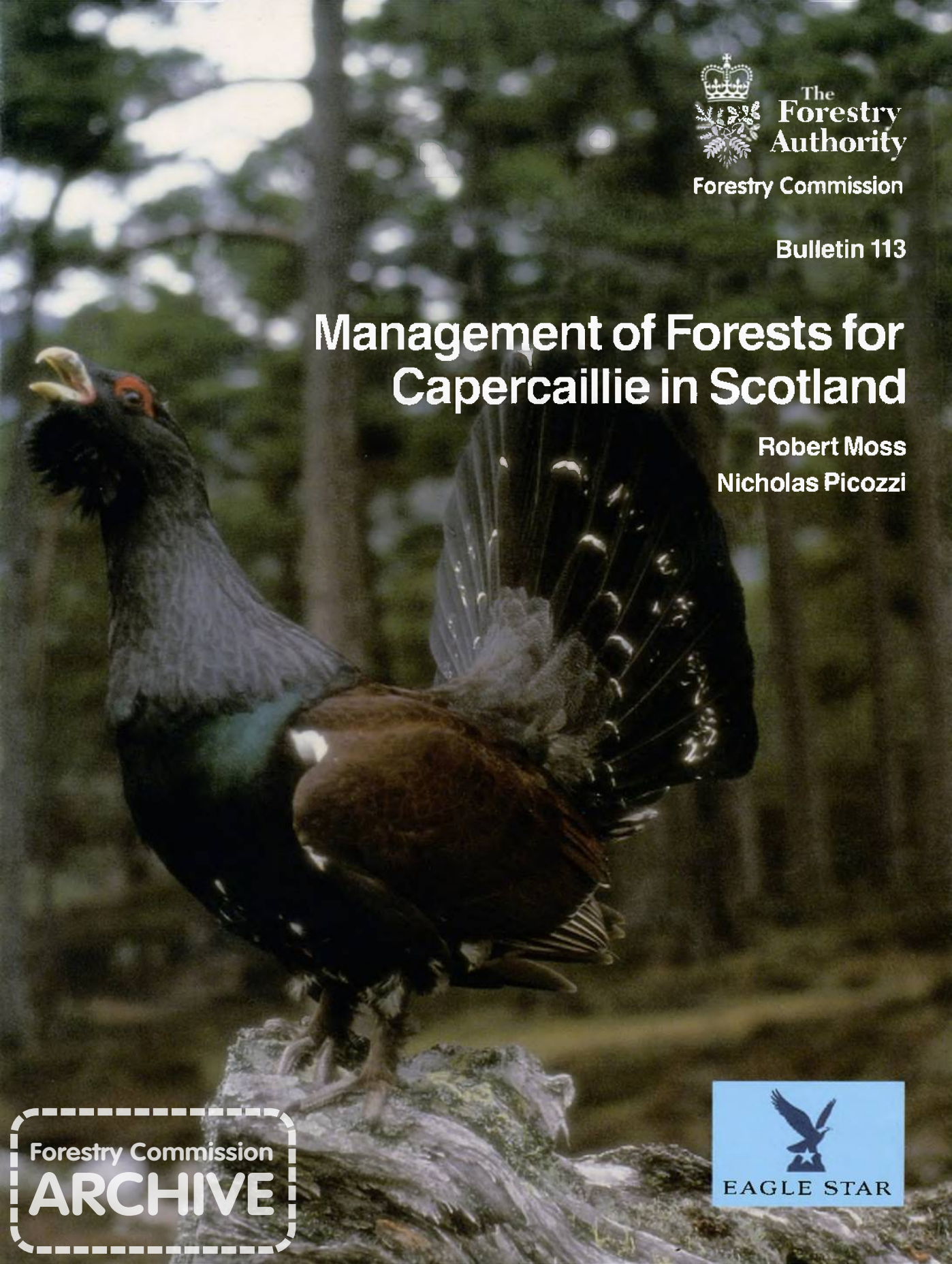

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Management of Forests for Capercaillie in Scotland

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Management of Forests for Capercaillie in Scotland

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Front cover: Cock capercaillie in full display (N. COOK)

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Management of Forests for Capercaillie in Scotland

Summary

The biology and status of capercaillie in Scotland are described. Both range and numbers are less than in the early 1970s. Possible reasons for the decline are discussed and recommendations for managing forests for capercaillie are made. In general, the winter diet comprises a wide range of conifers and in parts of Scotland the birds appear to eat Sitka spruce as readily as Scots pine. The association between capercaillie and old, semi-natural Scots pine forests is confirmed and it is suggested that this is largely because the open structure of such forests allows enough light to reach the ground to support heather and especially blaeberry (or bilberry). The structure of a forest may be more important than its tree species composition. Blaeberry is important as a chick food and also supports many of the insects upon which the chicks feed in their first weeks. Most plantations which support good populations of capercaillie are also rich in blaeberry and a major recommendation is that blaeberry should be encouraged. Guidelines for doing this are given. A few plantations with little blaeberry and heather also support capercaillie, so other ground vegetation may substitute for blaeberry, but the details are uncertain at present. Capercaillie are big birds with large home ranges and their management needs to be planned on a large scale. The impacts on capercaillie of changing climate, predators, mortality caused by fences, heavy grazing of ground vegetation by red deer and human disturbance are discussed.

La gestion des forêts au bénéfice des grands coqs de bruyère en Ecosse

Résumé

La biologie et le statut des grands coqs de bruyère en Ecosse sont décrites. Leur distribution et abondances sont plus faibles qu'au début des années septantes. Les causes possibles de ce déclin sont considérées et des recommandations pour la gestion des forêts au bénéfice des grands coqs de bruyère sont faites. En général, la diète hivernale comprend une grande variété de conifères et, dans certaines régions d'Ecosse, les oiseaux semblent manger du sapin Sitka ainsi que du pin sylvestre. La relation entre les grands coqs de bruyère et les vielles forêt semi-naturelles de pin sylvestre se confirme et il est suggéré que ceci est dû en grande partie à la structure ouverte de ces forêts qui permet que suffisament de lumière pénètre jusqu'au sol pour maintenir la bruyère et surtout le myrtillier. La structure d'une forêt peut être de plus grande importance que la composition en espèces de ses arbres. Le myrtillier est important comme nourriture pour les poussins et habrite aussi beaucoup d'insectes dont les poussins se nourrissent pendant les premières semaines de vie. La plupart des plantations qui habritent un bon nombre de grand coqs de bruyère sont riches en myrtilliers et une des recommandations faites est que le myrtillier doit être encouragé. Des indications sont données à cet effet. Certaines plantations avec peu de myrtillier et de bruyère contiennent aussi des grands coqs de bruyère, donc une autre végétation du sol peut remplacer le myrtillier mais, à présent, sa nature est indéfinie. Les grands coqs de bruyères sont de grands oiseaux avec de grands domaines vitaux et leur gestion doit être planifiée à grande échelle. Les effets sur les grands coqs de bruyère du changement de climat, des prédateurs, de la mortalité causée par les clôtures, les conséquences du pâturage excessif de la végétation du sol par les cerfs élaphes et de l'intervention de l'homme sont aussi considérés.

Forstpflege für Auerhahn in Schottland

Zusammenfassung

Die Biologie und der Zustand des Auerhahns in Schottland wird hier beschrieben. Sowohl Verbreitungsgebiet als auch Bestand sind heute geringer als Anfang der siebziger Jahre. Mögliche Gründe für den Rückgang werden diskutiert und es werden Vorschläge zur Forstpflege in Bezug auf Auerhähne gemacht. Im allgemeinen besteht die Winterdiät aus einer weiten Auswahl von Nadelbäumen und in Teilen Schottlands scheinen die Vögel Sitka Fichte ebenso bereitwillig wie Waldkiefer zu fressen. Die Verbindung zwischen Auerhähnen und alten, halbnatürlichen Waldkieferforsten wird bestätigt und es scheint, dies ist größtenteils auf die offene Struktur dieser Wälder zurückzuführen, die es erlaubt, daß genug Licht den Erdboden erreicht um den Wuchs von Heidekraut und Heidelbeere zu ermöglichen. Die Struktur eines Waldes könnte wichtiger sein, als die Baumartenkomposition. Heidelbeere ist ein wichtiges Kückenfutter und erhält außerdem viele jener Insekten von denen sich die Kücken in den ersten Wochen ernähren. Die meisten Pflanzungen, die einen guten Auerhahnbestand aufweisen, sind ebenfalls reich an Heidelbeeren und ein Hauptvorschlag ist die Unterstützung von Heidelbeerwuchs. Dafür werden Richtlinien gegeben. Ein paar Pflanzungen mit wenig Heidelbeere und Heidekraut unterhalten ebenfalls Auerhähne, es ist somit möglich, daß andere Bodenvegetation als Ersatz für Heidelbeere wirkt aber die Einzelheiten dazu sind im Moment unklar. Auerhähne sind große Vögel mit großen Ausbreitungsflächen und ihre Plege muß damit in großem Umfang geplant werden. Die Auswirkungen von Klimaänderungen, Raubtieren, Sterberaten durch Zäune, Abweidung der Bodenvegetation durch Rehwild und menschlichen Störungen auf Auerhähne werden ebenfalls diskutiert.

Manejo de Bosques para los Urogallos en Escocia

Resumen

Se desciben la biología y el estado de conservación de los urogallos en Escocia. Tanto el rango de distribución como los números de individuos son inferiores a los registrados a comienzos de la década de 1970. Se discuten las razones posibles de esta disminución y se hacen recomendaciones para el manejo de los bosques en favor de los urogallos. En general, la dieta invernal comprende gran variedad de coníferas; en algunas partes de Escocia, las aves paracen consumir abeto Sitka al igual que pino albar. Se confirma la asociación de los urogallos con los viejos bosques semi-naturales de albar y se sugiere que ésta se debe en gran parte a la estructura semi-abierta del dosel, que permite suficiente penetración de luz hasta el suelo para el desarrollo de brezo y arándano. Las estructura de un bosque puede tener mayor importancia que la composición de especies arbóreas. El arándano es importante como alimento para los polluelos, y también sostiene muchos de los insectos a partir de los cuales se alimentan los polluelos durante las primeras semanas de vida. La mayoría de las plantaciones que sostienen buenas poblaciones de urogallos, son ricas en arándano; una de las recomendaciones claves es que se estimule el desarrollo de esta planta. Se proporcionan los lineamientos para lograr esto. Algunas plantaciones con poco arándano y brezo también sostienen urogallos. Por lo tanto, otros tipos de vegetación baja pueden sustituir al arándano, aunque los detalles se desconocen hasta el presente. Los urogallos son aves de gran tamaño, que ocupan grandes extensiones. Su manejo debe ser planficado en gran escala. Se discute el impacto de diferentes factores sobre los urogallos: el clima cambiante, los predadores, la mortalidad causada por cercas, el pastoreo intensivo de la vegetación por parte de venados rojos y la perturbación de origen antrópico.

Management of Forests for Capercaillie in Scotland

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Background

The capercaillie (family Tetraonidae) is the biggest grouse in the world. It lives in Old World boreal and temperate forests and its range coincides largely with that of its main winter food, the Scots pine (Seiskari, 1962). Populations also occur in forests dominated by other species of pine, fir, spruce, oak, beech (Dement'ev and Gladkov, 1952; Semenov-Tjan-Schanskij, 1960; Jacob, 1988) and even in holly forests of the Spanish Pyrenees (Castroviejo, 1975). In Scotland, while usually associated with semi-natural and planted Scots pine, it also occurs in mixtures of pine and introduced conifers.

