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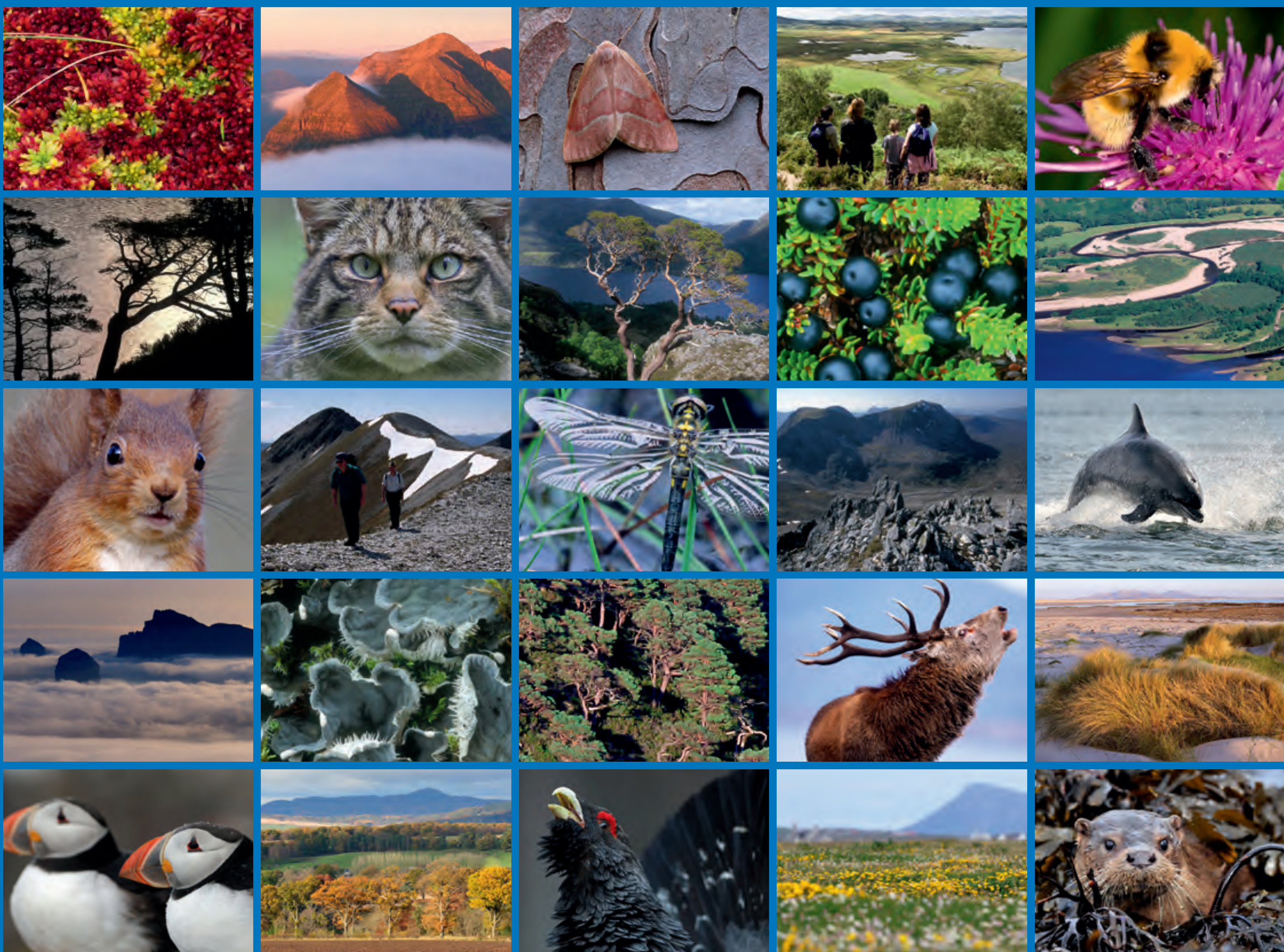
Commissioned Report No. 742

Correlates of capercaillie productivity in Scots pinewoods in Strathspey



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COMMISSIONED REPORT

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Correlates of capercaillie productivity in Scots pinewoods in Strathspey

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This report should be quoted as:

Summers, R.W., Golder, P., Wallace, N., Iason, G. & Wilson, J. 2015. Correlates of capercaillie productivity in Scots pinewoods in Strathspey. *Scottish Natural Heritage Commissioned Report No. 742.*

COMMISSIONED REPORT

Summary

Correlates of capercaillie productivity in Scots pinewoods in Strathspey

Commissioned Report No. 742
Project No: 14543
Contractor: RSPB
Year of publication: 2015

Keywords

Capercaillie; productivity; pinewoods; blaeberry; habitat; predators; human disturbance.

Background

In Scotland, the capercaillie population has declined to 1,000-2,000 birds since the 1970s, and is now largely restricted to the pinewoods of Strathspey. Poor productivity and increased adult mortality due to collisions with forest fences were previously identified (in 2000) as factors causing the decline. Whilst fence removal and marking have reduced mortality of full-grown birds, measures to improve breeding habitat and control of generalist predators have not led to an increase in the national population size in the last ten years.

Productivity of capercaillie varies across the key woods in Strathspey. This suggests that there may be other factors, which have not yet been addressed. Although the strong association of capercaillie with old-growth Scots pine and a blaeberry-rich shrub layer is well understood, and there is a correlation between productivity and blaeberry cover, it is possible that other important effects remain undetected. This study tested the relative contributions of habitat for food (pines in old woodland, blaeberry and cotton-grass) and cover from predators and rainfall (dense woodland, brash, bracken and juniper) in explaining variation in productivity across Strathspey woods. Human disturbance and the relative activity of predators (red foxes, pine martens, corvids and raptors) were also considered. Pine martens were of particular interest given their recent (mid-1990s) re-establishment as part of the pinewood community in Strathspey and direct evidence of predation on capercaillie clutches.

Blaeberry is recognised as an important plant for capercaillie: the leaves and berries are eaten by full-grown birds, and chicks eat the invertebrates (particularly moth caterpillars) that occur on blaeberry. The key Strathspey sites differ in woodland management and it has been hypothesised that this may cause differences in chemical composition in blaeberry and consequently insect abundance. As a secondary project objective, the chemical composition of blaeberry leaves from different stand types under different management regimes were measured and compared.

Main findings

- There were significant differences in capercaillie productivity amongst woods for the ten-year period (2004-2013); Abernethy East had the lowest productivity and Rothiemurchus the highest.

- Scots pine was the main tree species in all woods, but there was a small amount of non-native conifer in the plantation woods (Glenmore, Inshriach and Inverlaidnan).
- The abundance and frequency of heather, blaeberry, cowberry, grass, cotton-grass, bracken, brash and juniper reflected stand types in the different woods. Heather was most abundant in old open stands (e.g. at Rothiemurchus) and least in dense plantations (e.g. at Inverlaidnan). Blaeberry and cowberry were most abundant in old stands at Abernethy East and least at Inverlaidnan. Conversely, grass cover was most abundant in the plantations at Inverlaidnan and least at Abernethy East and Rothiemurchus. Cotton-grass was most abundant in wooded bogs at Abernethy West and least at Inverlaidnan. Bracken and brash were most frequent in old plantations at Craigmore and bracken least at Inverlaidnan. Juniper was most frequent at Abernethy West and least at Kinveachy.
- Indices of scat abundance showed that Abernethy had highest index for pine martens, whilst Inverlaidnan had the lowest. Inshriach and Abernethy East had the highest indices of fox activity and Rothiemurchus and Inverlaidnan had the lowest. In total, there were 8.6 times more pine marten scats recorded compared to fox scats. Variation in abundance of scats among woods in 2013 was strongly correlated with that in 2009, indicating a similar ranking of the woods in the two survey years. For both mammal species combined, twice as many scats on average were recorded in 2013 as in 2009 across the woods.
- The highest indices for corvids were in Craigmore and Inshriach and three out of the eight woods had no sightings. The index for raptors was highest in Craigmore and three out of the eight woods had no sightings.
- Glenmore and Rothiemurchus had the highest human disturbance index, whilst no people were sighted at Craigmore, Kinveachy and Inverlaidnan.
- At the wood scale, in univariate tests, a negative relationship was found between capercaillie productivity during 2009-13 and both cowberry cover and the pine marten scat index. However, cowberry cover and the pine marten index were themselves highly correlated. There was also a weak negative relationship between productivity and June rainfall.
- At the 1km square scale, in a multivariate model, capercaillie productivity was strongly inversely related to an index of change in warming rate during April, and weakly inversely related to the percentage of sample points with juniper, and to the pine marten scat index.
- A study of the chemical constituents of blaeberry leaves collected in different stand types (old-growth woodland and plantations that had been thinned) showed that tannins and phenols were highest in old-growth woodland at Abernethy and lowest in a thinned plantation at Inshriach.

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Acknowledgements

The study was funded by the Cairngorms National Park Authority (administered by J. Prigmore), Royal Society for the Protection of Birds (RSPB) and Scottish Natural Heritage (SNH) (administered by S. Haysom). Permissions to visit land-holdings were provided by W. Anderson and F. Law (for Inverlaidnan and Kinveachy), L. Ford and P. Ferguson (for Rothiemurchus), D. Forbes and C. Leslie (for Glenmore and Inshriach) and J. Roberts (for Abernethy and Craigmore).

Data on capercaillie productivity were provided by C. Leslie and K. Kortland of Forestry Commission Scotland (FCS) (for Glenmore and Inshriach), D. Baines of the Game and Wildlife Conservation Trust (GWCT) (for Inverlaidnan, Kinveachy and Rothiemurchus) and D. Dugan and T. Poole of RSPB (for Abernethy and Craigmore). SNH gave permission for use of data where they were co-owners. M. Hancock assisted with analyses.

The draft report was commented upon by A. Amphlett, D. Dugan, S. Haysom, J. Prigmore and M. Towers.

1. BACKGROUND

In Scotland, the capercaillie *Tetrao urogallus* population has declined to 1,000-2,000 birds since the 1970s (Catt *et al*., 1998; Wilkinson *et al*., 2002; Eaton *et al*., 2007; Ewing *et al*., 2012). As a result, the species is red-listed, an Annex I species under the EU Birds Directive, a Schedule 1 species under the Wildlife & Countryside Act, and a high priority species in RSPB's UK Species Recovery Strategy.

Poor productivity and increased mortality of full-grown birds due to collisions with forest fences were identified as factors causing the decline (Moss *et al*., 2000). Whilst fence removal and marking have been put in place to reduce mortality of full-grown birds (Summers & Dugan, 2001; Baines & Andrew, 2003), measures to improve productivity have proved less tractable. This is important, given that productivity is correlated with population growth (Summers *et al*., 2010).

Correlative studies across several woods, or over time at a single wood, have identified several, sometimes interacting, factors that are related to productivity. These include June rainfall (a negative effect) (Moss, 1986; Summers *et al*., 2004a), a change in April warming (Moss *et al*., 2001), abundance of blaeberry *Vaccinium myrtillus* (a positive effect up to a mean of 15-20% cover at the wood scale) (Baines *et al*., 2004) and predation by carrion crows *Corvus corone* and hooded crows *C. cornix* (a negative effect) interacting with rainfall (Summers *et al*., 2004a).

Despite conservation interventions that focused around breeding habitat management and control of generalist predators (red foxes *Vulpes vulpes*, and crows), the national population has not increased in the last ten years. The most recent estimate was only 1,285 individuals (95% CLs 822-1,882) in winter 2009-2010, with 75% of birds concentrated in Strathspey (Ewing *et al*., 2012).

Productivity varies across key sites. For example, it remains low at Abernethy despite efforts since 2000 to improve it through predator control and habitat management (Summers *et al*., unpublished). This suggests that there may be other factors which have not yet been addressed. Although the strong association of capercaillie with old-growth Scots pine *Pinus sylvestris* and a *Vaccinium*-rich shrub layer is well understood (Summers *et al*., 2004b), and there is a correlation between productivity and blaeberry cover (Baines *et al*., 2004), it is possible that other important habitat effects remain undetected.

It is also recognised that there are interactions between habitat composition and habitat selection by generalist predators, such as red foxes and pine martens *Martes martes* (e.g. Andrén & Angelstam, 1988). The pine marten is now of considerable interest given its recent expansion in range (Croose *et al*., 2013), and evidence that it is now the most frequent predator of capercaillie clutches at Abernethy (Summers *et al*., 2009). Feathers and eggs are, however, rare in pine marten scats (e.g. 0.7, 0.4, and 0.2 percentage occurrence for feathers in April, July and November, respectively, in scats at Abernethy) suggesting that birds are not important in the diet but are taken opportunistically (Summers & Denny, 2010).

There is anecdotal evidence that after major woodland disturbance events (e.g. thinning of trees by forestry operations) there is a "flush" in the abundance and nutritional quality of blaeberry leaves, perhaps because of the increased light entering the wood and nutrients recycled from the brash from the cut trees. This might influence the condition of adult capercaillie or insect prey for capercaillie chicks, given its importance as a food plant for adults and in supporting the invertebrates that are important chick foods. The proposed mechanism is that plants counter herbivory by producing secondary chemicals such as tannins that make leaves distasteful, poisonous or difficult to digest and may inhibit growth in their consumers (Iason, 2005). If such a mechanism is operating, it may offer an important approach to habitat management for capercaillie (i.e. thinning stands to encourage a "flush").

All key sites for capercaillie comprise Scots pinewood, either as native pinewood or mature plantations in varying proportions (Table 1). There is, however, variation in management due to differing forestry and conservation objectives. This results in largely non-intervention silviculture in native woods and thinning and felling in plantations. Further, different culling regimes for red deer *Cervus elaphus* and roe deer *Capreolus capreolus* may lead to varying deer densities and hence differences in the composition and quality of field-layer vegetation. To test the hypothesis that the quality of blaeberry varies between forest type with contrasting management, the chemical composition of blaeberry leaves was compared in different stand types under different management regimes.

Table 1. The study woods in Strathspey showing dominant woodland type and whether predator control takes place. Areas of the whole wood and the approximate area for brood counts are in brackets. Wood area was based on the amount of woodland within the described boundary lines in Annex 1.

Wood	Main woodland type	Predator control?	Area (km^2)
Abernethy	Native pinewood	Yes	38.83 (17)
Abernethy East	Native pinewood	Yes	9.33
Abernethy West	Native pinewood	Yes	29.50
Craigmore	Plantation	Yes	8.50 (3)
Glenmore	Native pinewood and plantation	No	19.02 (7.4)
Inshriach	Plantation	No	30.56 (10)
Kinveachy	Native pinewood	Yes	16.51 (11)
Inverlaidnan	Plantation	Yes	4.14 (0.9)
Rothiemurchus	Native pinewood	Yes	24.19 (9.7)

Recent studies have shown that human disturbance along forest tracks probably prevents capercaillie using the woodland closest to tracks for feeding (Summers *et al*. 2007, Moss *et al*. 2014). It is also possible that disturbance affects productivity, but this has yet to be examined.

Given the range of possible hypotheses, the aim of this study was to systematically map habitat (stand types and field layer vegetation) and management across the key capercaillie woods in Strathspey. These data were combined with data on weather, indices of predator activity and human disturbance to enable an overall multivariate assessment of the relative role of habitat, weather, predators and people as correlates of spatial variation in productivity.

2. OBJECTIVES

1. To obtain data on indices of predator activity, indices of human disturbance, field layer and stand level habitat structure and composition within key capercaillie woods in the Strathspey core range, and to use these measures to test whether these environmental variables are associated with variation in capercaillie productivity within and among woods.

2. To test the hypothesis that blaeberry quality varies as a function of stand structure and the occurrence and nature of recent forest management interventions (i.e. stand thinning).

3. To use the results to help to formulate improved management advice in support of capercaillie conservation.

3. METHODS

3.1 Study areas

The study was carried out in seven Scots pine woods in Strathspey (Abernethy, Craigmore, Glenmore, Inshriach, Inverlaidnan, Kinveachy and Rothiemurchus, Table 1, Figure 1 and Annex 1), which currently hold the bulk of capercaillie in Scotland (Ewing *et al.*, 2012). Most of the plantations are commercially managed by successive thinning followed by clear-felling. The plantations at Abernethy Forest, however, are not commercially managed. Stands of native pinewood are not felled.

