generalized linear mixed models, which showed that bilberry cover formed a significant quadratic relationship with all three measures of capercaillie breeding success (Table 5; and see Appendices 1 and 2) and explained more deviance than the indices of predator abundance. A simple scatter plot (Fig. 3a) showed that breeding success at first increased with bilberry cover, apparently declining when it exceeded 15–20%; however, a partial plot (Fig. 3b) that took the effect of predators into account showed no such decline.

MODELS WITH INTERACTIONS

We investigated interactions between year and forest descriptors (PRED1, bilberry and bilberry²) with a model that resembled model 2 (Table 5) except that year was entered as a fixed effect and not as a random one. We did this twice for each measure of breeding success, entering PRED1 both before bilberry cover and after it. No interaction term was significant in sequential analyses and we therefore consider main effects only.

Discussion

During the present study (1991–2001) capercaillie reared few young. Moss *et al.* (2000) used many of the same counts as us to calculate that the mean number of chicks reared per hen was insufficient to maintain a steady population, and concluded that the decline in capercaillie numbers in Scotland was due primarily to lower breeding success. In this study, we investigated whether variations in breeding success are affected by aspects of forest habitat and predator abundance. If so, it should be possible to increase capercaillie breeding success by altering forest management and so help to avoid the imminent prospect of a second extinction (Moss 2001). Moss *et al.* (2000) calculated that, to maintain a steady population, breeding success should average 1.1 chicks hen⁻¹ (95% CL 0.7–1.8), but that in the absence of adult mortality from flying into forest fences this need be only 0.6 (95% CL 0.3–1.0).

Breeding success of capercaillie differed between years, associated with variations in weather (Moss, Oswald & Baines 2001). In the present study, we focused on differences among forests and model year as a random effect. Scottish forests provide a range of habitats for capercaillie, differing in naturalness, structure, species composition and predator abundance.

BILBERRY AND BREEDING SUCCESS

Our data show a positive relationship between capercaillie breeding success and bilberry ground cover, at least up to about 15–20% cover (Table 5 and Fig. 3). Capercaillie are closely associated with old forest (Rolstad & Wegge 1987; Picozzi, Catt & Moss 1992) rich in dwarf shrubs, especially bilberry (Storch 1993, 1994, 2001). Such vegetation provides good cover (Kastdalen & Wegge 1991; Picozzi, Moss & Catt 1996), while bilberry supports abundant invertebrates, particularly lepidopteran larvae (Baines, Sage & Baines 1994), which, together with bilberry leaves and berries, comprise a large part of the chicks' diet (Kastdalen & Wegge 1985; Picozzi, Moss & Catt 1996). Indeed, larval consumption and brood survival were related (Picozzi, Moss & Kortland 1999). Our data showed no further improvement in breeding success above 15–20% bilberry cover, but we had no forest with bilberry cover greater than 24% and so cannot exclude the possibility of further improvement with greater cover. Alternatively, too much bilberry and other tall vegetation might hinder chicks from foraging.

We found no significant association between breeding success and habitat aspects, except bilberry cover. Our habitat measurements, however, were coarse-grained (on a 300–500-m grid, see the Methods) and without an explicit spatial component. It seems likely, for example, that a brood of small capercaillie chicks will do best if they have, within easy reach, food, water, cover from predators and places to dry out after rain. From anecdotal experience gained flushing chicks during brood counts, we estimate that 'easy reach' in this context is of the order of tens of metres, and that explicitly spatial habitat measurements, finer-grained than ours, would have revealed aspects of habitat, beneficial to capercaillie, that we did not detect.

PREDATOR ABUNDANCE AND BREEDING SUCCESS

Newton (1993, 1994), Côté & Sutherland (1995) and Smedshaug *et al.* (1999) summarized the literature, showing that in most studies of the effect of predator killing on birds and mammals, the breeding success of the prey increased with predator killing. In some studies the prey's breeding density also increased, but in others it did not. That killing of foxes and martens can improve breeding success in capercaillie was demonstrated experimentally by Marcstrom, Kenward & Engren (1988). Consistent with this evidence, capercaillie in Abernethy forest bred more successfully in summers when most crows and some foxes were killed (Table 5), and breeding success was negatively related to our index of predator abundance, PRED1. Interestingly, the Abernethy trial had no significant impact on brood size, in accord with the idea that crows exerted their impact on breeding success mostly through nest robbing (see Appendix 2). In studies of capercaillie

(Storaas & Wegge 1987) and black grouse *Tetrao tetrix* (Bernard 1982; Brittas & Willebrand 1991), predation was the main proximate cause of nest failure, but the role of predation in chick mortality is not well documented.

Our data on predator abundance and breeding success, however, show that not all predators are equally important to capercaillie. Thus, although pine martens certainly take capercaillie eggs and chicks, the index of pine marten abundance was unrelated to capercaillie breeding success (Table 5). Consistent with our observations, Smedshaug *et al.* (1999) found that, during a period when sarcoptic mange reduced fox numbers in Norway, pine martens and small game, including capercaillie, black grouse, willow grouse *Lagopus lagopus* and mountain hares *Lepus timidus*, all increased in abundance. Foxes kill martens and may also compete with them for food (Smedshaug *et al.* 1999). It seems likely that foxes have a bigger effect on capercaillie than pine martens, such that the killing of foxes benefits both capercaillie and martens.