Capercaillie became extinct in England in the 17th century (Cramp and Simmons, 1980). The last record of native Scottish capercaillie is from 1785 when two were shot on the occasion of a marriage rejoicing in Aberdeenshire (Pennie, 1950). By the second half of the 18th century, Scottish forests were at a low ebb following widespread felling of the native Scots pine (Harvie-Brown, 1888; Ritchie, 1920). By mischance, this coincided with the 'Little Ice Age' (Kullman, 1987), a period when summers were cold and wet. Such conditions are known to reduce the survival of capercaillie chicks (Moss, 1986). Continued shooting may then have hastened the end of the Scottish race. Extensive reafforestation which began in the late 18th and early 19th centuries was probably too late to save it from extinction.

The first successful reintroduction of capercaillie to Scotland was on Lord Breadalbane's estate at Taymouth Castle, Perthshire. Twenty-nine adult birds (13 cocks and 16 hens), followed soon after by another 20 birds, were trapped in Sweden and transported to the estate in summer 1837. A further 16 hens were imported in summer 1838. By 1839, it was estimated that between 60 and 70 capercaillie were at large on the estate and by 1862 the population there had grown to an estimated 1000–2000 birds. A good account of this and other reintroductions is given by Lever (1977, reprinted in Lovel, 1979). The success of the reintroduction seems to have been due to a combination of careful attention to details, zealous 'vermin' control, the good state of the habitat into which the birds were released, and the success of introducing capercaillie eggs into greyhen nests. The forest at Taymouth was largely of Scots pine but also contained mature larch. The spread of birds through the wooded river valleys of central and eastern Scotland was rapid, and helped by further successful introductions elsewhere in Scotland (e.g. at Cortachy, Angus in 1862, and Strathnairn, Morayshire between 1894 and 1900). Judging from bag records (Baines *et al.*, 1991), peak numbers were reached in the 1920s and 1930s. Shooting bags were often high: the record for Scotland was 150 in a day at Blackhall forest, Kincardineshire in 1908. Declines thereafter were associated with fellings of mature woodlands and semi-natural pinewoods, particularly during the Second World War. There was a second, lower peak in the 1960s and early 1970s, but since then a further sustained decline has led to gloomy speculation about the future of capercaillie in Scotland.

When abundant, capercaillie were regarded as pests for eating tree buds and freshly sprouted leaders. At such times their nests were destroyed, chicks crushed underfoot and shoots organised to reduce their numbers. But by the mid 1950s Palmer (1956) was advocat-

ing control only in exceptional circumstances. Indeed, the potential sporting value of capercaillie to a landowner (over £2000 per bird, see later) far outweighs any damage they might cause. In an attempt to conserve dwindling stocks few estates now shoot capercaillie, and rights to shoot them on Forestry Commission land have not been relet since 1982.

The aim of this Bulletin is to summarise the best current information about the birds' requirements and to provide guidelines for forest management which will benefit capercaillie. As far as possible, we base our recommendations on well-documented facts. Where hard data are not available, we make informed guesses based on anecdotal natural history and casual observations. Some of these guesses may be wrong; when we know more, we shall be able to improve upon them.

Description

Appearance

The capercaillie is a huge grouse; cocks in Scotland typically weigh about 4 kg and hens just under 2 kg. The cock has predominantly dark-grey plumage and dark-brown wings. The long, black tail forms a broad fan during display and is often flecked in individually distinct white patterns. He has a large, pale, hooked beak and massive head. The skull is reinforced for combat with other cocks in the mating season, but even so the powerful beak of the cock can inflict severe injuries, sometimes death, upon rivals. Skulls of both cocks and hens become progressively ossified with age, and this gives a method for telling a bird's age (Kirikov, 1944; Moss, 1987a). The hen is mainly brown, with warm-buff and white-barred body feathers and coverts, while orange-buff suffuses the chest and throat. She bears a superficial resemblance to a greyhen, but the latter is smaller and, in good light, can be seen to have whitish wing bars, white axillaries and a slightly forked tail, and to lack the orange coloration on chest and throat. The mortality rate of adult capercaillie is about 30–35 % a year (Moss, 1987b), but individual cocks have been known to live for up to 11 years.

Mating

The capercaillie's mating system is of the 'lek' type in which a number of cocks gather at a traditional display ground (lek) in spring to compete for the attention of hens. Old cocks may be seen displaying sporadically in any month of the year, except July when they are in heavy moult. The peak display period is very short, only a week or two in late April and early May. They begin to gather near the lek in late March. Leks are usually in open pole stage or mature woodland (Plate 1), but exceptionally on areas with trees less than 2 m high (Plate 2). Ground vegetation may be sparse, as in plantations, or dense, as in open semi-natural forest. Display begins just before first light and, if undisturbed, may continue until late morning when hens are present. Cocks in full display strut with head and neck erect, wings drooped and trailing stiffly along the ground, the tail spread upright in a broad fan. A round white spot shows prominently on each shoulder. Occasionally, cocks launch themselves 1–2 m off the ground and descend with wings beating rapidly and noisily. Such 'flutter-jumps' are often stimulated by hens arriving at the lek.

The cock's song seems strangely quiet for such a large bird. It consists of a series of accelerating double-clicks which culminate in an explosive 'pop' like a cork being drawn from a bottle, followed by a series of breathy wheezing noises: a knife being whetted is a popular description. However, the song is noisier than it seems to the human ear as a booming subsonic element has been detected using a tape recorder sensitive to low frequency sound (Moss and Lockie, 1979).

Early in the season, hens approach the lek alone or in small groups and sit on branches watching the cocks display (Plate 3). They may visit more than one lek. In the third week of April they come to the ground and most of them approach the dominant cock. When ready to mate, they crouch low by him. Surprisingly though, he shows no great eagerness

to mate and a harem of a dozen or more hens may develop, trailing him around the lek as they wait for service (Plate 1). Once mated the hen shakes herself, ruffles her feathers, preens, and soon leaves. She does not return unless her clutch is lost during egg-laying or soon after incubation has begun. The dominant cock mates with most of the hens, but such is the intensity of cock fights that today's dominant cock may be displaced by a rival, who may himself subsequently be displaced (N. Cook in Deeside and D. Dugan in Speyside, personal communications). Injured cocks may continue to display, but on the edge of the lek away from the main activity, and sometimes cocks are found dead at the lek. By early May the main display is over and, although some cocks still visit the lek, they tend to sit quietly and display infrequently.

Nest and chicks

Hens begin to lay their 5–11 (exceptionally up to 16) eggs in early May. The nest is usually within the forest and well concealed by ground vegetation. Occasionally, nests are on bare ground in dense woodland, or on clear-felled areas or heather moorland near to woodland. Chicks hatch synchronously 26–28 days after incubation begins, with most broods hatching in early June. When chicks are dry, they leave the nest with the hen and do not return. Cocks take no part in rearing the chicks, but there are records of cocks defending a brood against a predator (Semenov-Tjan-Shanskij, 1960).

Status of capercaillie in Britain

During 1990 and 1991, questionnaires were circulated to sporting estates, Forestry Commission rangers and nature reserve wardens as part of an ongoing joint project between the Institute of Terrestrial Ecology, Forestry Commission, Game Conservancy, Royal Society for the Protection of Birds, Scottish Landowners' Federation and Scottish Natural Heritage (Catt *et al.*, 1992). The survey aimed to determine the current status and distribution of capercaillie and to lay the foundations for estimating the total number of capercaillie in Scotland. Respondents were asked subjectively to categorise whether birds on their ground were scarce, regular or numerous. The results were then digitised using a Geographical Information System (GIS) ARC/INFO package (copyright 1987, 1988, 1989 Environmental Systems Research Institute, Inc. USA). The resulting map (Plate 4) shows the present range of capercaillie to be north of the industrial belt in Scotland, mainly from a line joining the Firth of Forth with the Firth of Clyde up to the Dornoch Firth, and from the Central Highlands eastward. They are more abundant in the east than in the west, with their main centres of population in Perthshire, Deeside, Speyside and the River Findhorn basin. Small, reportedly dwindling, populations are present in the west of their range at Loch Awe and Cowal in Argyll, Glen Garry and Glen Affric; only on the small islands of Inchmoan and Inchconnachan in Loch Lomond are densities still high in the west, although numbers there are small (Jones, 1990).

The picture over the last 20 years has generally been one of decline. A comparison between maps published in the first BTO Atlas for the period 1968–1972 (Sharrock, 1976) and in a Forestry Commission survey in 1983 (Tee *et al.*, 1985) shows a reduction in range north of the Great Glen. However, both maps show birds still present in the forests of the eastern coastal fringe from Aberdeenshire to Angus, but now (1994) there are none in this well-wooded region. Bag records (Baines *et al.*, 1991) indicate that the worst of the decline took place in the mid 1970s. Possible reasons for the decline will be considered later.

The capercaillie is now listed as a Red Data Book species (Batten *et al.*, 1990) and conservation measures through forest habitat management and continued careful control of shooting are necessary if numbers are not to decrease further.

Winter foods

Background

Comparing the winter diet of different populations of capercaillie with the proportion of dif-

ferent native tree species in the habitat shows that they prefer eating pine (Scots or Arolla pine) to fir, and fir to Norway spruce (Dement'ev and Gladkov, 1952; Gossow *et al.*, 1984; Jacob, 1988). However, they subsist on fir in the absence of pine, and spruce in the absence of fir and pine. In mixed forests they may prefer one species such as spruce for roosting, and another such as pine for feeding (Semenov-Tjan-Shanskij, 1960).

Most forest in Scotland now consists of introduced conifers and in recent decades Sitka spruce has been increasingly used. It is reasonable to expect the reintroduced Scottish capercaillie to eat Old World conifers, such as Norway spruce and larch, because some populations in Europe make much use of these species. However, capercaillie have had no evolutionary experience of New World species such as Sitka spruce and lodgepole pine. Whether they have adapted to eating these conifers to any extent is an interesting biological question and could be important for the birds' future in Britain, especially in forests where Sitka spruce is the main species. To tackle this question, the winter diet of Scottish capercaillie in forests where both spruce and pine occurred has been studied (Moss *et al.*, 1992).

Winter foods in Scotland

Six forests with capercaillie in Tayside Region were selected with different proportions of three main conifers: Scots pine, Sitka spruce and Norway spruce. Samples of droppings were collected in each forest and subjectively assigned to the bird's sex, usually on the basis of size but occasionally because the bird had been seen voiding it. Identification of conifer remains in the droppings was based on microscopic examination of the shape and pattern of stomata on the leaf epidermis (Plate 5 (a), (b)). These were quite distinctive, as were the remains of blaeberry and heather found in some faeces.

Scots pine, lodgepole pine, Sitka spruce, Norway spruce and larch were all found. Some other foods also occurred in small amounts: these included sedge seeds and heather and blaeberry leaves, stems and seeds.

Table 1 Main conifer species present (percentage by area of trees over 2 m in 1989 within 1 km of the lek) in six forest blocks in Tayside Region, and their frequency (%) in the winter droppings of capercaillie cocks and hens (in 1991–92).