It was recognised that the study was limited to a small number of woods, making it difficult to carry out correlative analyses. There was also limited information on capercaillie productivity. The site with the largest capercaillie data set was Abernethy. Therefore, to increase the sample size of woods, Abernethy was divided into East Abernethy (almost entirely native pinewood) and West Abernethy (a mix of native pinewood and plantation). The River Nethy was the dividing line. The River Nethy is a fast-running river about 5 m wide. There is also a stream (Crom Allt) and a 1 km band of less suitable habitat for capercaillie (grassland and young woodland) between the two sections. These features will lessen the chance of broods crossing between the two parts.

Glenmore and Rothiemurchus also have a common boundary, so are not independent woods, although are under different ownership. They have, however, been treated as independent in earlier studies (Baines *et al.,* 2011a, b), and the data collected on predators (though not capercaillie) are collected in well separated parts, so we retained this distinction of two woods.

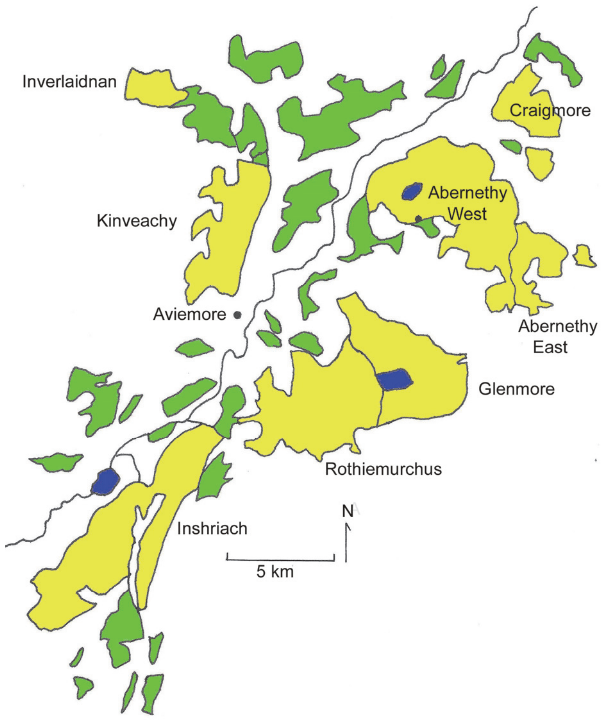


Figure 1. The locations of the study woods in Strathspey and weather stations at Aviemore and Abernethy West. Yellow – study woods, green – other woods, blue – lochs. The River Spey runs from southwest to northeast

Capercaillie are not evenly distributed through woods, but tend to occur only in specific areas. Consequently, we used transect survey data (see below), plus information of the locations of capercaillie during brood counts from 2009-2013 to define the broad regions of each wood used by capercaillie (Table 2). This allowed removal of habitat data where capercaillie did not occur, and provided a more appropriate analysis of the habitat data in relation to capercaillie productivity. Secondly, the 1 km grid squares where broods were located provided a finer scale of description of habitat in relation to capercaillie productivity.

Table 2. Dates and time spent surveying the different woods

Wood	Track survey time (hours)	Transect survey dates in 2013	Transect survey time (hours)	Number of transects (total points, points in capercaillie area)
Abernethy W	10.7	24 Jun-8 Jul, 3-4 Sep	74.5	17 (1094, 742)
Abernethy E	12.6	9-17 Jul	34.8	9 (402, 402)
Craigmore	14.1	23 May-7 Jun	29.3	11 (351, 150)
Glenmore	11.9	13-22 May	57.0	15 (740, 600)
Inshriach	15.3	2-22 Aug	83.4	21 (1223, 840)
Inverlaidnan	9.4	10-11 Jun	12.3	7 (161, 138)
Kinveachy	8.0	12-20 Jun	40.9	15 (652, 492)
Rothiemurchus	14.6	18 Jul-1 Aug	68.3	12 (905, 905)

3.2 Field data collection

Capercaillie productivity

Counts of female capercaillie with dependant young were carried out each July and August from 2004-2013 by teams of observers walking in a line abreast with dogs, which pointed and flushed females and their young. These data were collected by different organisations: FCS, GWCT, RSPB and SNH. Capercaillie productivity varies annually so the run of 10 years of data (2004-2013) was initially used to characterise the mean productivity in the different woods, except Inshriach which had brood data for only the last five years. A further analysis was carried out using the last five years (2009-2013), thereby including Inshriach in the analysis. Productivity was expressed as chicks per female, including females with no chicks.

Capercaillie distribution within woods

To determine the parts of each wood in which full-grown foraging capercaillie have used trees in the past year, a search of the ground in a 2 m radius around the nearest overstorey (tall) tree at each sample point (see below) was conducted for a maximum of one minute for capercaillie droppings that were composed of pine needles (Summers *et al*., 2007). Female capercaillies have droppings with a mean diameter of 8.7 mm (range 7.2-10.3 mm), and males 11.0 mm (9.2-12.9 mm) (Gjerde, 1990). Pine needles form most of the diet between September and April and a lesser proportion from May to August (Summers *et al*., 2004b). Droppings composed of needles last for many months, thereby reflecting past use. A small number of sightings of birds also distinguished locations used by capercaillie. Finally, brood records from 2009-2013 were obtained. Areas searched for broods were not representative of each wood (unlike the transect data), but did provide a large number of records of where broods occurred, ensuring that wood-scale analysis was restricted to where the birds occurred. Thus, the combination of information from droppings, sightings of birds and brood locations was used to define the parts of the woods used by capercaillie.

Habitat

Habitat assessments were made by walking parallel east-west transects (500 m apart; 250 m and 750 m up from the SW corner of each 1 km OS grid square) across all woods, collecting data at sample points 50 m apart, as determined by GPS (Garmin 60CX, accurate to within a few metres). All the habitat surveys were carried out by one person to avoid observer bias. The sampling effort was 2 km of transects per km^2 of woodland and 40 sample points per km^2. The number of transects and sample points (in brackets) are shown for each wood in Table 2. Transects were walked during May to early September when blaeberry was in leaf-burst or full leaf.

The following measures were made at each sampling point: top covers by different plants (blaeberry, cowberry *Vaccinium vitis-idaea*, heather *Calluna vulgaris*, grass and cotton-grass *Eriophorum* spp.) were estimated to 10% within a 2 m radius. A maximum height measurement was taken for heather and blaeberry within 1 m (if available) using a ruler. The ruler was pushed into the vegetation until there was resistance. For grass and cotton-grass, heights were assigned to one of three height classes: 1 = short (<5 cm), 2 = moderate (5-10 cm), 3 = tall (>10 cm) (Annex 2).

Woodland was defined as at least one live tree over 1 m high within 15 m of a sample point and was given a stand structure class based on tree density and size (Figure 2, Annex 3). The 12 stand types (Figure 2) were, however, reduced to six for the analysis by combining types 1, 2, 4 and 5 (oldest woodland); 3 and 6 (tallest woodland); 7 and 8 (young but not dense); and 10 and 11 (pre-thicket but not dense). Wooded bogs referred to areas with stunted pines growing on bogs with a ground vegetation of cotton-grass and *Sphagnum* spp. Any understorey trees were also noted separately from the overstorey trees. The dominant tree species was noted. If no woodland was present it was recorded as 0 for stand type and CF (clear-fell), G (grass) and H (heather) under "tree species". The species of any wind-blown trees was noted; e.g. WBLP (e.g. for wind-blown lodgepole pine *Pinus contorta*). Signs of recent woodland management (thinning racks) within 15 m were noted. Presence of brash and juniper *Juniperus communis* bushes (both over 1 m high) and bracken within 15 m was noted. These latter features may be important as brood cover.

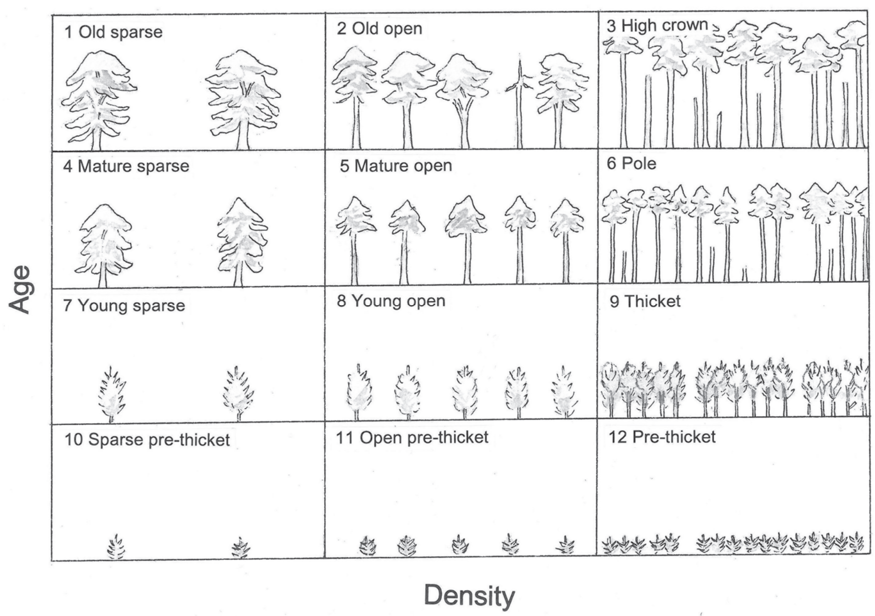


Figure 2. Sketches of the stand types based on age (size) and density, as recorded along the transects. See also Annex 3.

The assessment of ground cover by shrubs and grass took place from mid-May to the beginning of September 2013 (Table 2). Leaf burst of blaeberry was not complete during May because of the late spring in 2013. Assessments of early cover may, therefore, have been influenced by the incomplete leaf cover of blaeberry. Equally, grass cover assessments may have changed through the summer during its growth. To check for seasonal variation in cover assessments, 15 fixed plots were set in each of three areas (Loch Garten 1, NH973185; Loch Garten 2, NH978175; and Cuchanlupe, NJ005161) in Abernethy Forest with contrasting amounts of the different shrubs and grass. There was blaeberry and cowberry at all sites, but heather largely at Loch Garten and grass at Cuchanlupe. Assessments were made in mid-May (15th), late May (24th), mid-June (17th), mid-July (15th) and mid-August (15th).

Weather

It has been previously established that the productivity of capercaillie is poorer during wet Junes (Moss, 1986; Summers *et al*., 2004a). In addition, the way in which the weather warms in spring has been related to capercaillie productivity (Moss *et al*., 2001). If the air temperature rises quickly in early April, this is associated with higher productivity than Aprils in which the warming takes place later. The proposed mechanism for this effect is that early warming in April leads to better plant growth available for female capercaillie preparing for egg laying. Higher quality eggs then lead to more viable young (Moss *et al*., 2001).

Weather data (temperature and rainfall) were available for each year but not for individual woods. Instead, weather data from two local weather stations (Abernethy and Aviemore, Figure 1) were applied to two groups of woods, based on proximity – Abernethy weather station for Abernethy and Craigmore, and Aviemore weather station for the remaining woods.

Predators

Indices of predator activity were obtained by counting red fox and pine marten scats along gravel roads, tracks and footpaths (collectively called tracks) within each wood, following the protocol of previous studies (Baines *et al*., 2004, 2011a, b). Data for 2009, as collected by Baines *et al*., (2011a, b), were available for comparison with our 2013 data. The procedure involved a clear-up round in late April followed by four rounds of counting and collecting in mid-May, end of May, mid-June and end of June. Scats were removed during each survey, except the last. The data were expressed as the cumulative number of scats in May and June per km per day x 1000. The routes taken in each wood followed those initially selected by Baines *et al*. (2011a, b). New routes were chosen for Inshriach and an additional track was selected for West Abernethy, as these were areas not previously studied by Baines *et al*. (2011a) (Annex 1). Tracks were classed as un-vegetated vehicle tracks (UVT), vehicle tracks with vegetation growing up the middle (MVT), fully vegetated vehicle gravel tracks (VVT), overgrown vehicle gravel tracks (OVT), wide footpaths (WFP), narrow footpaths (NFP) and non-tracks (NT) (through woodland and across moorland) (Annexes 1 and 4). The ends of track sections were noted using a GPS, and their lengths obtained using GIS (ArcView).

The use of scat data in subsequent analyses makes the following assumptions:

1. That the distribution of the selected tracks was not associated with spatial patterns of use of forests by pine martens and foxes. By selecting tracks through the central portions of the woods, it was assumed this assumption would be fulfilled.
2. That the type of track did not influence their use by pine martens and foxes.
3. That the ability of observers to find scats was not influenced by the type of track.
4. That scats last for similar amounts of time on each track. It is likely that scats will last a shorter time if run over by vehicles, so scats on tracks used a lot by vehicles (e.g.

the track to Rothiemurchus Lodge) were unlikely to last long. In addition, annual variation in rainfall may make between-year comparisons unreliable because rain will help to disintegrate scats (Annex 5).

We felt that assumption 3 was especially unlikely to hold given the varying amount of vegetation growing on the tracks, so we tested the likelihood of detecting scats on different tracks. Fifty dummy scats (lengths of matt-black painted wooden dowling 50 mm long and 15 mm diameter) were set at random distances by an independent observer along 1 km sections of different track types ten minutes prior to the main observer walking the track. The percentage of dummy scats found provided a relative measure of scat detectability on different track types.

Scat identification was initially made in the field, based on the maximum diameter of scats, if they had not been squashed or started to disintegrate due to rainfall. Those which were $\leq$12 mm were classed as ’pine marten’ and otherwise ’fox’ (Summers & Denny, 2010). Flattened scats were identified on overall size. In an earlier study, an accuracy of 91% was achieved when identification was based on morphology and checked by DNA analysis (Summers & Denny, 2010). To establish the level of accuracy in this study, a further 100 scats were collected and checked using molecular techniques (O'Reilly *et al*., 2008; Mullins *et al*., 2010). To avoid potential bias in the selection of scats for molecular identification (e.g. collecting only ones that looked fresh), the first 60 classed as ’pine marten’ and the first 40 classed as ’fox‘ were sent for identification.

In addition to monitoring mammalian predators, corvids (crows, ravens *Corvus corax* and jays *Garrulus glandarius*) and raptors were noted during the day-time scat surveys along tracks. Most records of birds in woodland are made by hearing the calls, so scat and bird surveys were carried out at the same time. Surveys just after dawn, as carried out by Baines *et al*. (2011a, b), could not be carried out at all woods, as they may have disturbed capercaillie. To obtain a standard method for this survey, therefore, the corvid and raptor surveys were carried out during the daytime track surveys for scats. The data were expressed as numbers of encounters per hour x 100. Days with strong wind and heavy rain, when bird detection was likely to be poor, were avoided.

Human disturbance

Counts of people encountered on the track surveys provided a snapshot measure of human disturbance. Dogs with walkers were also counted. The indices were the number of groups (one or more people walking, cycling or driving) and numbers of people per hour. Weekends and public holidays were avoided when numbers of people were likely to be larger than week-days. It was assumed that the ratio of weekday to weekend human use was similar among woods.

Vaccinium chemistry in relation to stand structure and management

Collections of unbrowsed blaeberry leaves were made during June within examples of contrasting stand types: native (old open pinewood and high crown stands) and plantation thicket that had been thinned (data provided by the FCS). Samples from stands were taken from Abernethy East and West and from plantations in Inshriach. Thirty samples (>25 g wet mass) were taken from each stand type, weighed in plastic bags of known mass, and frozen. Samples were transferred in a frozen state to the laboratory and dried to obtain percentage dry mass. They were milled and analysed for tannin and phenolic content to assess whether stand structure and management has an effect on blaeberry leaf composition.
Condensed tannins were assayed by the Butanol-HCl method (Hagerman & Butler, 1978; Porter *et al*., 1986), standardised with blaeberry condensed tannin extracted and purified

according to Hagerman (2002). Total phenolics were assessed using the method of Salminen & Karonen (2011), using gallic acid as the standard.

3.3 Data analysis

Habitat

The seasonal changes in cover by shrubs and grass at the three sites in Abernethy were analysed using ANOVAs. Plots where a given plant was absent across all periods were deleted from the analysis of that plant. Site effects were examined only for blaeberry and cowberry because these plants were present at all three sites.

Capercaillie productivity amongst woods (wood scale analysis)

To describe variation in capercaillie productivity amongst woods, productivity (chicks per female) was analysed for the ten year period (2004-2013) for all woods except Inshriach, and for the five year period (2009-2013) for all woods. Poisson regression models were fitted using SAS (SAS Inst. 2000), in which wood and year were categorical fixed effects. The number of chicks in a given wood and given year was the dependent variable and the log number of hens was an offset variable. A log link was applied and overdispersion accounted for by adjusting the scale parameter.

Capercaillie productivity in relation to environmental variables

<u>Wood scale analyses</u>

Initially, the analysis in relation to environmental variables was carried out at the wood scale (n=8 woods; Table 1, using Abernethy West and East as separate woods), but excluding habitat data in those parts of the woods where capercaillie did not occur (Table 2).