GAMEKEEPERS, PREDATORS, LAND USE AND BREEDING SUCCESS

Gamekeepers, who kill crows and foxes to benefit game birds, were employed on estates encompassing 11 of the 14 areas of forest studied. A crude measure of gamekeeper density was related only weakly to crow and fox indices and did not contribute to explaining capercaillie breeding success. This is similar to findings for black grouse on moorland sites, where hens bred more successfully in better quality habitats irrespective of whether gamekeepers were employed to control predators (Baines 1996). One can speculate that our estate-based measure of gamekeeper density did not reflect the intensity of predator killing in the areas of forest studied, that some activities of gamekeepers adversely affect capercaillie (Cosgrove & Oswald 2001), or that the effects of habitat quality on breeding success outweigh those of predator killing (Baines 1996). We do not have the data to distinguish these possibilities.

More generally, numbers of potential predators of capercaillie, including crows, foxes and pine martens, have increased markedly in Scotland, particularly in the last three or four decades of the 20th century (Marchant *et al.* 1990; Corbet & Harris 1991; Hudson 1992). These increases corresponded with a two-thirds decrease in the number of gamekeepers employed in Scotland (Hudson 1992). Also, forest fragmentation in much of Scandinavia, due to human land use and changes in forestry practice, has resulted in increased levels of generalist predators such as foxes (Kurki *et al.* 1998) and crows (Andrén 1992). The way in which forest fragmentation might increase predation on ground nesting birds has been experimentally demonstrated using dummy clutches (Andrén & Angelstam 1988; Huhta, Mappes & Jokimaki 1996). Further evidence, from Finnish wildlife triangle censuses, showed that the proportion of forest grouse with broods in August

was negatively correlated with the degree of forest fragmentation (Kurki & Linden 1995; Kurki *et al.* 1997). Fragmentation in Norwegian forests has been associated with increases in clutch and chick loss (Wegge & Grasaas 1977; Storaas & Wegge 1987; Storch 2001). Given the small size and highly fragmented nature of many of the Scottish forests supporting capercaillie, and increasing numbers of predators, it is plausible that generalist predators may be having an increased impact on breeding capercaillie.

This broad inference needs qualification. Our data, together with that of Smedshaug *et al.* (1999), suggest that foxes and crows have a bigger impact on capercaillie than pine martens. Also, the easy inference that more gamekeepers would necessarily mean fewer predators, thereby benefiting woodland grouse, is substantiated neither by our data nor by that of Baines (1996).

CONCLUSIONS

The results from this study suggest that forest managers who wish to benefit capercaillie should aim for bilberry cover of 15–20% or more. The evidence from our and others' work provides no basis for changing the protected status of pine martens, nor does it show that increased numbers of gamekeepers would in itself necessarily benefit woodland grouse. If gamekeepers are to contribute to capercaillie conservation, they should routinely kill foxes and crows, by legal means, over as large an area as possible within core capercaillie forest. Fox snares, however, can kill capercaillie (Cosgrove & Oswald 2001) as well as other non-target species and so should not be used.

Although poor breeding success of capercaillie was probably the main cause of their recent decline in Scotland (Moss *et al.* 2000), better adult survival might have compensated for their reduced reproductive rate. A main cause of mortality is collisions with deer fences (Moss 1987; Catt *et al.* 1994) and calculations (Moss *et al.* 2000; Moss 2001) suggest that the decline might not have occurred in the absence of deaths from flying into forest fences. This assumes that the effects of reduced breeding success and the various causes of adult mortality are additive, as seems reasonable for this reduced population. Hence a current management priority for conserving capercaillie is to increase adult survival through reducing fence-associated mortality, marking fences to reduce collisions (Baines & Andrew 2003) or, preferably, removing fences altogether from core capercaillie areas (Forestry Commission 2001).

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Appendix 1: statistical notes

The overall measure of breeding success, chicks per hen (Table 5), comprised two components, broods per hen (Table A1) and brood size (Table A2). When summed by forest and year, the 114 data for chicks per hen were overdispersed relative to a Poisson distribution, as were those for broods per hen relative to a binomial distribution. After the parameter estimates for generalized linear mixed models were determined, the exponential family dispersion parameter for each measure of breeding success was assumed to be given by Pearson's chi-square statistic divided by the degrees of freedom, and statistics such as standard errors and likelihood

ratio statistics were adjusted accordingly. The function obtained by dividing a log likelihood function for a Poisson or binomial distribution by a dispersion parameter is not a log likelihood function but a quasi-likelihood function. Most asymptotic theory for log likelihoods also applies to quasi-likelihoods, so justifying such adjustments (SAS Institute 1996).

The covariance structure used for models 1 and 2 (Tables 5, A1 and A2) was simple variance components. We checked for AR(1) autocorrelation in successive residuals at each forest but found none.