	Present	*Cocks*	*Hens*
Drummond Hill			
Scots pine	30	100	81
Sitka spruce	35	t	14
Norway spruce	8	0	0
Lodgepole pine	0	0	0
(number of samples *n*)		(21)	(7)
Montreathmont			
Scots pine	49	78	57
Sitka spruce	35	19	40
Norway spruce	8	0	t
Lodgepole pine	2	3	3
(*n*)		(37)	(30)
Murray's Hill (Keillour)			
Scots pine	21	71	45
Sitka spruce	26	29	55
Norway spruce	37	0	t
Lodgepole pine	5	0	0
(*n*)		(21)	(22)
Bellour (Keillour)			
Scots pine	36	43	6
Sitka spruce	26	57	94
Norway spruce	20	0	0
Lodgepole pine	0	0	0
(*n*)		(14)	(16)
Aldie (Keillour)			
Scots pine	6	17	t
Sitka spruce	66	83	100
Norway spruce	15	0	0
Lodgepole pine	0	0	0
(*n*)		(18)	(16)
Blackcraig			
Scots pine	1	0	0
Sitka spruce	63	95	100
Norway spruce	21	5	0
Lodgepole pine	5	t	t
(*n*)		(19)	(7)

Notes The frequency above is the percentage of samples in which the indicated species predominated. The letter t means that the species occurred in one or more droppings but never predominated. Larch was eaten in autumn and spring but, being deciduous, not in winter. Blaeberry and heather occurred in some winter droppings, usually in small amounts; it was most frequent at Montreathmont where 22% of droppings had some blaeberry and 17% some heather. Spruce occurred more frequently in hens' than in cocks' droppings. Combining χ^2 values from four 2×2 contingency tables, using data from Aldie, Bellour, Murray's Hill and Montreathmont forests, gave $\chi^2 = 15.23$ ($p<0.005$).

Most samples comprised only one food species. Samples with more than one conifer species were assigned to the most abundant one for analysis (Table 1).

The composition of droppings ranged from mostly Scots pine at Drummond Hill to mostly Sitka spruce at Blackcraig (Table 1). The relative proportions of Scots pine and Sitka spruce broadly reflected the amounts available, but with some variation between forests. For example, there was an apparent preference for Scots pine at Drummond Hill and for Sitka spruce at Bellour. Norway spruce was eaten less frequently than expected from the amount present. Lodgepole pine occurred infrequently in the droppings, but was present only in small amounts in the forests. Larch was eaten in autumn and spring. Where capercaillie ate both Scots pine and Sitka spruce, the spruce was more often recorded in droppings classed as hens' rather than cocks'.

Conclusions on winter foods

The wide range of evergreen leaves eaten by capercaillie in different parts of their range illustrates their ability to adapt to different winter diets. In Scotland, Zwickel (1966) examined 99 crops of capercaillie obtained from game dealers and found that they contained 90% (dry weight basis) Scots pine needles, twigs and cones, but only a trace of Sitka spruce. Some years later, Jones (1982) examined 38 crops (using the same technique) and found 39% Sitka spruce in hens' crops but only 2% in cocks'. Our results also suggest that hens ate more Sitka spruce than did cocks (Table 1). Both earlier studies found only a trace of Norway spruce and no lodgepole pine. There might seem to have been a change in diet since 1966, with capercaillie now eating more Sitka spruce than formerly. However, the data do not really bear this interpretation since neither Zwickel (1966) nor Jones (1982) compared the birds' diet with the tree species available to them. Whether capercaillie could subsist entirely on a winter diet of Sitka spruce is not known. We know of no population in a monoculture of Sitka.

Moss *et al.* (1992) suggested that, although the site preferences of capercaillie in winter are probably related to the palatability of winter foods, this may sometimes be outweighed by other factors. Effects of palatability may be weak if the nutritive values of the different species are similar. Other potentially important factors are:

- ease of access to water
- a comfortable perch
- a place in the sun
- a good view of likely predators
- a good flight path
- good cover
- freedom from disturbance and competition.

These factors are related as much to the structure of the forest as to the tree species comprising it.

Summer foods

Ground vegetation (Plate 6 (a)) is much more common in the summer than in the winter diet (Cramp and Simmons, 1980). Dwarf shrubs, notably heather and the stems, leaves and berries of blaeberry, are particularly important. Although adults could probably survive the summer by eating conifer needles in a forest with little or no ground vegetation, chicks certainly could not. For chicks, blaeberry is not only a key food in itself, but also supports many of the insects which form much of the chicks' food in their first month of life, before they change to a diet largely of dwarf shrubs. Little information is available about the chicks' diet in Scotland, but work in Scandinavia indicates that caterpillars of moths (Plate 6 (b)) and sawflies, and small species of ants associated with blaeberry and heather, provide the bulk of their insect food (Kastdalen and Wegge, 1985, 1991; Spidsø and Stuen, 1988).

Big wood ants are probably not eaten much by small capercaillie chicks because they contain too much formic acid. Nonetheless, signs of broods — feathers, scrapes and droppings — are often found on the nests of wood ants,

probably because the birds use them for anting (Campbell and Lack, 1985).

As well as dwarf shrubs, adult capercaillie also eat young, tender tree shoots, and a variety of herbs, capsules of mosses such as *Polytrichum*, bracken shoots and fruiting heads of rushes and sedges. Hens are often seen feeding in larch trees in the spring and autumn. Newly growing larch needles and flowers probably provide a useful boost to the hens' nutrition prior to egg-laying.

Blaeberry in Scottish forests is generally associated with pine and sometimes with oak and birch. Spruce forests in Scotland have little or no dwarf shrub cover once the canopy closes. Although adults may be able to survive in such forests in summer, the absence of ground cover makes it unlikely that thicket and pole stages will provide habitat suitable for hens to rear chicks. However, hens and chicks do occur in some spruce-dominated forests in which there are large well-vegetated areas along rides and firebreaks, in clearings, and in restock and pre-thicket spruce. Similarly, broods seen in some Scots pine plantations with little blaeberry or heather (D. Baines, *in lit.*) might be relying on remnant patches of dwarf shrubs in adjacent habitats. These observations suggest that there is potential to manage spruce-dominated forests for broods. Patches of dwarf shrubs in restocked sites and other open areas might turn out to provide adequate food and cover even if blaeberry is otherwise scarce or absent. Potential foods for chicks, and for the insects which chicks eat, could include willow and birch leaves, raspberry leaves and berries, moss capsules, bracken, fireweed and other herbs. All this is speculative, however, and more research on the chicks' feeding habits in such atypical forests is needed before any conclusions can be reached. This research is currently in progress.

Spacing of capercaillie

Distance between leks

In continuous forest, leks are evenly spaced at roughly 2 km intervals (Picozzi *et al.*, 1992). One to over 20 adult cocks may attend a lek, with each cock's daytime territory typically radiating out about 1 km from the lek like wedges of a pie (Figure 1). When displaying in spring, the cocks move towards each other and concentrate at the centre of the pie (Hjörth, 1984; Wegge and Rolstad, 1986). However, their territories are quite variable, and the relatively small scale of many forest patches in Scotland may dictate a different territorial pattern. Nonetheless, the 2 km spacing between leks in Scotland is much the same as elsewhere in their range (Wegge and Rolstad, 1986), indicating the scale required when managing forests for capercaillie. The area of forest needed to support one lek is about 300–400 ha.

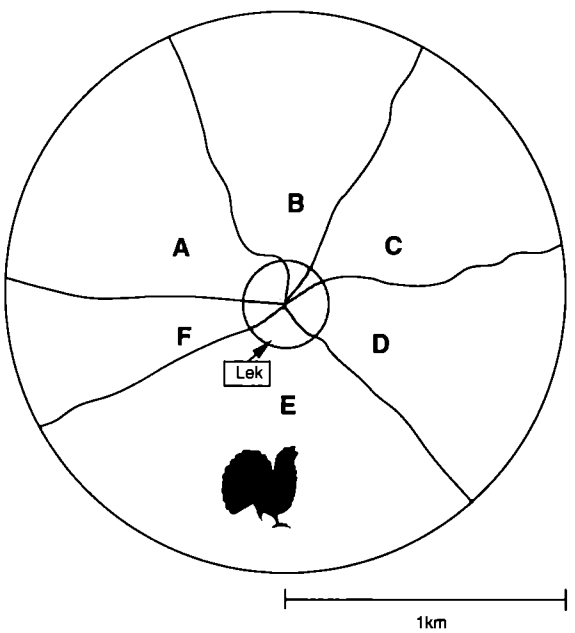


Figure 1 Capercaillie territories are arranged around the lek like wedges of pie (after Hjörth, 1984).

Dispersal

A single lek would not support a population of capercaillie in the long term, not least because problems of inbreeding might develop. Like many other species, capercaillie avoid inbreeding by dispersal. In the reintroductions, the hens were the first sex to colonise new areas, sometimes hybridising with pheasants and black game. This suggests that hens disperse more than cocks, and current studies are confirming this. We have been radio-tagging well-grown young and following their movements. There is much individual variation, but some hens (3/22 radio-tagged) have moved over 20 km from the area where they were caught as poults (well-grown chicks). Most movement has been in the spring, but dispersal from the natal area has also occurred in autumn. As yet, none of the 7 cocks marked as poults has moved more than 5 km from its natal area.

Two adult cocks radio-tagged in Perthshire in April 1992 remained within 1 km of their lek in small home ranges for the rest of the year and attended the lek in 1993. Both spent most of their time in or near patches of wind-thrown trees within pole-stage and mature Sitka spruce. In late summer, both visited adjacent restocked areas where the trees were 2 m or less in height. In April 1993 another four were marked. Two remained within 1 km of the lek, one later moved 2 km and the fourth 5 km from the lek. The latter two both spent the summer within 1 km of neighbouring leks. This study continues, but is already beginning to show how capercaillie utilise habitats provided by some Sitka spruce plantations.

Capercaillie habitat

Forest structure

To address the question of how best to manage a forest for capercaillie, we need a clear understanding of their habitat requirements, particularly the structure of the forests in which they live. Capercaillie are difficult to count at most times of year, but it is practicable to count the number of cocks displaying at a lek in spring. Such counts are likely to be related to the quality of the surrounding forest not only for adult cocks, but also for rearing chicks, because many of the cocks at a lek probably come from chicks hatched locally. Picozzi *et al.* (1992) related the number of cock capercaillie to the structure of the forest within a 1 km radius of each lek. This was intended to include the territories of adult cocks attending the lek.

Habitat characteristics and numbers were studied at 18 lek sites in 15 forests (Table 2). The forests included a full range of cock numbers and forest types (from semi-natural pinewoods to planted pine and introduced conifers) in the three main centres of population: Deeside, Speyside and Perthshire.

Forest structure and cock capercaillie numbers

Scandinavian workers have shown the importance of old forest to capercaillie (Rolstad and Wegge, 1987). As a start, we compared the number of cocks at each of the 18 leks with the percentage of forest with trees of any species older than 45 years in the 314 ha (1 km radius) about the lek. The correlation between cock numbers and old forest was very weak, mainly because counts at two leks were much higher than anticipated. When these leks were removed from the analysis, the correlation between the amount of old forest and the number of cocks attending a lek was statistically significant ($r_{14} = 0.66, p < 0.01$).

So, with some exceptions, the presence of older trees (irrespective of tree species) appears to be important for capercaillie in Scotland, as elsewhere. However, the analysis did not show what it was about old trees that was attractive, nor did it indicate whether younger forest can be managed to encourage capercaillie. Gossow *et al.* (1984) suggested that the birds can adapt to some younger forests. A new method of describing forest structure was therefore devised to shed light on these questions (Picozzi *et al.*, 1992). An abbreviated account and its practical application is given here in the Appendix. The end result of the new scheme is a single figure (the GRANNY score) which describes a forest in terms of 14 features thought to be important for capercaillie.