Statistical analysis was based on univariate Poisson regression models using SAS, in which the capercaillie productivity over five years (2009-2013) was related in separate models to each predator index, human disturbance and habitat variables in turn (see Table 3 for details). Productivity over five years was used rather than the year (2013) when the data on predators, disturbance and habitat were collected because few broods were found each year and the stochastic effects of annual variation in rainfall could distort the relative importance of each for wood as breeding sites for capercaillie. The response variable was the number of chicks, and the log of the number of hens was an offset variable, thereby expressing the dependent variable as chicks per hen. A log link was applied and overdispersion accounted for by adjusting the scale parameter. The values of the two weather variables for each wood were weighted by the number of broods (including broodless females) found in each wood in a given year, as follows:

$y = [y_1 * (n_1/N)] + [y_2 * (n_2/N]$ .... summed over all years.

Where y_1 = weather variable for a specified wood in year 1, n_1 = number of capercaillie broods in specificfed wood in year 1, N = total number of capercaillie broods in specified wood over all years (2009-2013).

No attempt was made to examine multi-variate models with all variables for this data set due to the small sample size of woods.

Table 3. Variables used in relation the productivity of capercaillie.

Variable	Units	Scale	Years available
Dependent variable			
Caper productivity	No. of chicks per hen	Wood or 1-km square	2004-2013 (2009-2013 Inshriach)
Independent variables			
June rainfall	Total mm	Groups of woods	2004-2013
April warming index	Units	Groups of woods	2004-2013
April temperature	Degrees centigrade	Groups of woods	2004-2013
Fox activity	Scats/km/day x 1000	Wood	2013
Marten activity	Scats/km/day x 1000	Wood	2013
Crow activity	Encounters/h x 100	Wood	2013
Raptor activity	Encounters/h x 100	Wood	2013
Stand structure	% of different stand types	Wood or 1-km square	2013
Field layer	% cover of each species	Wood or 1-km square	2013
Field layer	Heights of species	Wood or 1-km square	2013
Juniper/brash/bracken	% of sample points where present	Wood or 1-km square	2013
Human disturbance	Groups/km	Wood	2013

1 km grid square analyses

A further Poisson regression analysis was based on 1 km grid squares for which there were data on productivity of capercaillie. In this case, a mixed model was fitted, with wood set as an eight-level random effect. This provided a larger sample size for multivariate analysis to be carried out. Brood data from 2009 to 2013 were used for each 1 km square, and weather data for each square were weighted by the year-specific brood counts in each square as described above for the wood scale analyses. Some 1 km squares were on the edge of woodland and those with fewer than ten sample points for habitat data were removed from the analysis. The independent variables were: weighted June rainfall; weighted April warming; percentage of six different stand types; percentage cover of heather, blaeberry, grass and cotton-grass; percentage of points with juniper, brash and bracken; mean heather and blaeberry heights; indices for corvids, raptors, foxes, pine martens and human disturbance (walkers, cyclists and vehicles combined). These variables represented effects of weather and associations with food (e.g. blaeberry and cotton-grass), cover from predators (e.g. dense woodland, heather, brash and juniper), ease of flight within woodland (e.g. old woodland), risk of predation (red foxes and pine martens) or human disturbance. Data for habitat, predators and disturbance were from 2013 only, but assumed to vary little or consistently among woods across the years when the brood data were obtained (see Results).

In all, 80 1 km squares (10 from Abernethy East, 14 from Abernethy West, 4 from Craigmore, 11 from Glenmore, 10 from Inshriach, 3 from Inverlaidnan, 13 from Kinveachy and 15 from Rothiemurchus) were included in the analysis. There were a large number of habitat and management variables, which were initially tested singly. To reduce the number of habitat variables, only those whose univariate effects that were most significant (Pearson correlation coefficient, r >0.7 or <-0.7) were combined with the predator, disturbance and weather variables (11 in all) in the multivariate test. We preferred this approach to employment of ordination techniques to generate a subset of orthogonal explanatory variables because the latter approach generates composite variables that can be difficult to interpret from a management perspective. Backward selection from a full model (main effects only) was used to determine which combination was significantly correlated with capercaillie productivity. Once a final model was identified, residuals were calculated and subjected to a Moran's *I* test to assess whether there was any spatial structure in capercaillie productivity associated with analysis at the 1km square scale that had not been accounted for by the explanatory variables (Diniz-Filho *et al.,* 2003).

4. RESULTS

4.1 Capercaillie data

Capercaillie productivity

The mean productivity for the ten years 2004-2013 varied between 0.33 chicks per female for Abernethy East and 1.23 at Rothiemurchus (Table 4), with significant differences amongst years (χ^2=74.9, df=9, p<0.001) and woods (χ^2=19.5, df=6, p=0.0034) (Figure 3). For the last five years (2009-2013), which allowed the inclusion of Inshriach, there was a similar pattern. The mean productivity ranged from 0.51 chicks per female at Abernethy East to 1.22 at Inshriach. Within this smaller run of data, the significant difference among years remained (χ^2=38.1, df=4, p<0.001), but there was no detectable significant overall difference amongst woods (χ^2=8.41, df=7, p=0.30). Nevertheless, the ranking of woods was consistent for the 10- and 5-year runs of data (Spearman rank correlation=0.86, n=7, p<0.05).

Table 4. Mean productivity (chicks per female) of capercaillie in different woods in Strathspey during 2004-2013 and 2009-2013. Ranges are shown in brackets.

Wood	Productivity 2004-2013	Productivity 2009-2013
Abernethy W	0.44 (0-2.08)	0.74 (0-2.08)
Abernethy E	0.33 (0-0.92)	0.51 (0-0.92)
Craigmore	0.58 (0-1.78)	0.62 (0-1.33)
Glenmore	0.94 (0.29-3.15)	0.85 (0.50-1.08)
Inshriach	-	1.22 (0.33-2.17)
Inverlaidnan	0.50 (0-1.50)	0.75 (0-1.00)
Kinveachy	0.66 (0-2.00)	0.95 (0-2.00)
Rothiemurchus	1.23 (0.15-3.00)	1.02 (0.15-3.00)

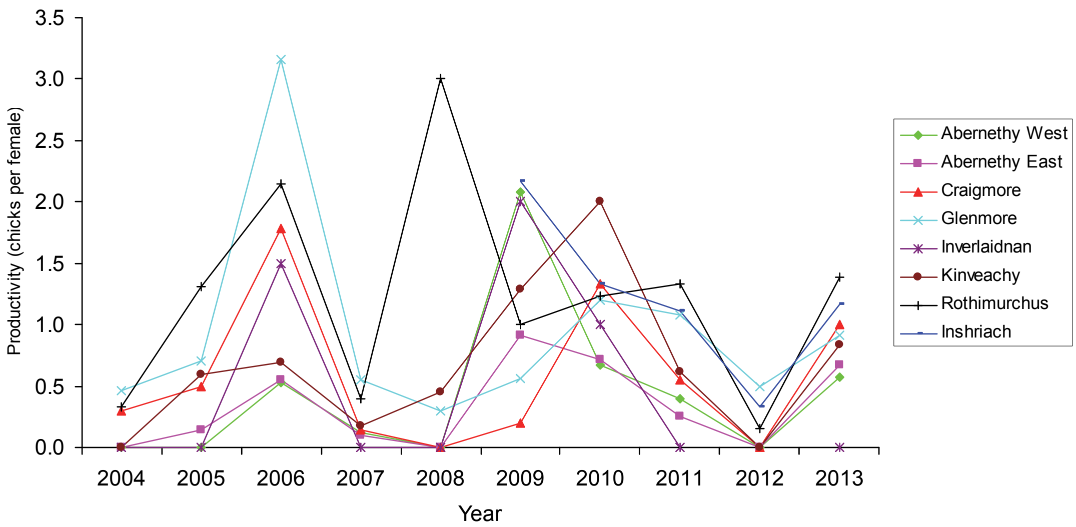


Figure 3. Capercaillie productivity for each wood from 2004-2013

4.2 Habitat data

Seasonal changes in ground cover

Assessments of ground cover at the same 45 plots between mid-May and August in Abernethy Forest showed that there were significant seasonal changes in the assessments of blaeberry ($F_{4,220}$=7.47, p<0.001) and grass ($F_{4,110}$=2.78, p=0.03), but not for heather ($F_{4,75}$=0.15, p=0.96) and cowberry ($F_{4,160}$=0.35, p=0.84). There was no site effect for blaeberry ($F_{2,218}$=0.96, p=0.38). The lowest cover estimates for blaeberry occurred in May, before the leaves were fully out. This was the converse of grass cover, suggesting that more grass was visible before blaeberry was in full leaf (Figure 4). The maximum cover of blaeberry occurred in June, so regression analyses were carried out with June values as the dependent variable ('y' in Table 5) and the cover values for other months as explanatory variables ('x' in Table 5). This provided regression equations which were used to correct the cover values greater than zero for the all the blaeberry assessments that took place outwith June (Table 5). A similar procedure was carried out for grass cover. All values were changed to a June standard before further analyses.

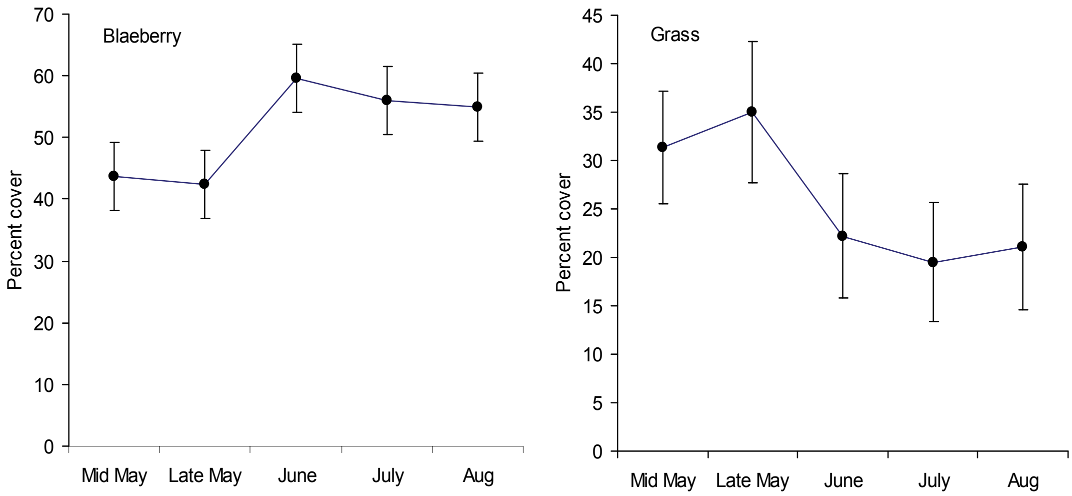


Figure 4. Seasonal changes in the mean percentage cover of blaeberry and grass at fixed plots in Abernethy Forest. The vertical lines show 95% CLs

Table 5. Regression equations used to correct cover scores of blaeberry and grass to a standard June value. y= score in June, x=score in period measured. Standard errors are shown in brackets

Plant	Period	Equation	*Pearson correlation coefficient*
Blaeberry	Mid-May	y = 2.39 (0.47)+ 0.82 (0.10) x	0.78
	Late-May	y = 2.04 (0.47) + 0.92 (0.10) x	0.81
	July	y = 1.54 (0.48) + 0.79 (0.08) x	0.83
	August	y = 1.47 (0.51) + 0.82 (0.09) x	0.82
Grass	Mid-May	y = -0.11 (0.32) + 0.62 (0.09) x	0.82
	Late-may	y = 0.91 (0.31) + 0.39 (0.10) x	0.63
	July	y = 0.49 (0.33) + 0.74 (0.15) x	0.72
	August	y = 0.52 (0.25) + 0.74 (0.11) x	0.82

Habitat composition and structure

Scots pine was the dominant tree species at most sample points in all woods (Figure 5). Wooded bogs were most frequent in Abernethy West and Rothiemurchus. Non-native conifers were most frequent in Glenmore, Inshriach and Inverlaidnan, reflecting stands of plantation woodland. The species composition of non-native conifers across all woods was 51% lodgepole pine, 21% Sitka spruce *Picea sitchensis*, 14% Norway spruce *Picea abies*, 9% larches *Larix* spp., 5% Douglas fir *Pseudotsuga menziesii* and 0.4% western hemlock *Tsuga heterophylla*. Broadleaf trees were most frequent in Inshriach and Craigmore. The broadleaf tree species composition throughout all woods was 79% birch *Betula* spp., 12% alder *Alnus glutinosa*, 4% rowan *Sorbus aucuparia*, 4% willows *Salix* spp., 1% bird cherry *Prunus padus* and 0.5% aspen *Populus tremula*.

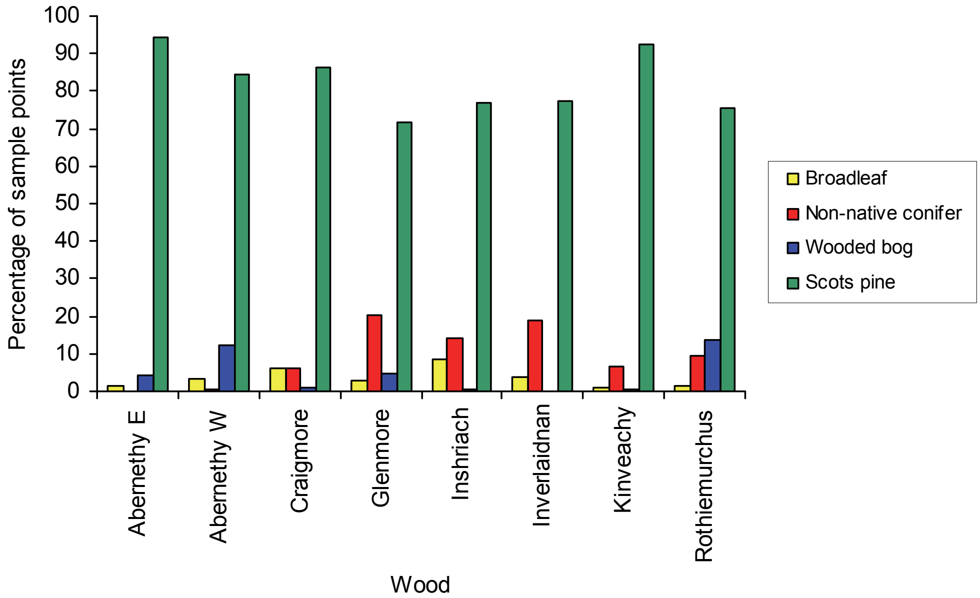


Figure 5. The percentage of dominant tree types at sample points in the different woods