We also checked whether the results (Tables A1 and A2) depended on the adjustments made for overdispersion. When expressed at the level of the individual

Table A1. Capercaillie breeding success (broods per hen). Details as in Table 5

	Parameter estimates \pm SE		Deviance explained		χ^2 (sequential)		χ^2 (partial)	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Total	–	–	274.6	274.6	–	–	–	–
Crow	-0.80 ± 0.52	–	260.3	–	6.9*	–	2.3	–
Fox	-0.22 ± 1.55	–	260.5	–	0.00	–	0.02	–
Raptor	-0.25 ± 0.45	–	260.7	–	0.36	–	0.30	–
Marten	0.25 ± 0.97	–	260.5	–	0.12	–	0.07	–
PRED1	–	-0.40 ± 0.15	–	262.8	–	6.4*	–	7.4**
Predator trial	3.03 ± 0.83	3.06 ± 0.81	226.9	227.9	11.3**	11.6***	13.3***	14.2***
Bilberry	0.15 ± 0.09	0.13 ± 0.07	217.8	219.7	5.0*	4.4*	–	–
Bilberry ²	-0.007 ± 0.003	-0.006 ± 0.003	207.0	207.9	5.5*	6.2*	–	–

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, otherwise not significant; –, row heading not applicable to this column.

Table A2. Capercaillie breeding success (brood size). Details as in Table 5

	Parameter estimates \pm SE		Deviance explained		χ^2 (sequential)		χ^2 (partial)	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Total	–	–	105.8	105.8	–	–	–	–
Crow	-0.04 ± 0.20	–	101.1	–	3.7	–	0.04	–
Fox	-1.15 ± 0.71	–	100.4	–	0.36	–	2.6	–
Raptor	-0.30 ± 0.16	–	95.3	–	5.6*	–	3.5	–
Marten	0.34 ± 0.39	–	95.1	–	0.34	–	0.80	–
PRED1	–	-0.21 ± 0.07	–	96.3	–	8.9**	–	9.3**
Predator trial	0.83 ± 0.51	0.80 ± 0.50	92.7	94.1	2.0	1.9	2.7	2.6
Bilberry	0.05 ± 0.03	0.06 ± 0.03	78.3	82.2	12.3***	8.6**	–	–
Bilberry ²	-0.003 ± 0.001	-0.003 ± 0.001	70.7	71.5	5.4*	8.5**	–	–

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, otherwise NS. –, row heading not applicable to this column.

hen, the 816 data for broods per hen and 279 for brood size were not overdispersed. We therefore enacted generalized linear mixed models at the hen level, equivalent to Tables A1 and A2 but with no adjustments for dispersion. Inconveniently, the GLIMMIX macro (Littell *et al.* 1996) would not accept forest as a repeated measure when there was more than one observation per forest per year. However, as there was no autocorrelation in the data (previous paragraph), we could achieve the same result by entering forest as a second random effect. Parameter estimates and standard errors from analyses done at the hen level were similar to those done at the forest level (Tables A1 and A2). Except for minor details (next paragraph), the same effects were significant. Biological inferences were identical and so our practical conclusions do not depend upon adjusted dispersion parameters.

Model 1 was less reliable than model 2 because of confounding among predator indices (main text). In the hen-level version of model 1 (as in Tables A1 and A2) the quadratic term (bilberry cover, squared) was not significant in the analyses for brood size or broods per hen. Parameter estimates and standard errors were similar to those in Tables A1 and A2, however, and in model 2 the term (bilberry cover, squared) was significant for both brood size and broods per hen. The effect of this term was to progressively reduce the slope of the

relationship between breeding success and bilberry cover (Fig. 3). Dropping it would not alter the conclusion that breeding success increased with bilberry cover. In addition, in the hen-level version of model 1, the effect for raptors (Table A2) was not significant in the sequential analysis.

In addition to the χ^2 statistics quoted in the text and tables, we calculated F -statistics and assessed their significance on the basis of degrees of freedom determined according to Satterthwaite's approximation (SAS Institute 1996), which adjusts for unequal group variances. The differences were trivial but we give the more conservative probabilities and significance levels from the F -tests.

Appendix 2: broods per hen and brood size

The predator index most strongly related to broods per hen (Table A1, model 1) was for crows, but in the case of brood size (Table A2, model 1) it was for raptors. Also, the trial at Abernethy, which involved killing most breeding crows but no raptors, had a significant effect on broods per hen (Table A1) but not upon brood size (Table A2), although the parameter estimate for brood size was in the expected direction. Crows rob nests, so leaving hens without broods, and probably take small chicks, so reducing brood size. Raptors are

not known to rob nests but do take chicks and hence reduce brood size. The above differences between Tables A1 and A2 are consistent with the idea that crows exert their effect upon breeding success more by robbing nests than by killing chicks.

Mean postdictions for broods per hen at Abernethy (from model 2; Table A1) were 0.04 (95% CL 0.01–0.18) in years without predator control and 0.48 (95% CL 0.37–0.59) in years with it. Brood sizes (from model 2; Table A2) were 1.3 (0.5–3.6) and 2.9 (2.6–3.3), respectively.