Table 2 Species composition in 1989 for trees taller than 2 m within 1 km of a lek at 18 leks in 15 forests, and mean maximum number of cocks counted at each lek in at least 2 consecutive years between 1989 and 1991.

Forest	*Mean cocks at lek*	*Tree species (%)*						
		SP	*LP*	*SS*	*NS*	*LA*	*BL*	*MI*
Abernethy	5	100	0	0	0	0	0	0
Alltcailleach	6	40	2	13	28	1	12	4
Ballochbuie	10	98	0	0	0	0	2	0
Birse	3	90	0	0	0	6	4	0
Cambus O' May	2	69	0	16	0	0	13	2
Coilacreich east	8	77	0	0	0	0	23	0
Coilacreich west	7	77	0	0	0	0	23	0
Dinnet	2.3	45	0	0	4	0	49	2
Glen Dye	2	66	0	6	6	16	2	4
Glen Tanar	12	87	0	4	0	0	0	9
Inver	5.5	76	2	5	1	16	0	0
Inverey	11	50	0	0	0	29	16	5
Keillour								
Aldie	10.5	6	0	66	15	9	3	1
Murray's Hill	1	21	5	26	37	6	2	3
Bellour	0.5	36	0	26	20	6	8	4
Revack	20+	81	0	<1	8	0	1	0
Tomvaich	6.5	78	0	3	13	0	6	0
Whitehaugh	0.5	3	4	68	9	16	0	0

SP, Scots pine; LP, lodgepole pine; SS, Sitka spruce; NS, Norway spruce; LA, larch spp.; BL, broadleaf, mainly birch; MI, miscellaneous.

The GRANNY scores for the 16 lek sites were compared with the number of cocks attending the lek (Figure 2); the two exceptional forests which had more cocks than expected from the amount of old forest were removed from the analysis. In general, the findings suggest that forest management for capercaillie should aim to produce a forest structure with features resembling those of a semi-natural pinewood (Plate 7), which has a high GRANNY score. However, the two exceptions show that other types of forest can support big leks. Neither resembled old semi-natural pinewood in structure. This is important, for it suggests that other management strategies might sustain capercaillie.

One of these forests, in Perthshire, was mainly of Sitka spruce but with many clear-felled and newly restocked areas. The older trees were mostly pole-stage or mature with patches of tangled windthrow. In the eastern Alps of Austria, even-aged spruce opened up by snow-break and windthrow is said to become habitable for capercaillie (Gossow *et al.*, 1984). The other exception was a younger plantation in Speyside comprising mainly Scots pine. It is relatively undisturbed while nearby Caledonian forest is popular with walkers and birdwatchers.

Forest structure and summer habitat

One value of open forest with a high GRANNY score is that enough light reaches the forest floor to allow vegetation, particularly dwarf shrubs, to develop. This, in turn, provides good habitat for capercaillie chicks. Scots pine has a more open needle and branch structure than spruce, and the ground vegetation is less often shaded out completely (Hill, 1979). Another desirable aspect of semi-natural forest is that it provides good ground cover for moulting cocks in mid-summer. Such cover may be provided by stands of juniper, by fallen trees or by hummocky ground covered with well-grown shrubs or bracken. In planted forest, patches of wind-

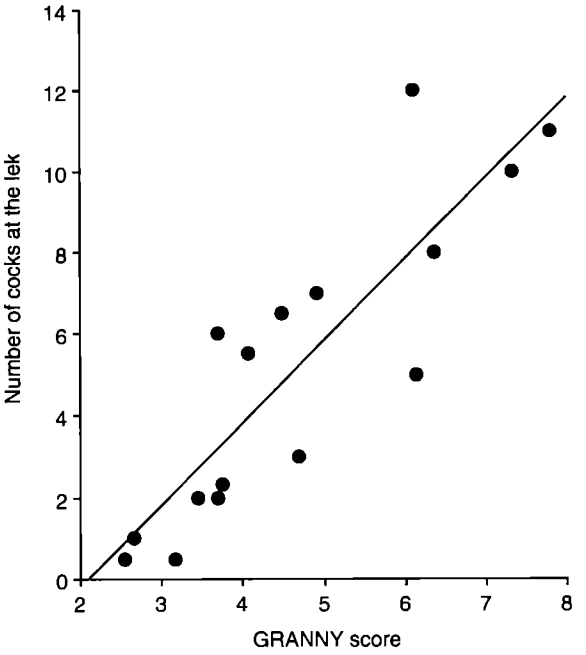


Figure 2 The mean number of cocks on leks at 16 sites with GRANNY scores between 2 and 8 (r_{14} = 0.87, $p < 0.001$). In two forests (omitted), the number of cocks was much bigger than expected from the GRANNY score. The higher the GRANNY score, the more closely a forest shares the characteristics of a semi-natural pinewood.
Regression equation: Number of cocks at the lek = 2 × GRANNY score – 4.3.

thrown trees or well-vegetated restocks may serve the same purpose.

Conserving and increasing the area of semi-natural pinewoods is widely accepted as beneficial for capercaillie in Scotland. It now seems that planted forests, even with a high proportion of exotic conifers, can in some circumstances provide suitable habitat. We do not yet know enough about the birds' ecology to understand fully why this happens, but in spruce woods the suitability of the habitat might be influenced by the amount of dwarf shrubs present in open or lightly shaded areas within the forest. It is also possible that other ground vegetation may be acceptable substitutes for blaeberry.

Features of a stand of trees likely to determine the presence of blaeberry and heather as an understorey are primarily related to the soil and secondarily to the amount of light reaching the forest floor. A forest manager will know whether his soil is suitable for dwarf shrubs. Both species occur on dry, well-drained, somewhat acidic soils such as podzols and iron-pan soils with a pH < 4.5. Blaeberry is more shade tolerant than heather and often replaces heather under a partial canopy. But both species may die out from lack of light as canopy cover increases (Hester *et al.*, 1991).

Here we consider the effects of shading on dwarf shrubs, based on a study in which the percentage cover of blaeberry and heather was estimated in 94 stands of Scots pine (61) and spruce (33, including both Sitka and Norway spruce) (Picozzi *et al.*, 1992). The stands covered a wide range of tree ages, heights and densities in the main capercaillie population centres. All measurements were made in plots of 10 main trees, as described in the Appendix. Plots did not extend into extraction racks, so estimates of stem density were based on woodland between racks.

In 25 of the pine plots, tree canopy cover was estimated by eye and ranged from 30 to 75%. It increased significantly as stem density increased (r_{23} = 0.54, p = 0.005). It also fell as the mean height of trees increased (r_{23} = –0.41, p = 0.04), but this was because the older plots had been thinned more heavily and so stem density tended to decrease as height increased. All heather was shaded out when canopy cover exceeded 65%, but in three plots blaeberry was still present when canopy cover was 75%. Grass remained as first heather, and then blaeberry, died out with increasing shade (Figure 3). Grass and moss are of undetermined value to capercaillie but they do eat some grass seed heads and moss capsules, notably of *Polytrichum*. A wide variety of invertebrates is present in such swards and these might be eaten by small chicks. However, grass provides little cover and, once a tight sward is established, the subsequent redevelopment of dwarf shrub cover may be hindered when the canopy is opened up. In all spruce plots, dwarf shrubs were shaded out completely when the trees were over 10 m tall.

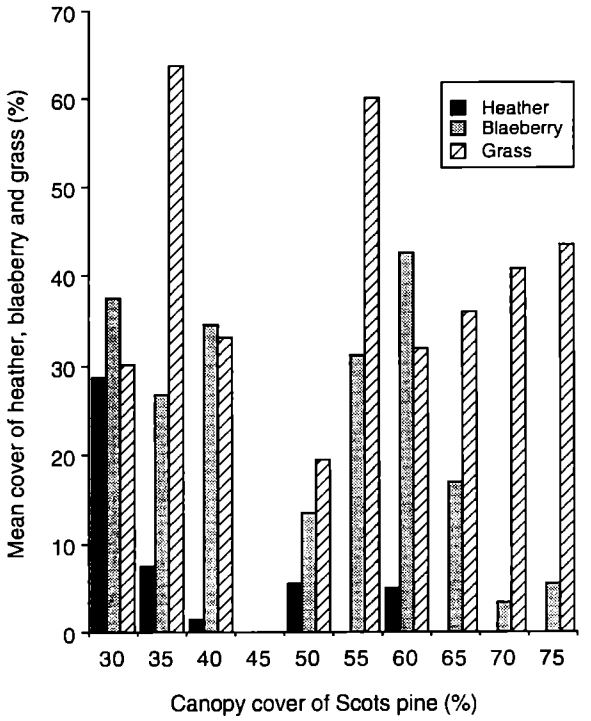


Figure 3 Mean cover of heather, blaeberry and grass under Scots pine in 25 sample plots with canopy cover from 30–75% (no data for 45% cover).

The cover of dwarf shrubs in the 61 pine plots was compared with mean tree height and stem density, and the conclusions are illustrated in Figure 4. Heights and densities to the left of the bold line should retain acceptable cover of both heather and blaeberry.

- The greatest cover of blaeberry was found beneath trees over 10 m tall and with a stem density of less than 1500/ha.
- The greatest cover of heather occurred
  - when trees were short (up to 5 m), reflecting the fact that the young plots sampled were established in heather moor;
  - when trees were over 10 m tall and stem densities were 500/ha or less (as in mature, well-thinned pinewoods).

Figure 4 also shows that heather tends to die out under pine when trees reach 10 m if densities are greater than 1500/ha. Management aimed solely at retaining the more shade-tolerant blaeberry could result in the loss of heather, but Figure 4 indicates how to manage Scots pines to retain both dwarf shrubs. In clear-felled areas, blaeberry may be retained, but is often replaced by heather and other ground vegetation.

Taller stands of pine tended to have lower stem densities, but this was not so for spruce. This resulted from a difference in their management, with spruce being kept at closer spacings than pine throughout a rotation, so that the ground vegetation was soon shaded out. Therefore, the maintenance of dwarf shrubs in a planted forest may depend largely on suitable thinning regimes for Scots pine, and upon retaining open spaces and lightly shaded areas in spruce forests.

Climate and weather

The disappearance of native capercaillie from Scotland in the 18th century coincided with the 'Little Ice Age'. This may have been fortuitous, but Höglund (1955) suggested that a decrease in the range of capercaillie in Sweden had been caused by increasingly wet weather, and Moss (1986) showed capercaillie in Scotland to be absent where the average rainfall in June exceeded 100 mm. The crucial period seemed to be the first 10 days in June, when most of the chicks hatch. It was the number of days with some rain, rather than the total rainfall in this period, that was most closely associated with chick survival. This might affect the amount of time available to chicks for foraging, because they spend more time being brooded by the hen in wet weather. If so, occasional exceptions to the association would be expected. For example, breeding might be unexpectedly good in an occasional wet year because a plethora of caterpillars makes foraging easy, or unexpectedly poor in a dry season through a dearth of insect food.