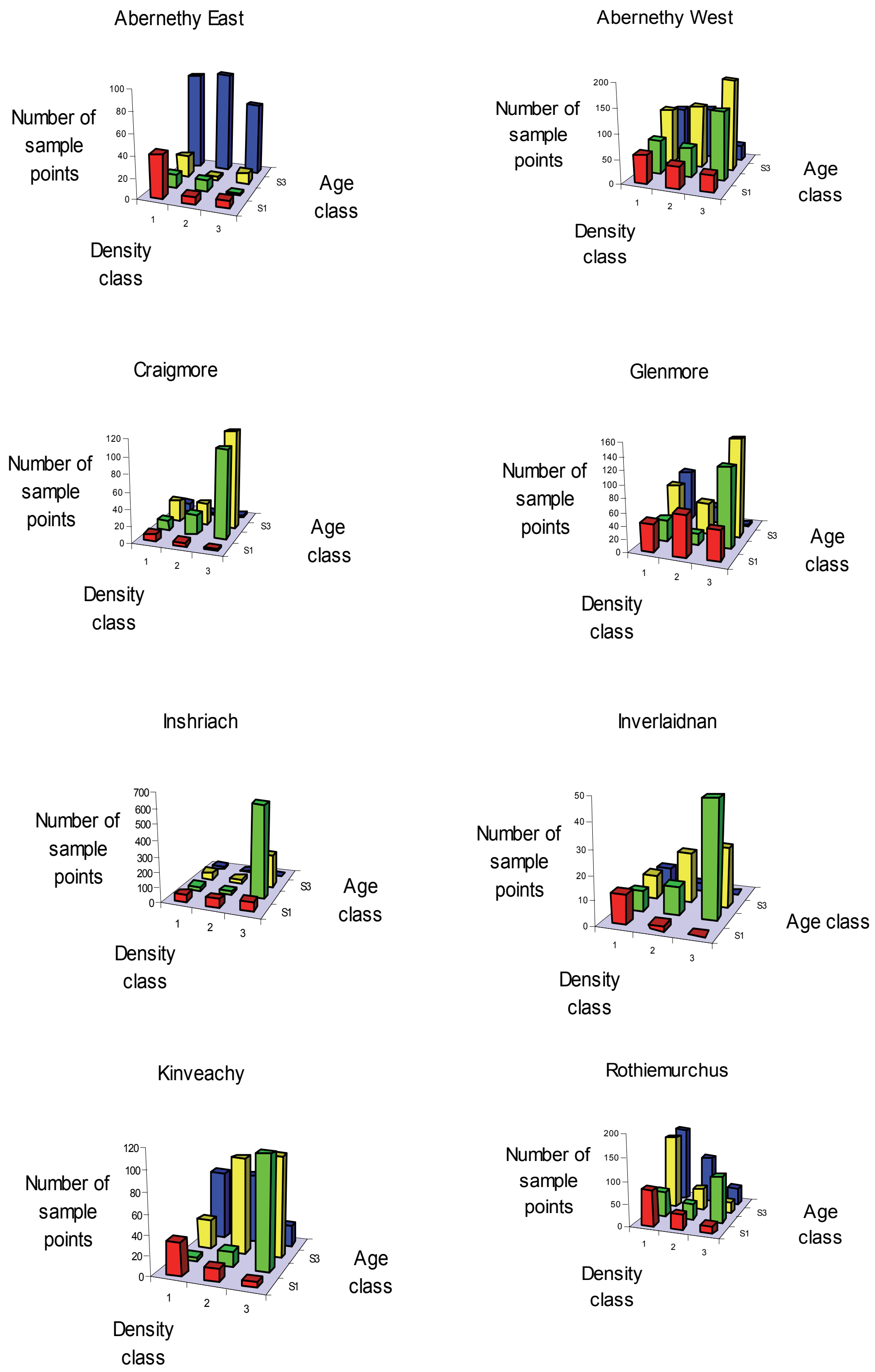
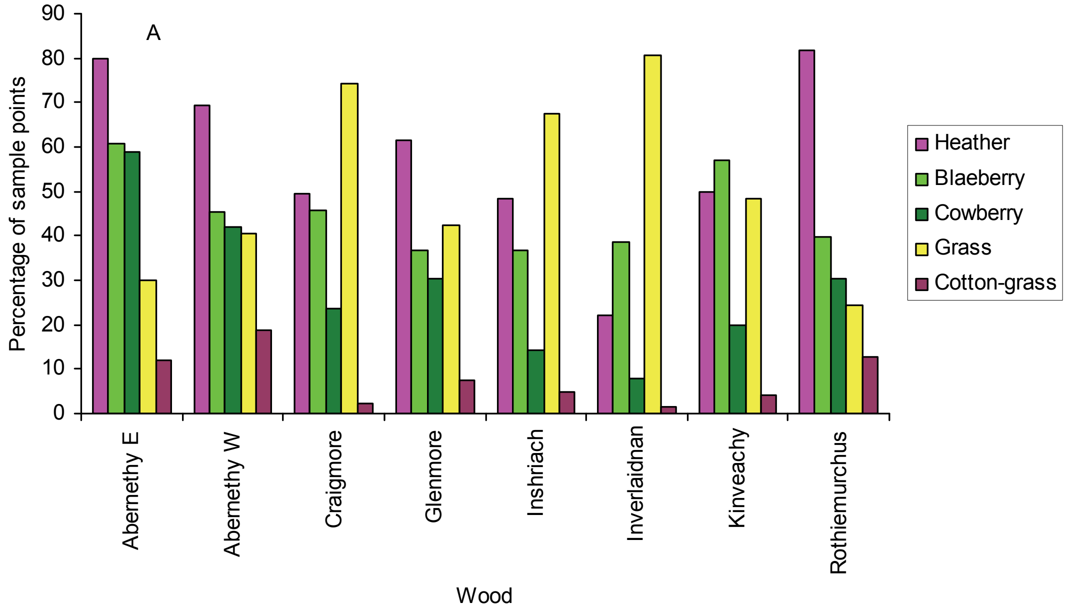


Figure 6. The frequency of different stand types at sample points in different woods in Strathspey. The colours show different age classes: red – class 1, green – class 2, yellow – class 3, blue - class 4

Abernethy East stood out in having mainly old trees (native stands) (Figure 6). There were both old-growth stands and younger stands in Abernethy West. By contrast, Inshriach was almost entirely composed of a high density of moderately old trees, typical of a plantation in the latter stages of the management cycle. The other woods had mixtures of old and young stands, reflecting separate areas of native old-growth and plantations. For example, Kinveachy had old-growth woodland on the western sides, but younger woodland (plantations) on the lower slopes on the east. Similarly, Glenmore had old woodland in the southern and eastern sections and younger stands in the northern sections.

The frequency of occurrence of heather varied from 22% of sample points in Inverlaidnan to 82% in Rothiemurchus (Figure 7). Likewise the mean cover of heather was lowest at Inverlaidnan and highest in Rothiemurchus (Figure 8). The high value at Rothiemurchus reflected the low density old-growth woodland. Likewise, localised abundance reflected areas of low density old-growth woodland (e.g. Kinveachy).

The mean maximum height of heather varied from 43.4 mm in Craigmore to 57.8 mm in Abernethy East (Figure. 9). There were significant differences among woods ($F_{7,3234}$=48.6, p<0.001). There was a correlation between heather height and heather cover (r=0.46, n=3394, p< 0.001). The large 95% CLs for heather at Inverlaidnan were due to the small sample size.



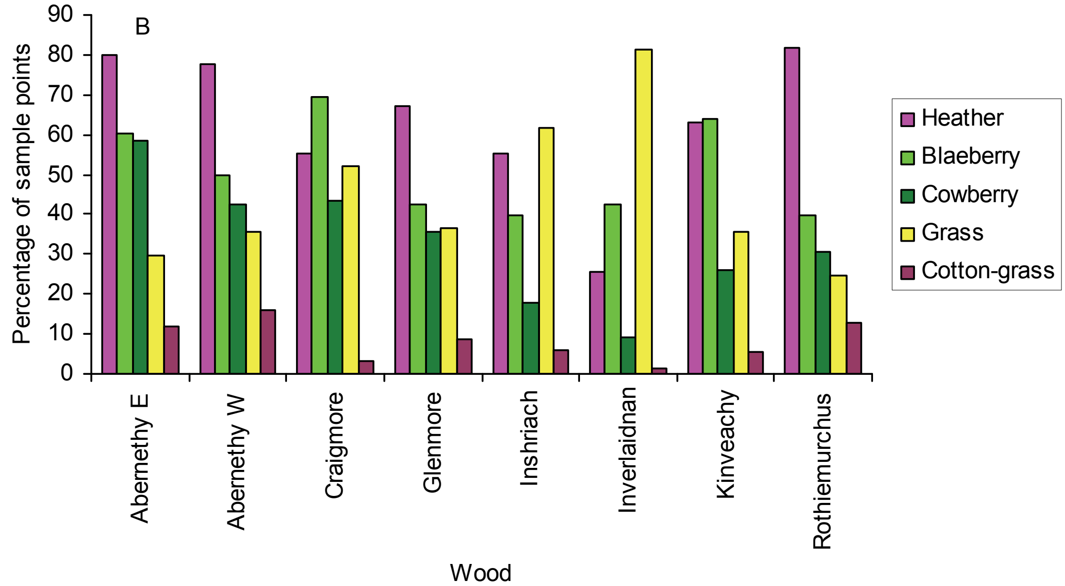


Figure 7. (A) The percentage of sample points with different shrubs, grass and cotton-grass in different woods, and (B) in those parts used by capercaillie

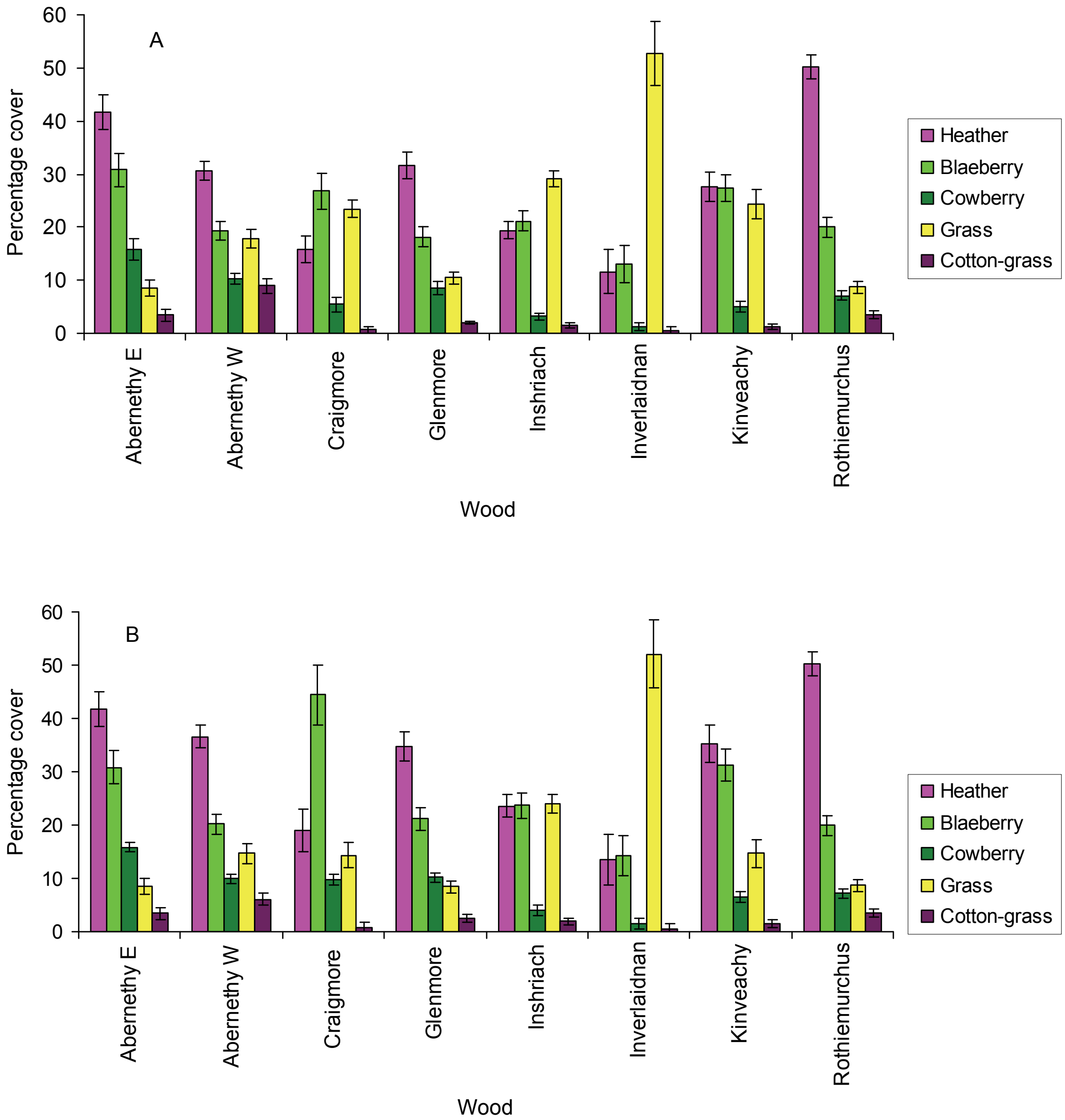


Figure 8. (A) Mean percentage cover (±95% CLs) of shrubs, grass and cotton-grass in the different woods, and (B) in parts used by capercaillie

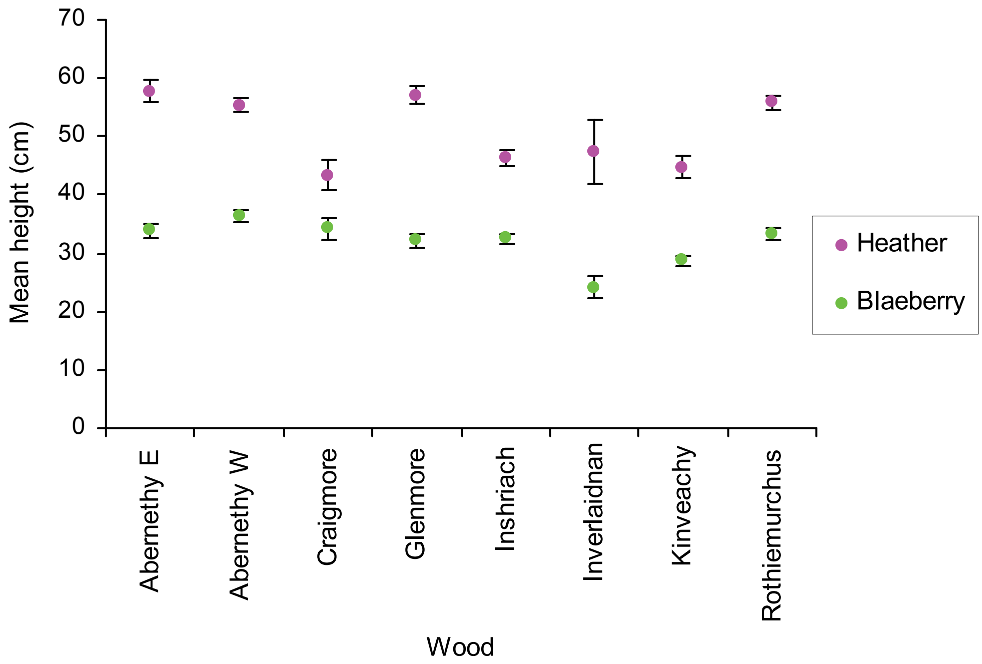


Figure 9. Mean maximum height (cm) of heather and blaeberry in different woods. The verical lines show 95% CLs

The frequency of occurrence of blaeberry varied from 37% of sample points in Glenmore and Inshriach to 61% in Abernethy East (Figure 7). The mean cover was lowest at Inverlaidnan and highest at Abernethy East (Figure 8). The mean maximum height of blaeberry varied from 24.1 mm in Inverlaidnan to 36.3 mm in Abernethy West, and there were significant differences amongst woods ($F_{7,280}$=22.5, p<0.001) (Figure 9). There was a correlation between blaeberry height and cover (r=0.32, n=2339, p=0.001).

The frequency of occurrence of cowberry varied from 8% of sample points in Inverlaidnan to 59% in Abernethy East (Figure 7). As with blaeberry, the mean cover of cowberry was lowest at Inverlaidnan and highest at Abernethy East (Figure 8). Cowberry was less frequent than blaeberry.

The frequency of occurrence of grass varied from 24% of sample points in Rothiemurchus to 81% in Inverlaidnan (Figure 7). Grass cover was least in Rothiemurchus and Abernethy East, and greatest at Inverlaidnan (Figure 8). The frequency of height classes indicated that grass was generally short, particularly at Inshriach. Woods where the grass was more tussocky were Glenmore and Inverlaidnan (Figure 10).

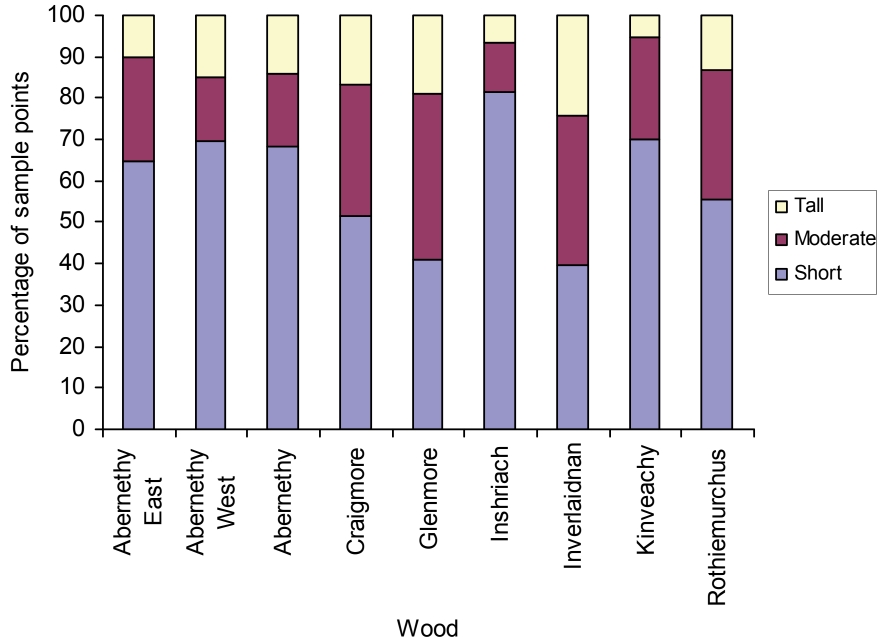


Figure 10. The percentage of points with grass at different height classes in different woods

The frequency of occurrence of cotton-grass varied from 1% of sample points in Inverlaidnan to 19% in Abernethy West (Figure 7). Cover was also greatest in Abernethy West (Figure 8), where it occurred mainly in the northwest of the wood. There was also a high frequency of cotton-grass in Rothiemurchus, particularly in the northern part. The frequency of height classes indicated that cotton-grass was generally tussocky (Figure 11).

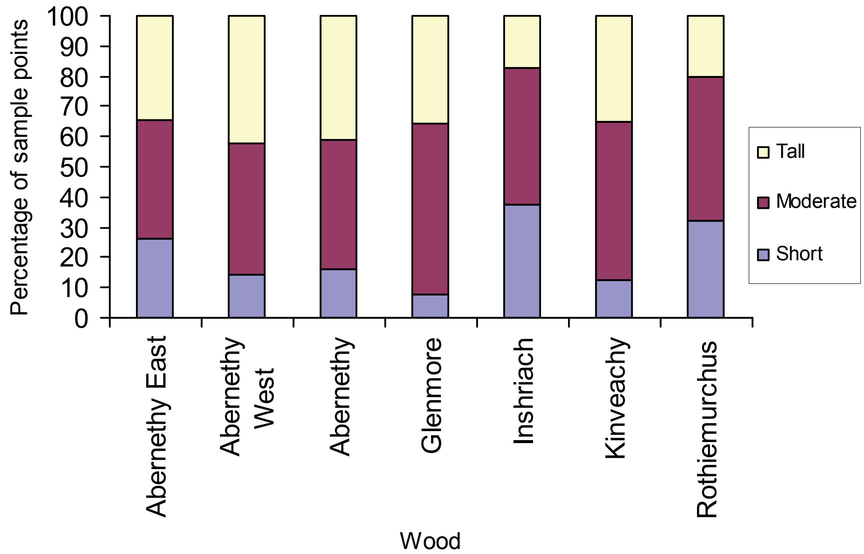


Figure 11. The percentage of points with cotton-grass at different height classes in different woods. There were too few values at Inverlaidnan and Craigmore for illustration

The frequency of occurrence of juniper varied from less than 1% of sample points in Kinveachy to 28% in Abernethy West (Figure 12). It was also common in Craigmore and Rothiemurchus, and sometimes localised; e.g. the western side of Rothiemurchus.

The frequency of occurrence of bracken varied from 1% of sample points in Inverlaidnan to 25% in Craigmore (Figure 12). In several woods, bracken was localised; in Rothiemurchus, it occurred along the rivers; in Kinveachy, it was in the eastern plantations; and in Glenmore, it occurred in the northern and central sections.

The frequency of occurrence of brash varied from 37% of sample points in Rothiemurchus to 79% in Craigmore, where there had been much brash creation by pulling over trees as part of habitat management (Figure 12).

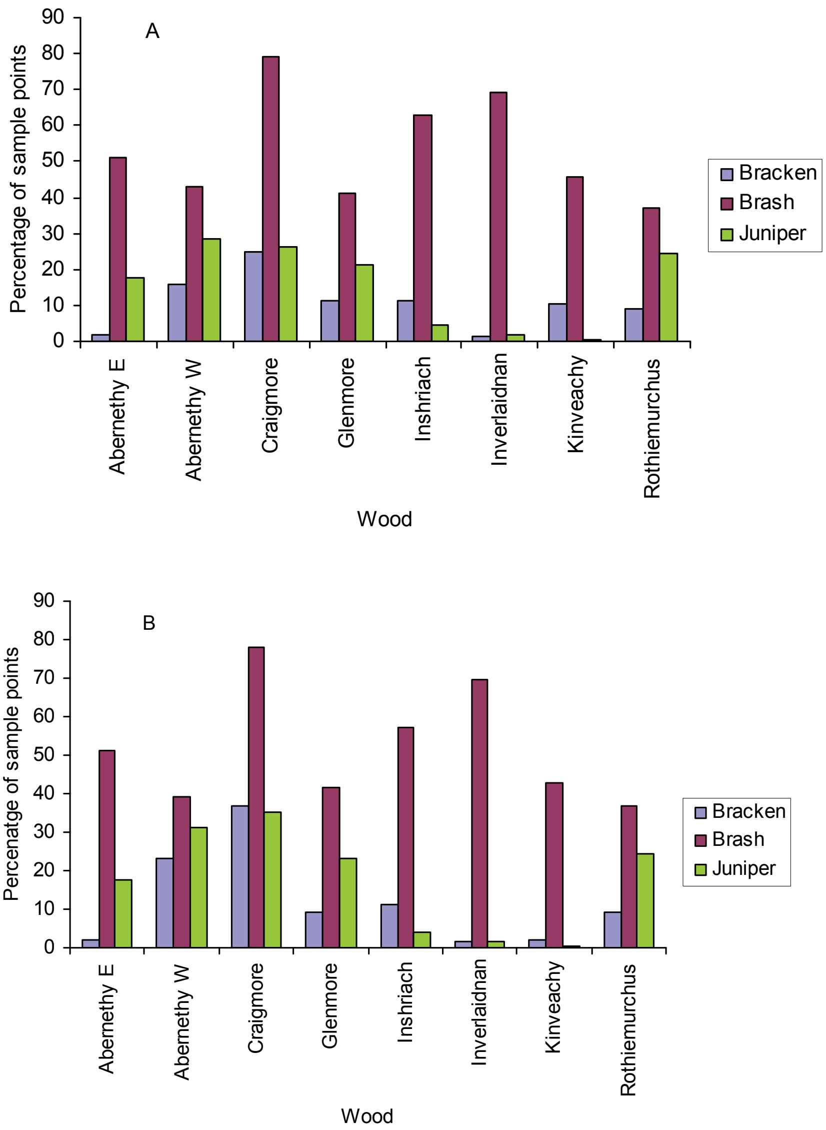


Figure 12. (A) The percentage of sample points with different types of cover in different woods, (B) those parts used by capercaillie

Habitat data were also summarised for those areas used by capercaillie. Comparisons of Figures 7B, 8B and 12B with the corresponding figures for the whole woods (Figures 7A, 8A and 12A) show little difference within the different woods.

4.3 Weather

Weather data for 2004-2013 at Aviemore and Abernethy are shown in Table 6. The wettest year was 2007 and the driest was 2010. There was a high correlation between rainfall at Aviemore and Abernethy (r=0.83, n=10, p<0.01).

The mean April air temperature ranged from 10.02°C in 2011 to 4.50°C in 2012.

The April warming index was lowest in 2008 and highest in 2013. Most values were negative. The warming index and mean April temperature were not significantly correlated (r=-0.26, n=10, p>0.05). For example, although the warming index was highest in 2013, the mean temperature was low.

Table 6. Total June rainfall (mm) in June as recorded at the Aviemore and Abernethy, and the April warming index and mean April air temperature (based on Aviemore data).

Year	Aviemore rainfall	Abernethy rainfall	Percentage difference between Aviemore and Abernethy	April warming index	Mean April temperature °C
2004	74.0	127.7	73	-0.21	7.61
2005	62.8	71.7	14	-0.15	6.73
2006	45.2	49.4	9	0.23	5.63
2007	78.0	133.0	71	-0.41	9.76
2008	68.9	68.7	-0.3	-2.07	5.29
2009	71.0	59.1	-17	-1.68	8.45
2010	39.0	39.4	1	-0.29	6.88
2011	73.2	68.6	-6	0.03	10.02
2012	59.6	100.8	69	-0.85	4.50
2013	46.2	53.2	15	2.82	4.94

4.4 Predators

Scats of red foxes and pine martens

The lengths of each track type in each wood are shown in Table 7. Some woods, such as Abernethy and Inshriach, had fairly similar track types throughout, whereas Craigmore and Rothiemurchus had a greater variety of track types. Some sections, as originally selected by GWCT, were through woodland or over moorland, and defined as non-track (NT) in our study (Table 7).

Table 7. Lengths (m) of different track type in each wood

	UVT	MVT	VVT	OVT	WFP	NFP	NT	Total
Abernethy	7849	8348	0	0	0	0	0	16197
Abernethy W	2943	5005	0	0	0	0	0	7948
Abernethy E	4906	3343	0	0	0	0	0	8249
Craigmore	2359	2528	2521	661	0	0	2031	10100
Glenmore	9012	720	0	29	0	0	0	9761
Inshriach	10421	2170	0	0	0	0	0	12591
Inverlaidnan	6318	0	0	0	0	0	0	6318
Kinveachy	3719	3399	1816	0	0	0	0	8934
Rothiemurchus	3359	0	0	0	3998	2359	3998	13714

Detectability of dummy scats

Tests of the detectability of dummy scats showed that it was relatively easy to see scats on un-vegetated vehicle tracks, but it became progressively more difficult to detect them as tracks became more vegetated (Table 8). It was also easy to see dummy scats on footpaths, probably because the search width was smaller than along vehicle tracks. There was, however, a particularly eroded and braided footpath in Rothiemurchus (from NH951057 to NH953067) where the detectability was poor.

Table 8. Tests of the detectability of dummy scats along tracks of different types

Wood	Track type	Code	Percent of dummy scats found
Abernethy	Un-vegetated vehicle track	UVT	92
Abernethy	Un-vegetated vehicle track	UVT	96
Abernethy	Vehicle track with vegetation up the middle	MVT	78
Craigmore	Vehicle track with vegetation up the middle	MVT	72
Craigmore	Fully vegetated vehicle track	VVT	56
Craigmore	Fully vegetated vehicle track	VVT	28
Craigmore	Overgrown vehicle track	OVT	29
Rothiemurchus	Wide footpath	WFP	92
Rothiemurchus	Narrow footpath (eroded)	NFP	46
Rothiemurchus	Narrow footpath	NFP	98

Identifying scats

Scats were identified on size when initially counted. To check on the accuracy of identification, 95 scats were identified molecularly (Table 9). The identification of five scats was not determined. Three (9%) of 34 fox scats were incorrectly identified as pine marten, and eight (15%) of 61 pine marten scats were incorrectly classed as fox. Thus, 88% were correctly identified, similar to the 91% recorded correctly by Summers & Denny (2010). The tendency to mis-identify scats did not vary significantly for the two species (Yates' corrected $\chi^2=0.085$, df=1, $p=0.77$). The mean width of pine marten scats was 10.2mm (SD=4.7, $n=38$) and the mean width of fox scats was significantly greater (19.6 mm, SD=4.8, $n=32$; $t=9.2$, df=68, $p<0.001$). To correct numbers of scats identified in the field, those classed as pine marten were multiplied by (53/56 = 0.95) and those classed as fox were multiplied by (31/39 = 0.79) and the differences from the numbers classified were added to the other species.

Table 9. Numbers of pine marten and red foxes identified in the field and later identified on DNA

	Pine marten by DNA	Red fox by DNA	Total
Pine marten in field	53	3	56
Red fox in field	8	31	39
Total	61	34	95

Scat indices

To ensure comparability with the study by Baines *et al.* (2011a, b), we calculated the scat indices in the same way. A direct comparison between the data for the seven woods showed a strong correlation between the data for 2009 and 2013 (Figure 13). This indicated that the ranking of the relative abundances of foxes plus pine martens amongst the different woods had not changed. Abernethy Forest and Craigmore had the highest indices and Inverlaidnan the lowest. It was also notable that the indices were significantly higher in 2013 compared to 2009 (paired *t*-test = -5.4, df=5, *p*=0.003). Indices for the six woods were, on average, 2.0 (range 1.2-3.6) times greater in 2013 compared to 2009.

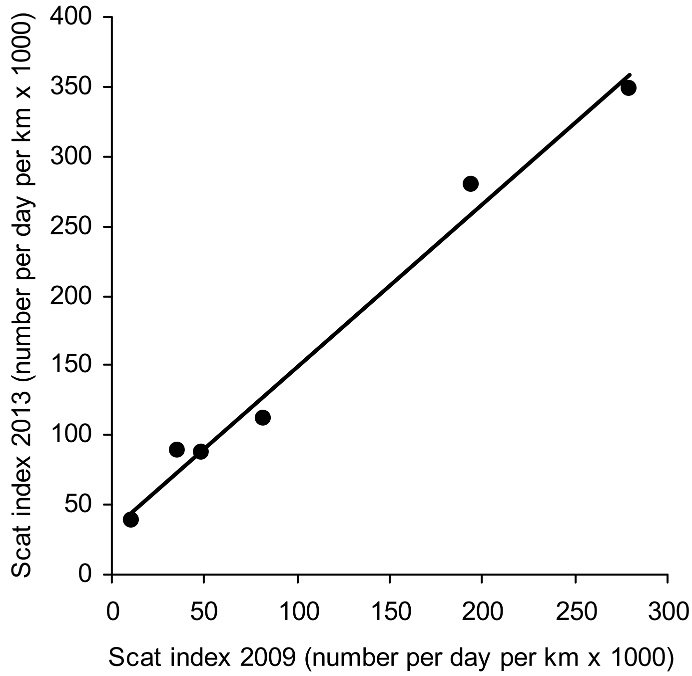


Figure 13. The relationship between the total mammal scat indices in 2013 and 2009

Before further analysis, the data for 2013 were modified. Given the variation in the detectability of dummy scats on different track types, it is likely that the detectability of pine marten and fox scats also varied between track types. There were insufficient tests made of detectability to provide correction factors for each track type. Instead, track types with low scat detectability were deleted from the data set in the calculation of scat indices. These were the overgrown vehicle tracks, fully vegetated vehicle tracks, the eroded footpath at Rothiemurchus (which was also largely outside woodland), and routes through woodland and over moorland (Table 7).

After deletion of data from the tracks where scats were difficult to detect, a total of 482 scats were collected during the clear-up round and 1321 during the four collections. The number of pine marten and fox scats counted during the four rounds was 1184 and 137 respectively, after correcting for mis-identified scats.

Corrected indices for pine marten and fox scats along the tracks for each wood are shown in Figure 14. Abernethy, and particularly Abernethy East, had the highest pine marten scat index, whilst Inverlaidnan had the lowest. The fox indices were consistently lower than pine marten indices. The fox indices were highest in Inshriach and Abernethy East, and lowest in Rothiemurchus and Inverlaidnan.

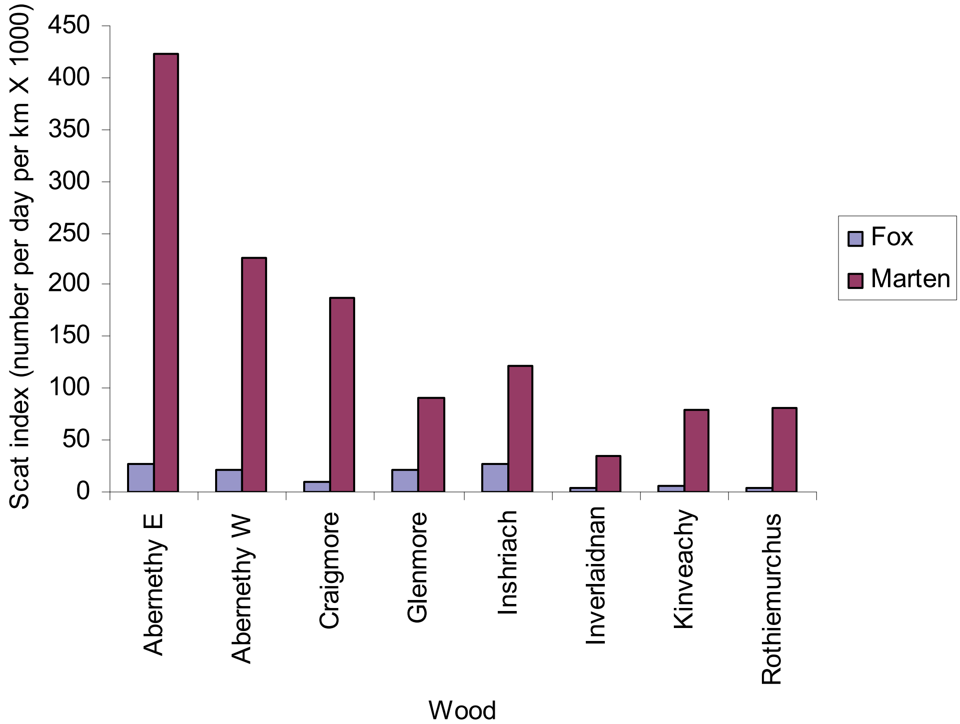


Figure 14. Indices of corrected red fox and pine marten scat abundance for 2013 after deleting tracks with low scat detectability

Raptors and corvids

The index of abundance of raptors observed along tracks was highest at Craigmore and raptors were not observed at several woods (Table 10). The raptors encountered were all buzzards *Buteo buteo* (15 encounters). The index of abundance of corvids observed along tracks was highest at Inshriach and Craigmore, and zero at several woods (Table 10). The corvids were 70% hooded and carrion crows, 10% ravens and 20% jays. Jays occurred mainly in Inshriach.