Black grouse have a more westerly range than capercaillie in Scotland. One of the reasons could be that black grouse chicks are less vulnerable to rain than capercaillie because

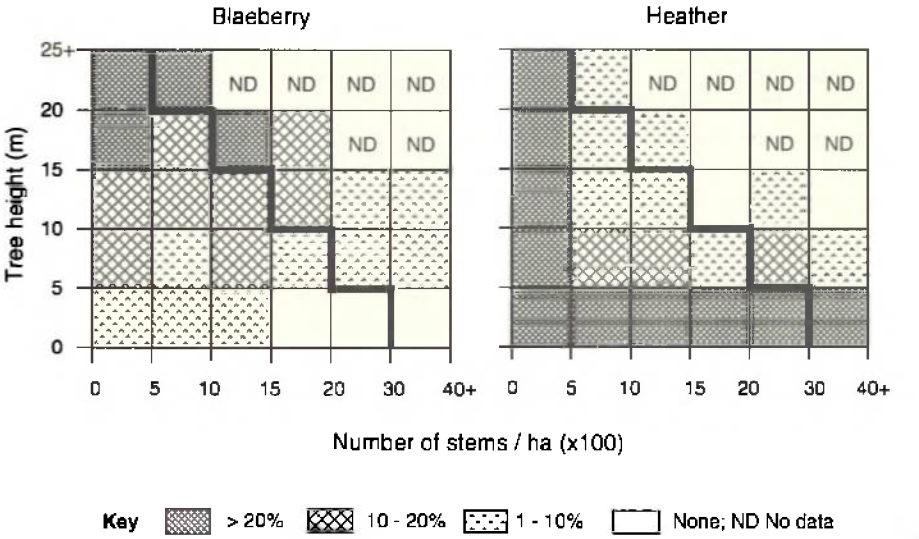


Figure 4 Mean cover (%) of blaeberry and heather under Scots pine in relation to mean tree height and stem density. Height and stem density classes to the left of the bold line are those which should retain cover of dwarf shrubs. Blaeberry tolerates shade better than heather. Note that these densities do not include extraction racks. This is a rough guide and will be modified by local conditions.

they are smaller. They grow more slowly and therefore need less food and probably need to spend less time foraging. So the same reduction in the time available for foraging during wet weather may have a more severe effect on capercaillie chicks than on black grouse. A similar size-related effect occurs within capercaillie broods: male chicks are bigger and grow faster than females and, in years of poor breeding, it is usual for fewer cocks than hens to be reared (Moss and Oswald, 1985).

If, as a possible result of global warming, summers were to become wetter, then there is a strong possibility that the range of the capercaillie might be further restricted. Conversely, were summers to become drier, their range might expand. The recent decline in numbers has been associated with an increase in rainfall. A 28% increase in annual rainfall occurred over the 20-year period 1969–1988 in the River Clyde catchment area (which includes Loch Lomond) in the west of Scotland (Curran and Robertson, 1991). More detailed analysis of climatic trends in Scotland will be necessary to see whether this crude annual increase was accompanied by an increase in the number of days with rain in the first 10 days of June. Deteriorating climatic conditions for capercaillie could override any improvements in habitat quality.

Hazards and enemies

Fences and wires

Young trees and dwarf shrubs are vulnerable to browsing by domestic stock, rabbits and deer. Where these animals are present, newly planted trees are fenced until they are well established. Fences are also used in mature forests where browsing by deer is preventing the growth and development of natural regeneration, especially in semi-natural pinewoods. Unfortunately, while fences reduce browsing they do present a considerable hazard to capercaillie, especially when a fence runs through a forest (Plate 8). Moss (1987b) showed that hitting fences was a common cause of death to

capercaillie; and of the 7 cocks and 22 hens we have marked with small radio transmitters in Deeside, 2 of the cocks and 8 of the hens have died by flying into fences or, in one case, a power line (see also Bevander, 1990). Most of the deaths were on deer fences but 2 were on 1 m high stock fences, and so all fences, irrespective of their height, are dangerous.

It is often assumed that capercaillie fly into fences because they do not see them or because they are panicked. This is partially true, but we have seen adults and chicks flying directly at multi-strand fences and adjusting their flight path to fly between the wires. A slight error of judgement, or a strand of barbed wire, can result in serious injury or death.

Fences are of two main types: multi-strand fences with droppers, and wire mesh fences (Pepper, 1992). There are many variations on these themes, but all of them are dangerous to birds. Large-square-mesh wire netting may be more dangerous than the small-sized hexagonal mesh more frequently used in the past. Hexagonal mesh fences do kill birds, but survival following a collision may be more likely if the impact is better absorbed. There is scope for more investigation into the value of electric fences, although Pepper *et al.* (1992) consider that they are not at present an effective barrier against deer. Current research is investigating how often grouse collide with fences and looking at ways of altering fences to reduce collision rates.

Predators

Gamekeepers are less numerous than formerly and predator control is less effective than it used to be. Foxes for example, once rare in eastern Aberdeenshire, are now abundant. Many potential predators of adult and young capercaillie are protected by law. This includes all birds of prey and some mammals. The goshawk is an important predator of capercaillie in continental Eurasia. It was lost as a breeder in Britain largely through deforestation and finally by intense persecution by game preservers in the 20th century. In recent years it has become re-established through deliberate releases and birds lost by falconers (Marquiss and Newton, 1982). The pine marten, another protected species, is also a predator of capercaillie, particularly their nests and chicks. Once rare, it is now spreading eastwards from its west Highland strongholds. Anecdotal evidence suggests that capercaillie can breed well in the presence of pine martens as long as there is plenty of ground cover. This is an important principle and may apply to other predators too. Good ground cover may allow ground-nesting birds, such as capercaillie, to survive in situations where they might otherwise be much reduced or even eliminated by predators.

The fox and the crow are two common predators that can legally be controlled. Both take eggs and chicks, and the fox may kill nesting hens, birds roosting on the ground and occasionally cocks at the lek. The effects of predation on the Scottish capercaillie population have not been documented.

Disturbance

While there is no firm evidence, most workers feel that continued disturbance has a deleterious effect on capercaillie populations. Because the birds are so big they may be more vulnerable to disturbance than other, smaller birds. The chicks must grow as fast as broiler chickens, but on a poorer diet which they must find for themselves. Continued interruptions to their feeding may result in slow starvation, even when the food supply is otherwise adequate. In wet weather, they may become chilled if separated from the hen for too long. Probably because they grow so fast, the chicks are more sluggish than chicks of smaller grouse species and soon become exhausted when forced to run or fly. They are therefore particularly vulnerable to dogs which are not on leads. In winter, the birds have only a few hours to take in a large weight of food (about 600 g for a cock). Continued flushing by cross-country skiers who leave forest trails could reduce the birds' food intake and result in slow starvation, especially in cold weather.

Enthusiastic birdwatchers anxious to view a lek are an increasing cause of disturbance to capercaillie. The effect of such activities has not been studied, but is likely to be harmful unless carefully controlled.

Plate 1. *Capercaillie cock displaying to hens at a lek in Aberdeenshire. The wood is a well-spaced mixture of mature larch and pine.*
(N. COOK)

Plate 2. *Lek site in Sitka spruce restock and thicket in Perthshire. The trees were thinned in 1993 to prevent full canopy closure and so retain the attraction of the site to displaying birds.*

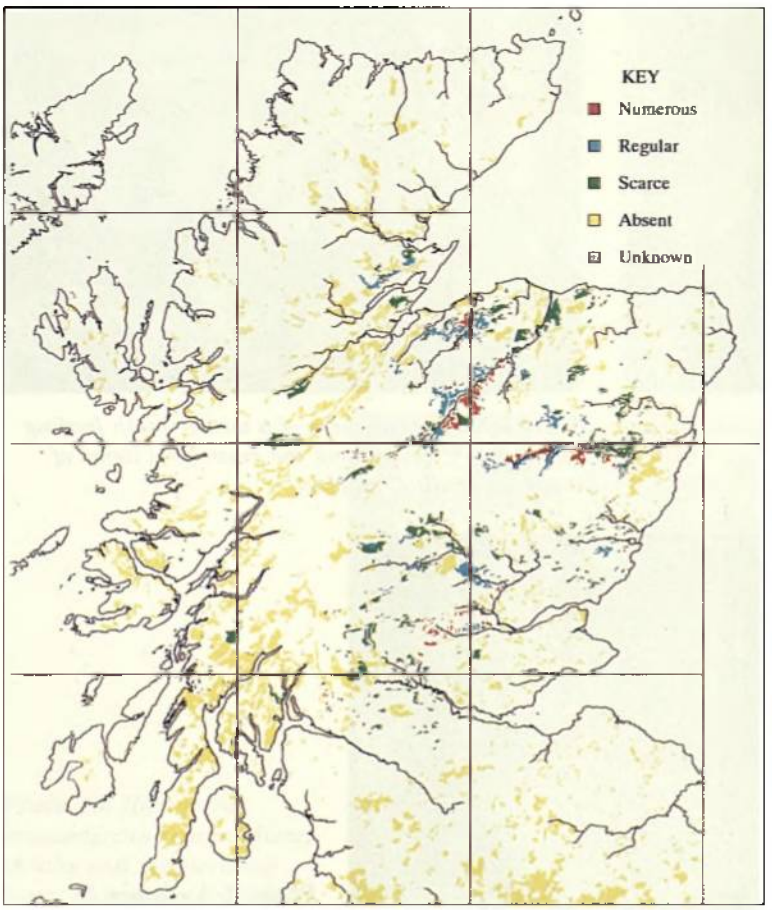


Plate 4. *Distribution and relative abundance of capercaillie in Scotland in 1992. Some original map data copyright Bartholomew and Son, Ltd.*

Plate 3. *Hens may visit several leks and watch the displaying males from surrounding trees.*

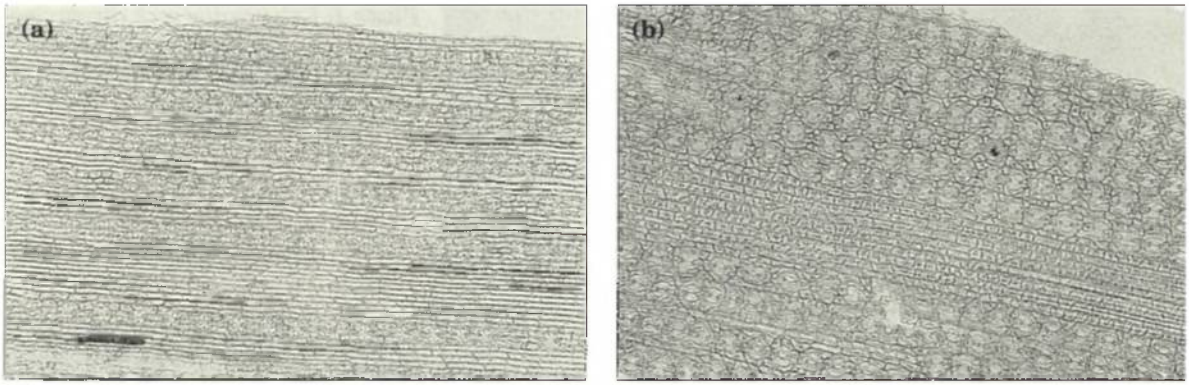


Plate 5. *Microscopic examination of epidermal cells on leaf surfaces shows clear differences between conifer species. Undigested leaf fragments from capercaillie droppings showed that they had been eating: (a) Scots pine, (b) Sitka spruce.* (A. LUCAS)

Plate 6(a). *Blaeberry is an important food plant for capercaillie adults and chicks.*

Plate 6(b). *Larvae, here of a winter moth feeding on blaeberry, are among the main food items of small capercaillie chicks.*

Plate 7. *A mature plantation of Scots pine with a complete ground cover of heather and blaeberry to match a semi-natural pinewood.*