Table 10. Indices (numbers of encounters per hour x 100) of avian predators whilst surveying scats on tracks

	Raptors	Corvids
Abernethy	0.86	0.43
Abernethy W	1.86	0.93
Abernethy E	0.00	0.00
Craigmore	5.67	2.13
Glenmore	0.84	0.84
Inshriach	0.00	1.31
Inverlaidnan	0.00	0.00
Kinveachy	3.73	0.00
Rothiemurchus	0.68	0.68

4.5 Human disturbance

The indices of human disturbance were greatest in Glenmore and Rothiemurchus, and least in Craigmore, Inverlaidnan and Kinveachy (Table 11). Of the 39 groups of walkers encountered, 12 (31%) had dogs. Most had only one dog so, in addition to 70 walkers, there were 16 dogs.

Table 11. Indices (number of groups per hour x10, and total number per hour x10) of human use along tracks in each woods/sub wood

	Groups				Numbers			
	Walkers	Vehicles	Cyclists	All	Walkers	Vehicles	Cyclists	All
Abernethy	4.29	2.14	0.86	7.29	5.15	2.14	0.86	8.15
Abernethy W	7.45	0.00	0.93	8.39	9.32	0.00	0.93	10.25
Abernethy E	1.59	3.97	0.79	6.36	1.59	3.97	0.79	6.36
Craigmore	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glenmore	12.57	0.00	10.06	22.63	31.84	0.00	20.95	52.79
Inshriach	0.65	0.00	1.96	2.61	0.65	0.00	2.61	3.26
Inverlaidnan	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kinveachy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rothiemurchus	8.89	3.42	7.53	19.84	13.00	4.10	20.52	37.63

4.6 The relationship between capercaillie productivity and environmental variables

At the wood scale (*n*=8), significant negative correlations were found between mean capercaillie productivity and both cowberry cover and the pine marten scat index (Table 12, Figure 15). Cowberry cover and the pine marten scat index were themselves, however, strongly correlated (r=0.85, n=8, p< 0.01), probably because of the high amounts of both in Abernethy. There was also a weak relationship with the weighted June rainfall (negative relationship) (Table 12).

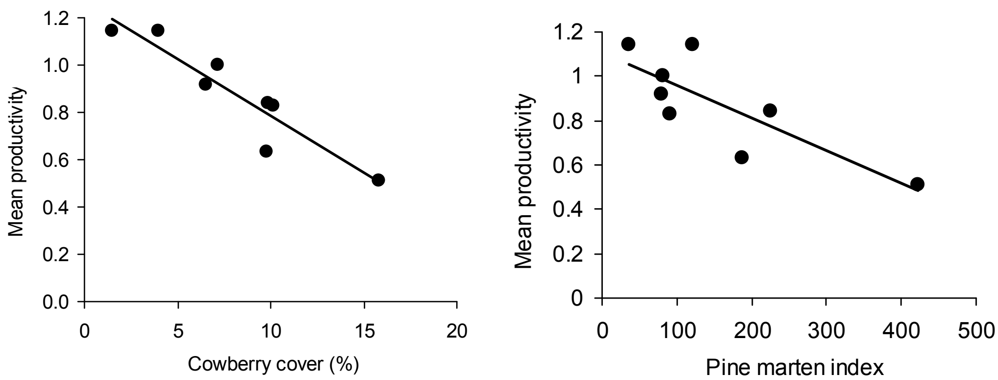


Figure 15. The relationship between the mean capercaillie productivity for 2009-2013 and the mean percentage cover of cowberry, and the pine marten scat index in different woods

Table 12. Results of Poisson regression models examining associations between mean capercaillie productivity across 2009-2013 with the percentage of sample points with blaeberry, cowberry and the index of pine martens

	Estimate	se	χ^2 (*p*)
Intercept	0.3635	0.1469	6.12 (0.013)
Cowberry cover	-0.0616	0.0168	13.44 (<0.001)
Scale parameter	1.0		
Intercept	0.0859	0.0958	0.8 (0.370)
Pine marten index	-0.0017	0.0006	8.6 (0.003)
Scale parameter	1.0333		
Intercept	2.0455	1.1316	3.27 (0.071)
Weighted June rainfall	-0.0374	0.0193	3.77 (0.052)
Scale parameter	1.2867		

For the multivariate analysis at the scale of the 1 km squares (*n*=80), a correlation matrix of all the explanatory variables is given in Table 13, showing numerous significant correlations. Some showing high correlation coefficients (>0.7 and <-0.7) can be regarded as different expressions of the same variables; for example the percentage of points with heather and mean heather cover. There was a similar pattern for cotton-grass. Others included negative associations between two types of ground cover; for example heather and grass. The correlation between management and stand type D reflects the stage where stands of this type are managed by thinning. Before multivariate modelling, therefore, the number of habitat variables was reduced using univariate tests (see Methods). The final model generated by backwards selection is presented in Table 14 and shows additive, inverse relationships between capercaillie productivity and both juniper occurrence and the April warming index, as well as a weak inverse relationship with the pine marten scat index. Moran's tests showed no significant spatial structure in model residuals.

Table 13. Pearson correlation coefficients among independent variables in 1km squares during 2009-2013 in different woods. With n=80, all coefficients greater than c. 0.217 and less than c. -0.217 are statistically significant, but only those greater than 0.7 and less than -0.7 are highlighted.

	% heath	% blaeb	% cowb	% grass	% Cottgr	Heath Ht	Blae Ht	Tall grass	% junip	% brash
% blaeb	-0.21									
% cowb	0.06	0.38								
% grass	-0.74	0.19	-0.01							
% cottgr	0.33	-0.38	-0.09	-0.37						
Heath Ht	0.40	-0.11	0.20	-0.39	0.18					
Blae Ht	0.31	0.15	0.29	-0.22	0.01	0.35				
Tall gras	0.22	-0.35	-0.29	-0.12	0.14	0.09	-0.13			
% junip	0.05	0.16	0.14	0.06	-0.13	0.46	0.43	0.00		
% brash	-0.56	0.43	0.05	0.55	-0.30	-0.14	-0.17	-0.23	0.18	
% brak	-0.15	0.25	0.14	0.29	-0.14	0.12	0.32	-0.18	0.48	0.17
Mgmt	-0.62	0.07	-0.03	0.65	-0.34	-0.28	-0.03	-0.33	-0.09	0.50
Fox	-0.03	0.00	0.10	0.04	0.11	0.25	0.30	-0.20	0.10	0.05
Marten	0.16	0.18	0.39	-0.05	0.18	0.33	0.33	-0.17	0.31	0.13
Crow	0.09	-0.01	-0.05	0.11	-0.03	0.07	0.18	-0.08	0.27	0.22
Buzz	-0.15	0.30	0.15	0.07	-0.07	-0.21	-0.01	-0.01	0.07	0.07
Disturb	0.37	-0.23	0.07	-0.29	0.12	0.32	-0.02	0.23	0.22	-0.22
Heath cov	0.85	-0.42	-0.12	-0.74	0.27	0.39	0.06	0.32	-0.03	-0.64
Blae cov	-0.31	0.90	0.27	0.25	-0.37	-0.19	0.14	-0.38	0.14	0.48
Cow cov	0.30	0.32	0.72	-0.31	0.05	0.32	0.23	-0.14	0.15	-0.03
Gras cov	-0.72	0.07	-0.09	0.90	-0.30	-0.41	-0.27	0.00	-0.03	0.47
Cott cov	0.27	-0.38	-0.10	-0.28	0.95	0.15	0.02	0.14	-0.06	-0.25
Stand A	0.38	0.04	0.07	-0.42	0.10	0.19	-0.05	0.24	0.18	-0.30
Stand B	-0.36	0.33	-0.06	0.36	-0.20	-0.17	-0.09	-0.23	0.01	0.39
Stand C	0.06	-0.19	0.17	-0.11	0.34	0.11	0.24	0.05	-0.01	-0.14
Stand D	-0.49	0.06	-0.08	0.51	-0.25	-0.26	-0.09	-0.29	-0.17	0.46
Stand E	0.38	-0.38	-0.14	-0.32	0.21	0.03	0.05	0.19	-0.12	-0.48
Stand F	0.19	-0.24	0.03	-0.05	-0.01	0.22	0.23	0.13	-0.01	-0.21
Apr warm	-0.03	0.00	0.11	0.01	0.07	-0.14	-0.13	-0.11	-0.16	-0.14
June rain	-0.14	0.30	0.14	0.15	-0.25	0.05	-0.03	-0.17	0.18	0.32
Apr temp	-0.05	0.18	-0.06	-0.02	0.02	0.16	0.07	0.09	0.19	0.23

	% brak	Mgmt	Fox	Marten	Crow	Buzz	Disturb	Heath cov	Blae cov	Cow cov	Grass cov
Mgmt	0.20										
Fox	0.07	0.26									
Marten	0.07	-0.22	0.46								
Crows	0.26	0.29	-0.29	-0.10							
Buzz	0.26	-0.09	-0.42	-0.22	0.18						
Disturb	-0.04	-0.25	-0.40	-0.34	0.40	-0.19					
Heath cov	-0.25	-0.70	-0.20	-0.02	-0.08	-0.15	0.38				
Blae cov	0.26	0.18	0.05	0.14	0.08	0.31	-0.21	-0.50			
Cow cov	-0.03	-0.16	0.22	0.45	0.01	-0.03	0.21	0.04	0.19		
Gras cov	0.23	0.59	-0.04	-0.14	-0.07	0.00	-0.35	-0.66	0.08	-0.39	
Cott cov	-0.13	-0.27	0.19	0.18	-0.04	-0.06	0.05	0.18	-0.37	0.04	-0.20
Stand A	-0.07	-0.74	-0.32	0.07	-0.29	0.12	0.23	0.52	-0.09	0.09	-0.36
Stand B	0.31	0.29	0.28	0.14	0.07	0.17	-0.39	-0.48	0.44	-0.08	0.20
Stand C	0.00	0.08	0.05	0.17	0.18	0.07	0.04	-0.02	-0.23	0.16	-0.05
Stand D	-0.01	0.85	0.18	-0.24	0.20	-0.19	-0.19	-0.55	0.16	-0.19	0.48
Stand E	-0.29	-0.31	-0.05	-0.08	-0.09	-0.17	0.24	0.44	-0.40	0.02	-0.25
Stand F	0.02	-0.01	0.11	-0.01	0.22	-0.15	0.16	0.10	-0.19	0.14	-0.08
Apr warm	-0.12	-0.01	-0.10	-0.13	-0.12	0.07	0.04	0.02	0.03	0.14	-0.04
Jun rain	0.16	0.22	0.15	0.12	0.10	0.11	-0.18	-0.20	0.25	0.11	0.07
Apr temp	-0.09	-0.10	0.14	0.27	-0.15	-0.11	-0.16	-0.08	0.13	-0.08	0.03

	Cott cov	Stand A	Stand B	Stand C	Stand D	Stand E	Stand F	Apr warm	Jun rain
Stand A	0.08								
Stand B	-0.20	-0.36							
Stand C	0.29	-0.32	-0.30						
Stand D	-0.20	-0.75	0.06	0.08					
Stand E	0.16	-0.07	-0.30	0.05	-0.22				
Stand F	0.04	-0.25	-0.08	0.10	-0.02	0.09			
Apr warm	-0.04	0.16	-0.09	-0.27	0.01	0.02	-0.08		
Jun rain	-0.28	-0.08	0.29	0.04	0.11	-0.35	-0.21	-0.39	
Apr temp	0.18	0.01	0.09	0.02	0.02	-0.18	-0.04	-0.47	0.26

Table 14. Results of multivariate Poisson regression mixed models examining associations between capercaillie productivity with independent variables

	Estimate	se	*t* (*p*)
Intercept	0.265	0.13400	1.97 (0.089)
April warming index	-0.334	0.10700	-3.12 (0.003)
Percent of points with juniper	-0.012	0.00540	-2.25 (0.028)
Pine marten scat index	-0.002	0.00008	2.03 (0.046)

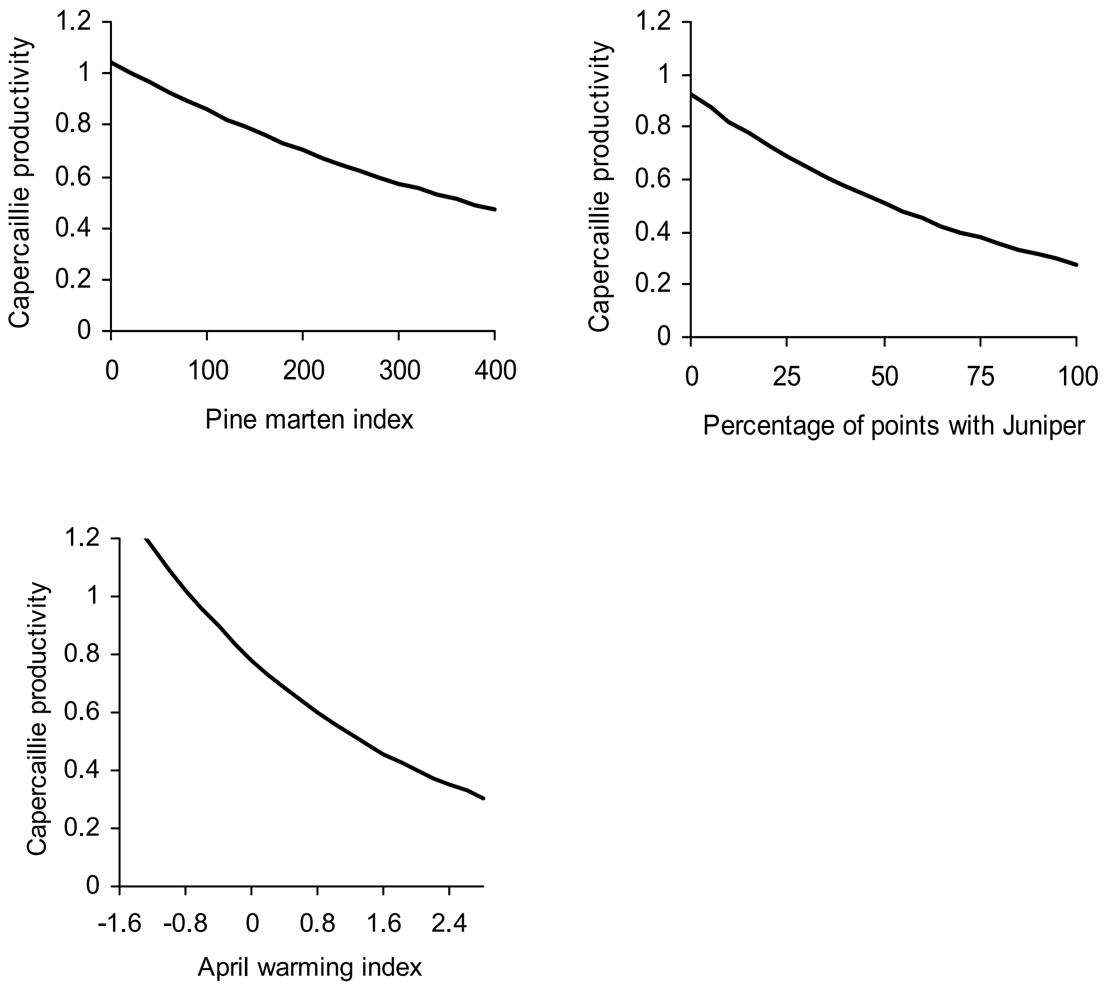


Figure 16. Modelled relationships between capercaillie productivity and the significant independent variables, as shown in Table 14. Mean values were used for the two variables not shown within a given graph

4.7 *Vaccinium* chemistry in relation to stand structure and management

A comparison among three stand types showed that blaeberry leaves in the old-growth stands at Abernethy (high crown and old open) had a higher percentage of dry matter, condensed tannins, total phenolics and lower oxidative capacity of phenolics than the blaeberry leaves in the thinned plantation at Inshriach (Table 15). This supports the hypothesis that the leaves in the old-growth woodland were better defended against herbivores than the leaves in the plantation.

Table 15. Mean values for chemical attributes of blaeberry in different stand types. Standard errors are given below the means.

	High crown	Old open	Thinned plantation	$F_{2,98}$	*p*
Number of samples	30	30	39		
Percent dry matter (%)	30.21	31.50	26.45	20.25	<0.001
SE	0.63	0.63	0.55		
Condensed tannins (% dry matter)	4.87	5.87	3.66	10.32	<0.001
SE	0.37	0.37	0.32		
Total phenolics (mg/gDM)	65.68	68.66	56.85	6.03	<0.01
SE	2.71	2.71	2.38		
Oxidative phenolics (mg/gDM)	23.55	25.43	24.21	0.29	>0.05
SE	1.36	1.36	1.19		
Oxidative capacity of phenolics (% of total phenolics)	35.64	37.02	42.58	8.27	<0.001
SE	1.38	1.38	1.21		

5. DISCUSSION

The study provided a wide ranging ecological audit of the capercaillie woods in Strathspey, describing tree species composition, woodland structure and associated frequency, abundance and height of the major ground flora. In this respect, it supports the general contrasts already acknowledged between the native pinewoods and plantations (Steven & Carlisle, 1959; Summers *et al*., 1999; Mason *et al*., 2004), but now provides quantified assessments and data on patterns of distribution.

5.1 Capercaillie distribution

The study provided a description of the capercaillie distribution in the different woods, potentially allowing associations to be examined between habitat characteristics and parts of the woods where capercaillies resided. This was not, however, the main focus of the current study, so is not reported.

5.2 Predator indices

It was notable that the scat counts in 2013 were highly correlated with the scat counts in 2009, indicating that the ranking of the woods in terms of the activity of foxes and pine martens had not altered over this five-year period. This provided assurance that the use of scat data from one year provided predator indices over a longer period, as used in the analysis of capercaillie productivity in relation to predator activity.

More scats were counted in 2013 than 2009. The difference could have been due to an increase in predator numbers, but could equally have been due to differences between observers in detecting scats, or the dry weather in 2013 allowing scats to be detectable for longer. Scats can vary in their condition, from fresh whole scats to broken and flattened smears that can be difficult to identify as scats, even if detected (Annex 5). Clearly, as scats break down, there will be a point along the scale of disintegration when they will no longer be recognisable. How one defines a scat is therefore crucial in assessing their abundance. It does, though, indicate that the definition of a scat should be clear and the ability of observers to detect scats should be measured if making comparisons between years. Weather variables during scat surveys also need to be considered otherwise changes in numbers of scats cannot be confidently interpreted as a change in mammal activity.

5.3 Weather

All the study woods were close together and there were only two weather stations covering the woods, making it difficult to detect strong weather effects among woods. Although the data for rainfall for the two weather stations were highly correlated, there were three years in which the rainfall was much higher at Abernethy compared to Aviemore. There was no corresponding large difference when Aviemore was wetter than Abernethy. It is therefore possible that the low productivity at Abernethy can be partly related to the differences in local weather, thereby explaining the association between productivity and June rainfall (Table 12).

5.4 Capercaillie productivity in relation to environmental variables

An initial examination of a series of the explanatory variables representing food, cover, and risk of predation or disturbance at the wood scale, found that capercaillie productivity was negatively associated with cowberry cover and the pine marten scat index. There was also a weak negative effect of rainfall. It is not obvious why cowberry would have a negative effect. These were, however, univariate comparisons, so need care in interpretation, especially since some variables were themselves correlated (e.g. cowberry cover and the pine marten index). By contrast, the correlation with June rainfall is well established (Moss, 1986; Summers *et al*., 2004a), even though the mechanism by which chicks die is not known. It could be due to direct wetting of the chicks, reduced prey availability, or increased calling by chicks to be brooded, thereby alerting predators (Wegge & Kastdalen, 2007).

The multivariate analysis at the 1 km grid square scale showed that capercaillie productivity was inversely correlated with three variables: April warming, the percentage of sample points with juniper, and the pine marten index. The larger sample size in this analysis allowed for the possibility of variables to be included in the model after accounting for the variance explained by the first variables within the model. The absence of cowberry in the multivariate analysis, therefore, is probably because it was strongly correlated with the pine marten index, so did not explain any further variance after the pine marten index was included in the multivariate model, even though cowberry was significantly correlated with capercaillie productivity in a univariate model. The fact that the pine marten index was present in both the wood scale and 1 km grid square analyses lends support to the strength of this correlation.

The negative correlation between capercaillie productivity and the percentage of sample points with juniper is surprising at first sight, because juniper can be regarded as having positive attributes, such as providing cover for broods. If, however, juniper is used as cover for moulting females after brood loss rather than cover for broods, this could account for the observed relationship.

The negative relationship between capercaillie productivity and the April warming index is also surprising, because an earlier study had found a positive association, for which there was a plausible explanation; more nutritious plants for egg-laying females (Moss *et al*., 2001). There are, however, no supporting data in terms of changes in the nutrition in the vegetation associated with April warming, nor evidence of more robust chicks when the warming index is high.

A likely explanation for the negative relationship between capercaillie productivity and the index of pine marten activity is that pine martens predated capercaillie clutches and chicks. There is direct evidence for this in Abernethy where pine martens took at least a third of clutches during 2003-2007 (Summers *et al*., 2009). Previous Scottish studies had failed to find a correlation between capercaillie productivity and pine marten abundance (Baines *et al.,* 2004; Summers *et al*., 2004a), perhaps because pine marten numbers were still increasing in Strathspey, having been locally extinct for much of the 20th century (Forsyth, 1900; Birks, 2002).

It was notable that some woods had a higher pine marten index than others. While some urge caution in using scat indices as a measure of pine marten abundance (Birks *et al*., 2004), it seems that there may be more pine martens in some woods compared to others. There is evidence that pine marten densities are affected by woodland fragmentation, with densities increasing up to an optimum level of fragmentation before declining (Caryl *et al*., 2012). It is thought that fragmentation results in a greater abundance of field voles, perhaps through more grassland being made available to voles; the primary food of pine martens in the UK (Birks, 2002). In this case, one might expect a correlation between the pine marten index and abundance of grassland in the different woods.

Given the results of our study there is a need to understand more about pine marten populations and their ranging patterns. One estimate has been made of the pine marten numbers in Abernethy and Inshriach based on genotyping hair samples from hair traps (Kubasiewicz, 2014), and preliminary work has been carried out on measuring home ranges and habitat use by marking three pine martens in Abernethy with GPS tags (RSPB unpublished data). Such information would help to design a scheme to test possible interventions such as diversionary feeding.

It is worth noting some of the variables, such as the crow, raptor and disturbance indices are dependent on the short period of time that the observer records them. As such, they are likely to be rather weak as explanatory variables compared to habitat measures and even scat indices which integrate over longer time periods and may be more reliable measures. This may explain why there was no evidence of an effect of crows, even though such effects have been found in previous studies (Summers *et al*., 2004a; Baines *et al*., 2004).

5.5 Disturbance

There was no evidence that capercaillie productivity was related to human disturbance. There is, however, growing evidence that human disturbance affects the distribution of capercaillie (Summers *et al*., 2007; Thiel *et al*., 2008, 2010; Moss *et al*., 2014). By denying capercaillie a proportion of woods, capercaillie are probably limited in their ability to expand in range and numbers.

5.6 Vaccinium chemistry in relation to stand structure

By having greater amounts of tannins and phenolics, blaeberry leaves in old-growth woodland were found to be better defended against herbivores than the leaves in the plantation. There is the possibility that insects, or the capercaillie themselves, will find leaves in old woodland more difficult to digest than leaves in plantations, and this could account for differences in capercaillie productivity between Abernethy and Inshriach. Additional work at Inshriach found, however, that insect damage to blaeberry leaves was greatest in the thinned racks compared to the blaeberry between the racks where the leaves had lower levels of secondary compounds than between the racks (Ross, 2014). It seems, therefore, that insects are responding largely to the increased light and warmth along the racks rather than the levels of secondary compounds. A fuller account of this work is in preparation (Iason *et al*., unpublished).

5.7 Conclusions

This study faced the difficulty of the range restriction of the capercaillie by carrying out a univariate analysis at wood level, recognising that the small sample size would prevent a fuller exploration of the data. We then broke the data down to a large number of 1 km squares recognising that we may be conflating variables that explain productivity with those that explain brood foraging habitat selection. Nevertheless, our study found relationships which had been found before, others that were interesting enough to warrant further investigation, and some difficult to interpret. For example, the negative effect of juniper on productivity is surprising, as it is generally regarded as good cover. If, however, females that lose broods seek the cover of juniper when they moult, this would account for the relationship we found.

The negative effect of high rainfall in June is well established. Our finding that some wet Junes were particularly wet at Abernethy is intriguing and may help to account for the low productivity at Abernethy in some years. A check of past weather records will establish whether Abernethy does tend to receive more rain. It would be worth establishing basic weather stations at all Strathspey woods to obtain wood-specific information, even if this were only for June rainfall. This would also help to test whether the close-by Craigmore has different weather from Abernethy.

The correlation between capercaillie productivity and the pine marten index needs further investigation. This includes establishing whether there is a relationship between pine marten density and the scat index. Some observers are highly sceptical of the use of scat numbers as an index of pine marten population size (Birks *et al*., 2004). We also need to know more about the habitat use of pine martens. Do they target grasslands for foraging within and outside woodlands? This would make them less likely to encounter capercaillie nests or broods. Furthermore, do pine martens venture onto adjoining farmland to hunt, and what proportion of pine martens do this? This basic information about pine martens is crucial for making further management decisions about capercaillie conservation.

The information on blaeberry chemistry has shown that differences do exist in key components of the blaeberry leaves in different stand types according to how they are managed. Even blaeberry in the two types of old-growth woodland in Abernethy differ, presumably because of the differing light levels. This now needs to be followed up by examining how this affects insect abundance.

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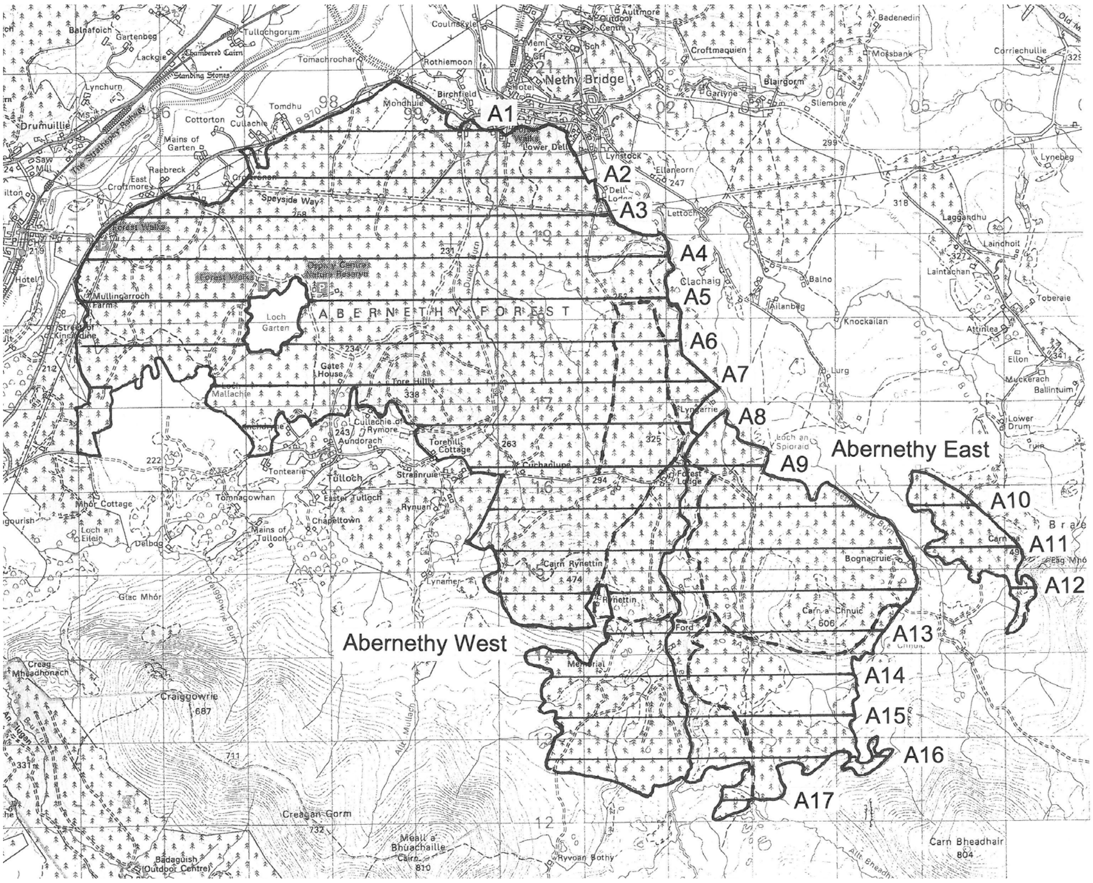
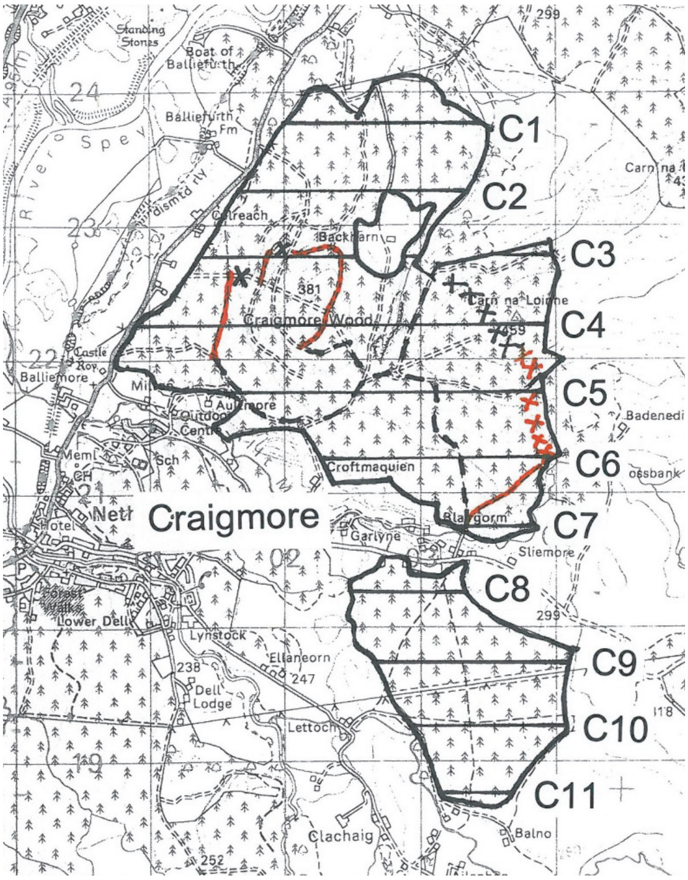
ANNEX 1. MAPS OF THE STUDY WOODS SHOWING THE PARALLEL EAST-WEST TRANSECTS (LABELLED WITH A LETTER FOR THE WOOD AND NUMBER) FOR HABITAT DESCRIPTIONS, AND TRACKS FOR SCAT AND AVIAN PREDATOR SURVEYS

Track colours: black dashes = un-vegetated vehicle track, or with vegetation in the middle, red = totally vegetated vehicle track, red crosses = overgrown vehicle track, dotted and dashed line = wide footpath, dotted line = narrow footpath, black crosses = woodland (no track).