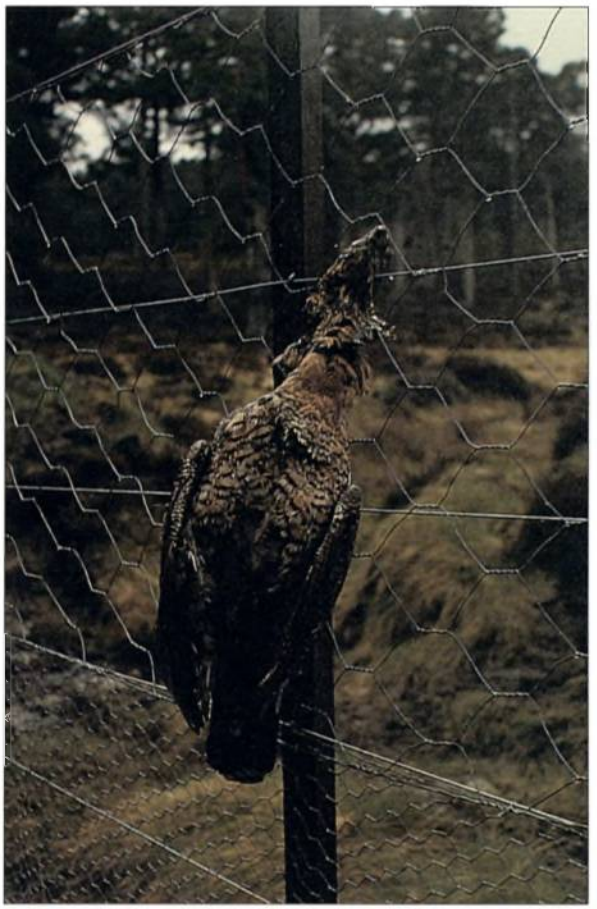


Plate 8. *Deer fences sited through forests are an important cause of death and injury to woodland grouse. Here, a hen capercaillie has hit the fence.* (N. COOK)

Plate 9. *This old semi-natural pine forest, classic capercaillie habitat, comprises young, old and dead trees, and has a rich understorey of dwarf shrubs and juniper.*

Plate 10. *Heavy deer browsing can repress dwarf shrubs and regenerating trees. This enclosure has been in place for 20 years and shows a dramatic change to the ground vegetation when deer are excluded.*

Plate 11. *In this forest ride, heather is the main shrub in the open. The more shade-tolerant blaeberry is abundant next to the trees, while in the denser shade under the trees, the blaeberry dies out and is replaced by grass.*

Plate 12. *Making fences more conspicuous may reduce deaths from birds flying into them. The central strand of barbed wire here is an added danger, snagging birds which attempt to fly through the fence.*

Plate 14. *Capercaillie shooting is a potential source of revenue but few estates now let shooting since stocks are low.*

Plate 13. *Seasonal notices at the entrance to a forest alert visitors to conservation measures being taken.*

The decline in numbers

Several factors have probably contributed to the recent decline. The overriding fact is that insufficient young have been reared and recruited into the population to sustain it in much of Scotland.

Habitat deterioration has probably played a role. Of the 35 semi-natural pinewoods recorded by Steven and Carlisle (1959), 22 were larger than 100 ha (J.S.G. Gill, personal communication) but now there are only 18 of this size (Bain, 1987). As pinewoods and pine/larch plantations have been felled some have been replaced by the fast growing Sitka spruce, which eventually shades out ground vegetation. Moss *et al.* (1979) showed that in Abernethy forest (Speyside) from 1968 to 1976, the felling of old, 'granny' pines (Plate 9) was followed by a marked reduction in the numbers of capercaillie shot relative to nearby Kinveachy forest, where few old pines were felled. However, bags also declined at Kinveachy, though not to the same extent: so presumably other factors also contributed to the decline. Moss *et al.* (1979) also showed that breeding performance was generally worse in planted than in semi-natural forests, and this they attributed to the greater cover of blaeberry on the floor of the old forests. Some Scots pine plantations are today not thinned as often as formerly, so they support less blaeberry and heather than more traditionally managed, frequently thinned stands. Red deer have increased in numbers (Red Deer Commission, 1987) and heavily browse the ground vegetation of some old pine forests (Plate 10). This can affect the cover of dwarf shrubs to the point where they provide much reduced food and cover for chicks. There is limited evidence (R. Moss, unpublished) that breeding has been poorer and the decline in numbers steeper in one heavily browsed forest than in another, nearby, forest where browsing has been much lighter.

There may also have been an increase in predation. There are now fewer gamekeepers to control predators on private estates than formerly (Hudson, 1986). The Forestry Commission no longer kills foxes and crows as a general policy, but targets situations where there is a clear local need. Hence many plantations provide safe havens for predators. These factors have probably contributed to an increase in predators, particularly foxes and crows.

Fences are an important cause of capercaillie mortality. There is no documentation showing that fence deaths have increased in the last 20 years, but a level of mortality which has little effect on a thriving population might have a bigger impact on an ailing one.

The weather may have deteriorated. In particular, the number of rain-days in early June is inversely associated with capercaillie breeding success. The possibility that changes in weather may have contributed to the recent decline has yet to be checked.

So, the reasons for the decline may be many. We must now consider what action can be taken to maintain and improve our present stock. The next section discusses how forests can be improved for capercaillie.

Management

Scale

Capercaillie are big birds with large home ranges and can disperse long distances. Forest management for capercaillie therefore needs to be strategically planned on a large scale, such as entire catchments, rather than on a local forest or estate level. The smallest subunit of population it makes sense to consider for management purposes is a lek. This covers 300–400 ha of good forest habitat. To be viable, a population should include several lekking units. A reasonable guess is that it would take a minimum of 1000 ha of good habitat (3–4 leks) to support a population of breeding capercaillie. Good habitat need not be continuous but must provide for both adults and chicks.

Improving forests for capercaillie

The widely held understanding that semi-natural pinewoods are the key habitat for capercaillie in Scotland is probably as true

today as in the past. This is due largely to their open structure which allows the development and retention of dwarf shrubs so important to chicks (Plate 9). However, capercaillie are not confined to semi-natural pinewoods, but occur in a range of planted woodlands including some spruce-dominated forests. We consider that the quality of these planted woodlands can be substantially improved for capercaillie. Adult capercaillie can probably exist in many open pole-stage or older coniferous habitats; the limiting factor appears to be suitable chick habitat. Therefore, the following recommendations concentrate on how to improve habitats for chicks, with some advice on managing forests for adults. Pine and spruce are the main forest types within the range of the capercaillie in Scotland. Because they have different growth characteristics each is treated separately.

Pine forests

The more a pine plantation can be managed to resemble semi-natural pinewood, especially in terms of wide spacing and/or clumping to encourage dwarf shrubs, the more capercaillie it should hold (Plate 7). Management should aim to increase the GRANNY score, which can be done by thinning. Table 3 was calculated from the GRANNY score equation (Figure 2) and should be appropriate for most forests where there is already a stock, or a nearby source, of capercaillie. But capercaillie may not appear as if by magic in numbers appropriate to the GRANNY score. They have to come from somewhere and in unfavourable circumstances this could take many years. On the other hand, some exceptional forests may have more birds than expected from the GRANNY score.

The main reason for increasing the GRANNY score is to encourage dwarf shrubs. Although blaeberry will not thrive in all situations it is a resilient shrub that grows on most acidic soils on which much modern planting has taken place. It does not do well in wet conditions, and on more fertile soils may be ousted by grasses. Given the right soil conditions, the main factor to consider is light (Plate 11). Thinning encourages the retention of heather and especially the more shade-tolerant blaeberry (Figure 4). When the aim is to create woodland with uneven tree density, areas where blaeberry and heather are present should be targeted for heavier thinning. The development of a dense grass sward should be avoided as this will discourage subsequent regeneration of dwarf shrubs. A rough guide to the tree heights and densities which should allow the retention of both blaeberry and heather under pine is given in Table 4.

Table 3 Score for forest structure and the number of capercaillie cocks expected to attend a lek in such a forest (see caption to Figure 2 for the equation from which the number of cocks was calculated).

GRANNY score	*Cocks at lek*	*GRANNY score*	*Cocks at lek*
2.5	1	5.5	7
3.0	2	6.0	8
3.5	3	6.5	9
4.0	4	7.0	10
4.5	5	7.5	11
5.0	6	8.0	12

Table 4 Approximate stem densities of Scots pine which should allow the retention of dwarf shrubs at tree heights from 5 m to over 20 m.

Tree height (m)	*Stem density (per ha)*
5	*c.* 2000
10	1000–1500
15	500–1000
>20	up to 500

Spruce forests

Capercaillie were abundant in one spruce-dominated forest where pole-stage and mature crops were relatively open and included patches of windthrow. This gave the birds the opportunity to move in and through the canopy fairly readily. They also used the wind-thrown patches and fed on fresh side shoots which grew from the blown trunks. This research is beginning to indicate that some spruce-dominated forests can provide suitable winter habitat for capercaillie.

Whether such forests in Scotland have the potential to become good *summer* habitat for capercaillie is less certain. Hens and chicks occur in some of these forests, but they might be relying on remnant patches of dwarf shrubs. Since there is little chance of retaining ground vegetation during the thicket and pole stages, attention should be focused on other areas within these forests to provide good chick habitat:

- Create permanent areas with good ericaceous vegetation. Ideally these should be scattered throughout spruce forests in different-sized patches. They can include wide open spaces alongside burns, or along roads and rides that have been selected and perhaps widened because they already have some dwarf shrubs. Avoid creating narrow, linear habitats as these will help avian predators to find their prey. Open areas with a mixture of heather and blaeberry will benefit by the planting of some trees in patches, especially if the trees used cast a relatively light shade and can be used by adult capercaillie for food: for example, Scots pine, larch, aspen and rowan.
- Create long-term retentions on sites that will support dwarf shrubs. Ideally, species other than spruce should be selected to provide alternative foods for adult capercaillie. However, on the right sites, old widely spaced spruce with gaps in the canopy can allow blaeberry to flourish.
- When designing clear-felling programmes, choose the smallest practicable coupe size, with the greatest possible separations in both space and time within the forest. Aim to create a fine-grained patchwork of different-aged tree stands. This will ensure that adults and chicks have a wide range of habitats available to them. The value to capercaillie of non-ericaceous vegetation on restocked sites is not known, but broadleaved shrubs and herbaceous plants are likely to be of greater value than grasses because of their palatability and associated insects.

Collectively, such areas are likely to comprise 20–30 % of the area of a forest at any one time, and may provide a substantial resource for adult and young capercaillie.

Habitat initiatives and grant schemes

The following initiatives are already providing an opportunity to improve habitats for capercaillie.

The Woodland Grant Scheme

Under this scheme a higher rate of grant is available to those who wish to establish new pinewoods of natural character outside existing ones, or to manage existing native pinewoods. This scheme applies within the former natural distribution of pine–birch forest north of the Forth and Clyde valleys. Restocking also qualifies for a grant if the conditions can be met. At present (1994) the full grant is paid for at least 1100 Scots pine plants per ha, distributed in a way which reflects the natural habitat variation within the site. They must not be evenly spaced. This initiative offers a major opportunity to increase the diversity of a forest to the benefit of capercaillie. It is administered by the Forestry Authority.

Forest Enterprise initiatives

Forest Enterprise are responsible for the management of more than 3000 ha of semi-natural pinewoods in Scotland (25 % of the total area of such woodland) distributed among 15 locations. Some of these woods have been managed for conservation for up to 40 years. In 1992 a new initiative was launched (Anon., 1992). This aims to extend conservation management to all Forestry Commission semi-natural pinewoods, creating regeneration zones totalling another 3000 ha by the year 2000. Principal woodlands will be designated as Caledonian Forest Reserves covering more than 12 000 ha of forest, loch, bog and mountain.

Forest Enterprise also manages 40 500 ha of planted Scots pine in north Scotland Region. This area is likely to be maintained or extended in future. It is expected that the age

class structure of these woods will continue to mature and that more stands will be retained beyond their economic rotation length as part of the diversification process now vested in Forest Design practice and Forestry Policy. Some Scots pine plantations have been identified as capercaillie 'reserves' where management is specifically tempered to favour capercaillie.

Fences and wires

The ideal way of maintaining and recreating native pinewoods and establishing new woodlands is to reduce deer stocks to a level where natural regeneration can occur. This has been achieved but is not always practicable. It may need a co-operative effort by landowners over large areas. When stocks of deer or sheep are high and cannot be reduced, fences are used to exclude them. What can be done to minimise bird strikes? There are few hard data on this problem (Catt *et al.*, 1994). Here, we summarise the best current opinion, based largely on anecdote and uncontrolled observations.

Controlling disturbance

The consensus based on anecdote and experience is that capercaillie can tolerate occasional disturbance with little adverse effect, but that repeated disturbance can lead to local extinctions. They can probably become accustomed to vehicles, bicycles and walkers that keep to regularly used roads, tracks and paths.

In late March to early May, the cocks gather at the lek for their short, intense display season. A capercaillie lek is a great attraction for birdwatchers. Disturbance on consecutive mornings is very disruptive and may even cause the birds to desert an area. If this problem exists then consider siting a large, semi-permanent hide so parties can view a lek. Access to and from a hide would need to be well shielded from the lek. It might be better to guide visitors in this way than to attempt to deny them access. Forestry operations can also disturb a lek. The manager should plan to avoid forest operations within 1 km of a lek from March to May.

Temporary notices at forest entrances to the effect that this is a conservation area can be helpful in reducing disturbance from walkers and cyclists (Plate 13). The notices can request visitors to avoid marked areas, to

Minimising bird strikes

- The first rule is to remove any fences immediately they have served their purpose. This includes both stock and deer fences.
- Avoid siting fences to pass through woodland, especially where blaeberry or other food plants are plentiful.
- Fencelines sited in the open should be at least 10–20 m out from the edge of the trees.
- Fences should not follow ridges but be sited so that birds have a good chance of flying over them without taking avoiding action.
- Bird strikes are often concentrated along certain sections of fence. Walk fencelines at regular intervals (perhaps three or four times a year) to identify these sections, then consider alterations to the alignment or construction of the fence to make it more visible.
- There are several ways of making fences more visible.

  1. Large corks, tightly tied bundles of heather and brightly coloured plastic webbing (at least 25 cm wide) are easily attached along the top of a fence (Plate 12).

  2. Coloured rope may be threaded through the top part of a fence, but make sure that it is knotted at frequent intervals, otherwise a single knot becoming untied can lead to a long unravelling and eventual loss of the rope.

  3. Thin plastic strips or short plastic ribbons can soon become detached in high winds and are then unsightly. Any markers must be very securely fastened.

- All methods of marking require maintenance, as the markers will otherwise fall off; and none so far tried has been completely effective.
- Overhead wires are also hazardous. If possible, they should be sited outside woodland. If they are to run through a wood, then set them in very wide rides and mark the wires to make them obvious.

keep to the tracks and to keep dogs on a lead. Badly controlled dogs are a menace when hens are laying and incubating (May) and when they have chicks (June–August). Notices can be erected in late March and taken down in late August. This will cover the most vulnerable period and have more impact on visitors than permanent notices.

Controlling predators

The Forestry Authority does not recommend the indiscriminate killing of predators. Therefore, the need for predator control should be carefully considered. Two examples illustrate extremes. If a high density of capercaillie were present in a forest surrounded by heavily keepered land, then killing crows and foxes within the forest at the right time of the year might reduce predation on capercaillie and other ground-nesting birds. But in an extensive forest with no predator control on adjacent land it is unlikely that killing foxes and crows will significantly reduce predation.

Foxes and crows are the only important predators of capercaillie that may legally be controlled by the landowner or his agent. Both are probably more abundant in the modern countryside than they would be under natural conditions. Farming provides them with sources of food year-round.

Our understanding of the legal position for dealing with foxes and crows (Department of the Environment DoE Poster ref. no. 91 EP 0183: see References) is as follows:

- Cage traps can be used for members of the crow family. Decoy birds can be used in the trap but must not be injured and must be provided with food and water. Captured birds must be humanely killed, non-target species released and traps inspected daily. The Larsen trap seems to be particularly effective.
- Crows may be shot and their nests and eggs destroyed. Protected species such as long-eared owl, kestrel and merlin breed in disused crow nests, therefore first establish that the nest is occupied by a crow before shooting into it.
- Foxes can be shot, or snared with a humane free-running type of snare provided it is checked daily. Snares should be set to avoid non-target species (which if inadvertently caught must be released).

In practice, the legal requirements for snaring foxes are difficult to meet. Non-target species, including capercaillie, are regularly killed by snares set for foxes. The advice of the Forestry Authority is not to set snares other than in exceptional circumstances. When fox control is necessary the recommended method is to spotlight them at night by dens, or at middens of carrion, and to shoot them. This should be at the time of year (March–July) when it will have the greatest effect in reducing fox numbers and predation on ground-nesting birds. Indiscriminate fox control at other times of year is considered ineffective and wasteful of time and resources (Chadwick and Ratcliffe, in preparation).

Dense forest and excessive stocks of red deer reduce ground vegetation and cover for sitting hens, eggs and chicks of ground-nesting birds. Animals use cover to escape from predators and where it is sparse, they are vulnerable. Providing good cover may also reduce predation and hence the need for strict predator control, but there is little evidence to date. Cover can be provided by dense ground vegetation, shrubs such as juniper and uneven ground and fallen trees. All improve the chances of a hen escaping predators and rearing her chicks.

Shooting

The decline of capercaillie throughout its range in Scotland has led to the virtual, though not complete, cessation of shooting. Were numbers to recover to the point at which shooting could again be offered to sportsmen (Plate 14), the value to the landowner of a stock of capercaillie would be over £300 per ha (Table 5). Moss *et al.* (1979) produced a model for the allowable cull. This indicated that if breeding performance is in the order of two fledged young birds per hen, then one day's shooting, which would result in a 15% cull, would be acceptable. If breeding performance is only one young bird per hen, then the model predicts a 10% drop in numbers

even without shooting. Unfortunately, in recent years, a breeding success of two young per hen has seldom been achieved in the areas where it has been studied.

Table 5 The value of a stock of capercaillie.

1. The value of a day's capercaillie shooting was equivalent to a day's grouse shooting.
2. One day's good capercaillie shooting produced a bag of 20 birds; one good day's driven grouse, about 100 brace.
3. The capital value of a stock of grouse, based on the average bag, is around £3000 per brace. So the capital value of a capercaillie is, on average, £15000 per bird shot.
4. A thriving capercaillie population could be shot once a year and, on a typical drive, one bird was shot for every seven on the ground.
5. The capital value of a capercaillie on the ground is therefore about £2150 (£15 000/7).
6. A good capercaillie population is typically 10–20 birds/km^2. This comes to £323/ha (15 × £2150/100).

Capercaillie disperse long distances and management on the basis of local breeding performance in one estate or forest is not the best approach to conservation. An area which has good breeding one year may export birds, so topping up numbers at a neighbouring estate where they have not done so well; the next year, it might be the other way round. A sensible approach would be to have country-wide monitoring of breeding success each year, and to conduct shooting that year in accordance with the number of young birds available nationally. Of course, it could be argued that an estate should shoot following local good breeding, irrespective of what is happening elsewhere, because otherwise many birds would disperse to neighbours. This would not, however, be in the long-term interests of the capercaillie.

Key points for managing capercaillie

- Think big: the cocks attending one lek need 300–400 ha. The minimum area of good habitat to sustain a viable population is at least 1000 ha.
- Adult capercaillie can probably exist in a wide range of native and introduced conifers, including spruce.
- The limiting habitat factor for capercaillie appears to be suitable feeding areas for chicks.
- Ground cover is important for adults and chicks and may help reduce predation.
- Areas of blaeberry are the most important chick habitat. Other ground vegetation such as heather, broadleaved shrubs such as willow and birch, and herbaceous plants may also be valuable.
- Blaeberry thrives in open pine forests. These can be achieved by promoting natural regeneration so that an uneven canopy develops, or by a suitable thinning regime.
- Vary thinning intensity in pine to create uneven stem density by targeting areas with existing blaeberry for heavy thinning.
- In spruce forests, blaeberry and ground vegetation suitable for chicks can be encouraged in suitable open spaces, areas with other tree species such as Scots pine, young restocked sites and open long-term retentions.
- Avoid draining boggy areas and try to create new ones. These are important for chicks as they are often rich in insect food.
- Patches of windthrow within pole-stage spruce crops provide cover and feeding areas for adult capercaillie. Retain any small patches of windthrow.
- Remove fences when they are redundant. Carefully site new fences away from the forest and make them as visible as possible.
- Check fencelines regularly and, if sections where grouse collisions occur are located, mark these with brightly coloured material or heather bundles to make them more obvious. Inspect and maintain fence markers regularly.
- Carefully consider whether control of foxes and crows, the main predators of capercaillie, is necessary. If it is, then start in March–April, before capercaillie lay, and continue until late July when chicks are well grown.
- Do not shoot capercaillie while numbers are low. If populations recover in future, plan shooting nationally in relation to the number of young reared. Capercaillie can easily be overshot. They need to produce a little over one chick per hen just to maintain numbers.

Appendix

Describing the structure of a stand

Forest stands are often described in terms of their stage of development: establishment and restock (typically up to 8 years); pre-thicket (9–16 years); thicket (17–28 years); pole (29–44 years) and high canopy (mature) forest (45+ years). A new method of forest description (Picozzi *et al.*, 1992) designed to assess structure preserves these distinctions but is more precise and quantitative. Each stand may be assigned to one of the 28 'boxes' in a grid (Figure 5) using a key (Tables A–F). Each box has two scores PRIN1 and PRIN2 depending upon its position in the grid (Table 6). A high PRIN1 score (good for capercaillie) would be obtained for a stand in which trees are well spaced with thick trunks and branches, which tend to be clumped, and have an open canopy with a good field layer of dwarf shrubs.