C1
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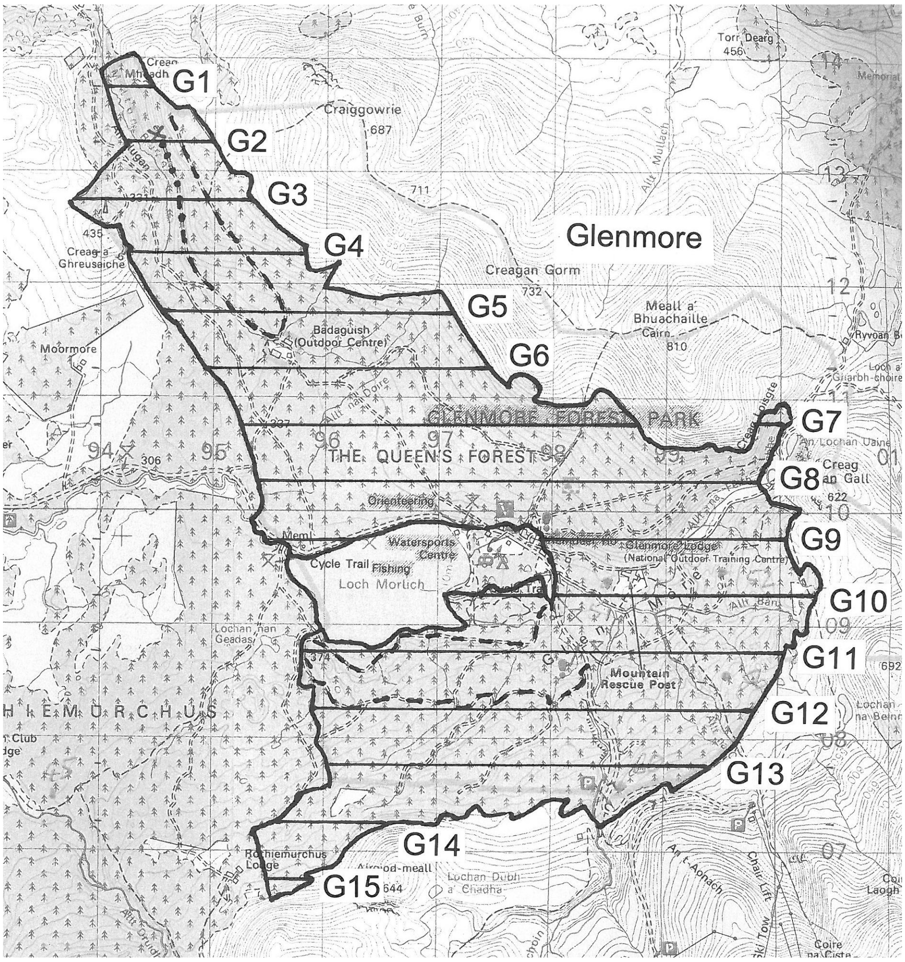
C3
C4
C5
C6
C7
C8
C9
C10
C11
Craigmore
Craigmore Wood



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G4
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G6
G7
G8
G9
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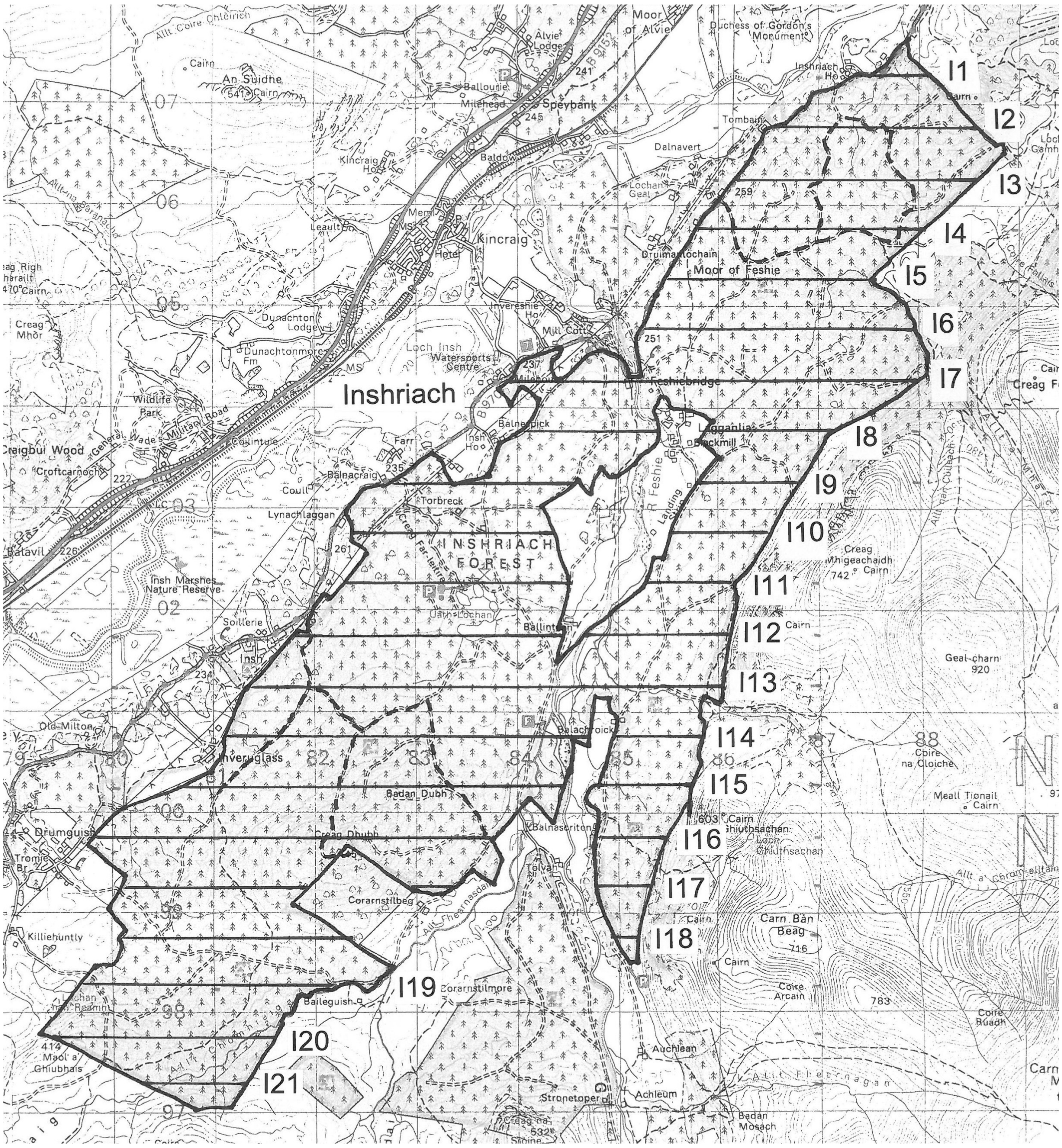
G12
G13
G14
G15
Glenmore
GLENMORE FOREST PARK
THE QUEEN'S FOREST
Loch Morlich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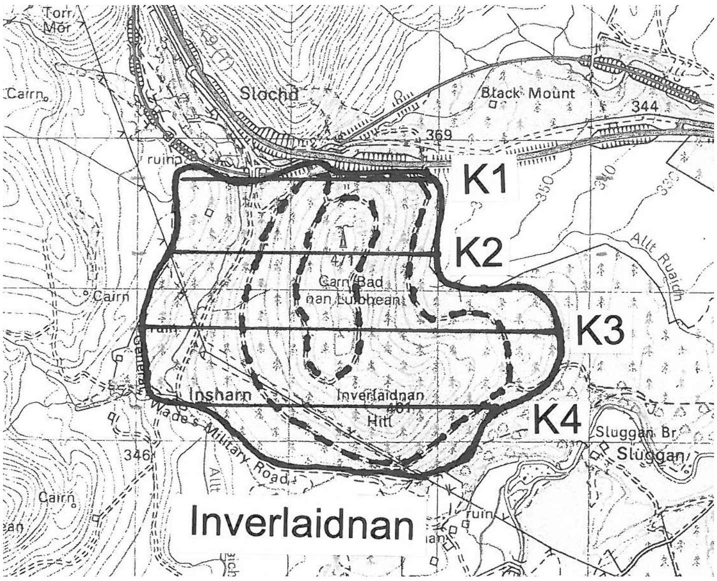
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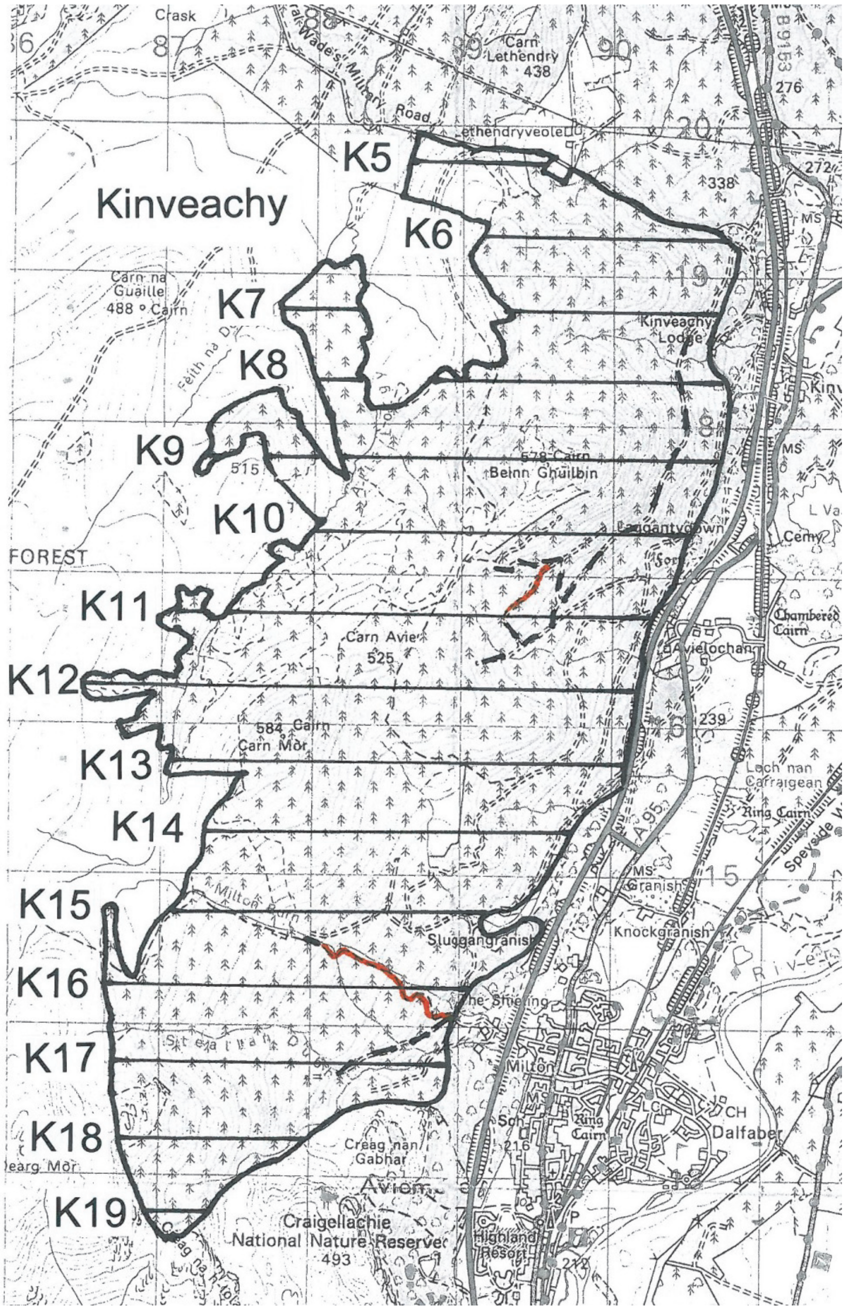

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K8
K9
K10
K11
K12
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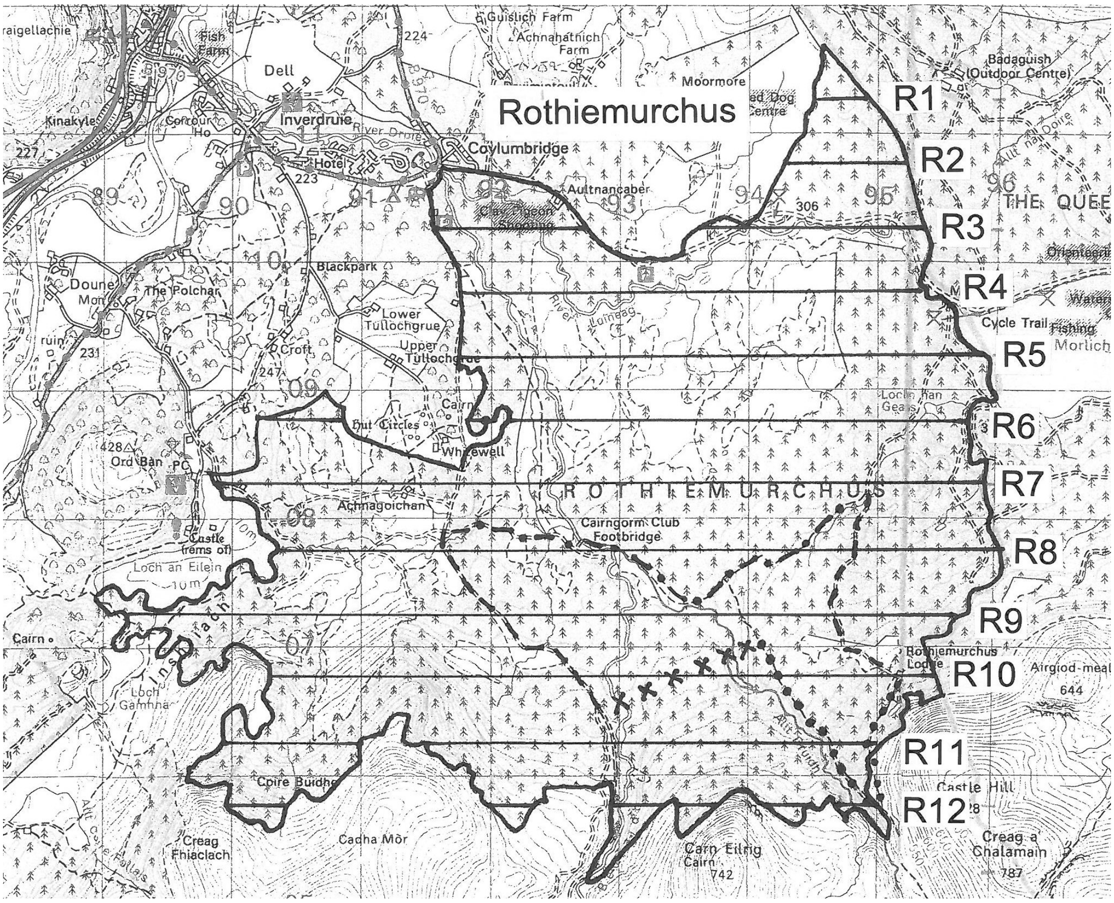
K15
K16
K17
K18
K19
Carn Lethendry
438
Carn na Guaille
488 Cairn
Wade's Military Road
Lethendryveole
Kinveachy Lodge
578 Carn
Beinn Ghuilbin
515
FOREST
Carn Avie
525
584 Cairn
Carn Mor
Chambered Cairn
Avielochan
239
Loch nan Carraigean
Ring Cairn
A95
Sluggangranish
Knockgranish
Milton
The Shieling
Ring Cairn
216
Dalfaber
Creag nan Gabhar
Craigellachie
National Nature Reserve
493
Highland Resort
B9153
276
272
338


Rothiemurchus
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ROTHIEMURCHUS
Coylumbridge
Inverdruie
Aviemore
Dell
Blackpark
Lower Tullochgrue
Upper Tullochgrue
Whitewell
Achnagoichan
Cairngorm Club Footbridge
Rothiemurchus Lodge
Loch an Eilein
Loch Gamhna
Coire Buidhe
Cadha Mòr
Carn Eilrig
Creag Fhiaclach
Creag a' Chalamain
Castle Hill
Badaguish (Outdoor Centre)
Moormore
Aultnancaber
Clay Pigeon Shooting
Doune
The Polchar
Ord Ban
Cycle Trail
Fishing
Airgiod-meall

ANNEX 2. EXAMPLES OF GRASS IN DIFFERENT HEIGHT CLASSES


Class 1(<5 cm high)


Class 2 (5-10 cm)


Class 3 (> 10 cm)

ANNEX 3. PHOTOGRAPHS OF STAND TYPES. SEE ALSO FIGURE 2


1 - Old sparse with 12 - pre-thicket


4 - Mature sparse with 12 - pre-thicket


2 - Old open


5 - Mature open


3 - High crown


6 - Pole

8 - Young open - bog pines

9 - Thicket

10 - Sparse pre-thicket, 6 - pole behind

11 - Open pre-thicket

12 - Pre-thicket

Clear-fell

ANNEX 4. PHOTOGRAPHS OF TRACK TYPES

Un-vegetated vehicle track (UVT)

Vehicle track with vegetation up the middle (MVT)

Vegetated vehicle track (VVT)

Overgrown vehicle track (OVT)


Wide footpath (WFP)


Narrow footpath (NFP)

ANNEX 5. PHOTOS OF SCATS AT DIFFERENT STAGES OF DISINTEGRATION. PHOTOS BY R. DENNY

1.

2.

3.

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