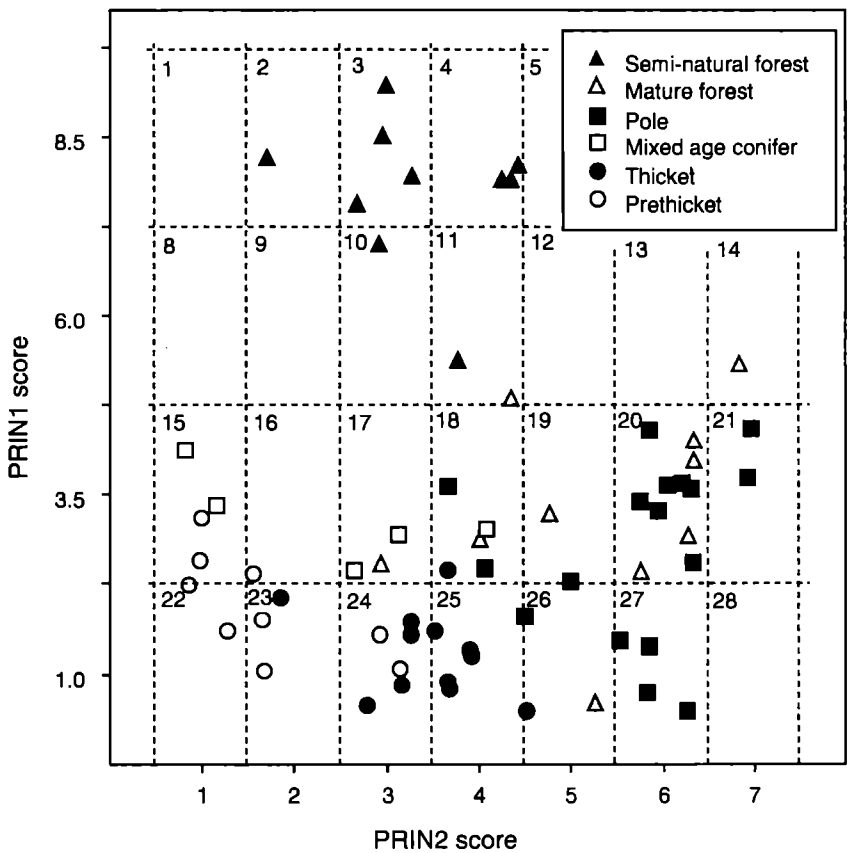


Figure 5 Plot of the first two principal component scores for 64 sample plots in four forests. A grid with the box numbers used in the key (Tables A–F) has been superimposed. Some of the boxes have no trees in them, and trees equivalent to some empty boxes probably do not exist.

Tables A–F Key to forest stand classification, based on a circular plot containing 10 main trees (see Table 7) which were representative of the stand. Mean values for variables apply throughout.

Table A

1[a]	*Vaccinium myrtillus* >10%; mean nearest neighbour distance ≥3 m; diameter thickest branch >6 cm	Table B
	Vaccinium myrtillus <10%; mean nearest neighbour distance <3 m; diameter thickest branch <6 cm	2
2	*Calluna vulgaris* <15%	4
	Calluna vulgaris ≈15%	3
	Calluna vulgaris >15%	Table C
3	Grass <20%; height to first live branch >5 m	Table C
	Grass >20%; height to first live branch <5 m	Table E
4	Mean height of trees ≤5 m	Table C
	Mean height of trees >5 m	5
5[b]	Branch interlock above 10 m >5%; ground vegetation ≤5%	Table D
	Branch interlock above 10 m <5%; ground vegetation >5%	Table E

[a] If at least two of these three criteria are met, then go to Table B; if not met, then go to step 2.

[b] If these two criteria are opposed, use branch interlock above 10 m as the overriding consideration for advancing either to Table D or Table E.

Table B

1	Nearest neighbour distance >4 m; branch interlock at 5–10 m and 10+ m <10%	2
	Nearest neighbour distance ≤4 m; branch interlock at 5–10 m and 10+ m ≥10%	3
2	Height to first live branch <5 m; trees very clumped, index ≈5	Box 2
	Height to first live branch >5 m; trees clumped, index ≈3	Box 3
3[a]	Height of trees ≤15 m; height to first live branch <8 m; diameter of thickest branch >9 cm	4
	Height of trees >15 m; height to first live branch >8 m; diameter of thickest branch <9 cm	Box 4
4[a]	Height of trees <13 m; height to first live branch <3 m; trees very clumped, index ≈5	Box 9
	Height of trees >13 m; height to first live branch ≥3 m; trees clumped, index ≈3	Box 10

[a] Decision based on at least two criteria being met.

Table C

1	Height of trees <10 m	2
	Height of trees >10 m	Box 11
2	*Calluna vulgaris* <60%; grass >15%	3
	Calluna vulgaris >60%; grass <15%	4
3	Height of trees <4 m; branch interlock up to 2.5 m <25%	Box 22
	Height of trees >4 m; branch interlock up to 2.5 m >25%	Box 23
4	Height of trees <7 m; branch interlock up to 2.5 m >10%	Box 15
	Height of trees >7 m; branch interlock up to 2.5 m <10%	Box 16

Table D

1	Branch interlock up to 2.5 m and 2.5–5 m <30%	3
	Branch interlock up to 2.5 m and 2.5–5 m ≈30%	2
	Branch interlock up to 2.5 m and 2.5–5 m >30%	5
2	Diameter at breast height >20 cm; height of trees >15 m	3
	Diameter at breast height <20 cm; height of trees <15 m	5
3	Height of trees <20 m	Box 20
	Height of trees ≥20 m	4
4[a]	Diameter at breast height ≤30 cm; branch interlock 5–10 m >15%; nearest neighbour distance ≈2 m	Box 21
	Diameter at breast height >30 cm; branch interlock 5–10 m <15%; nearest neighbour distance ≈3 m	Box 14
5	Branch interlock at 10+ m ≈10%; height to first dead branch ≈0.5 m	Box 26
	Branch interlock at 10+ m ≈20%; height to first dead branch ≈1.0 m	Box 27

[a] Decision based on at least two criteria being met.

Table E

1	Grass cover <20%	5
	Grass cover ≈20%	2
	Grass cover >20%	3
2	Height to first dead branch 1–2 m; diameter at breast height >15 m	3
	Height to first dead branch 0.5 m; diameter at breast height <15 cm	5
3	Mean tree height ≤10 m; height to first live branch <4 m	Box 17
	Mean tree height >10 m; height to first live branch >4 m	4
4	Branch interlock up to 2.5 m and 2.5–5.0 m >10%; height to first live branch ≤7 m	Box 18
	Branch interlock up to 2.5 m and 2.5–5.0 m ≤10%; height to first live branch >7 m	Box 19
5	Height to first live branch <3 m	Box 24
	Height to first live branch ≈3 m	6
	Height to first live branch >3 m	Box 25
6	Branch interlock at 5–10 m ≈15%	Box 24
	Branch interlock at 5–10 m ≈30%	Box 25

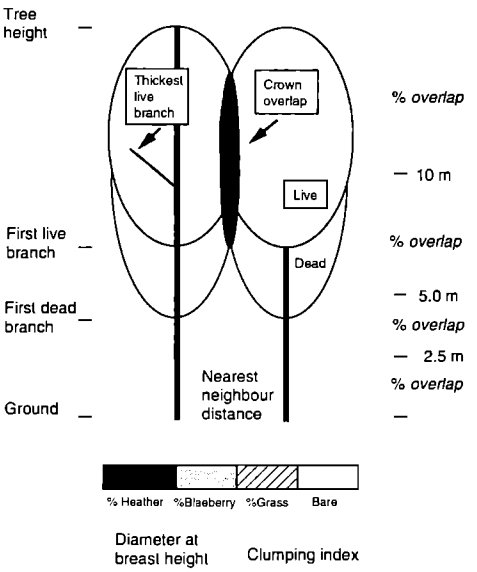
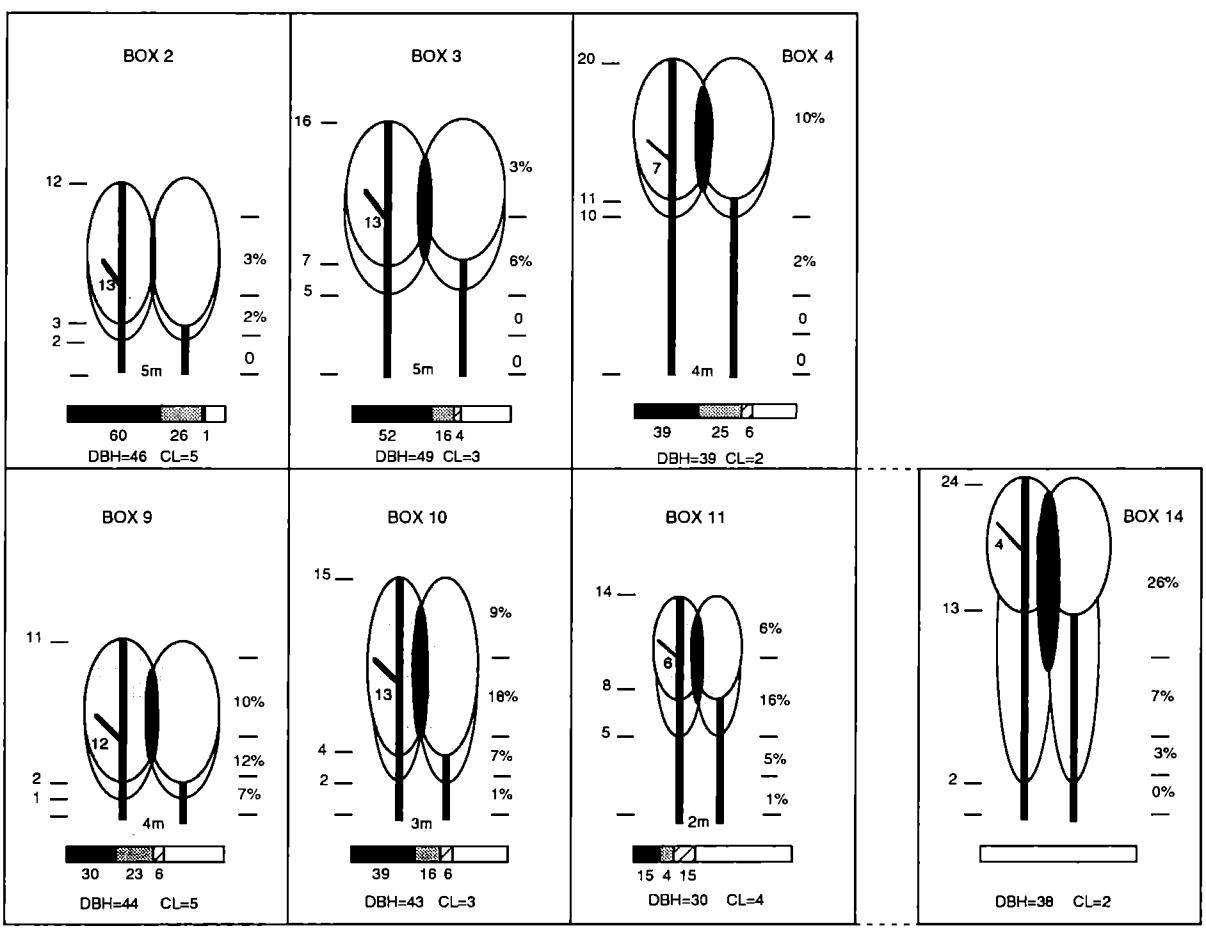
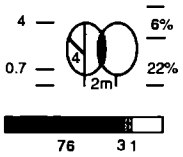


Figure 6 Diagrammatic representations of stand structures. The values given are means from Table F. Crown overlap refers to that of a tree with all its neighbours. Stands with a clumping index of 1 have a completely regular distribution of trees; a value of 5 means trees are extremely clumped.

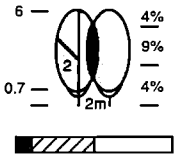


BOX 15



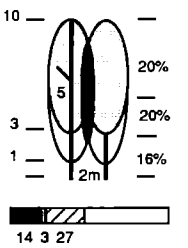
DBH=9 CL=3

BOX 16



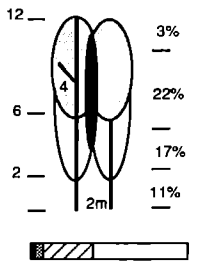
DBH=9 CL=4

BOX 17



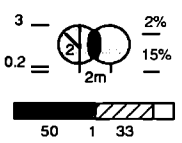
DBH=22 CL=2

BOX 18



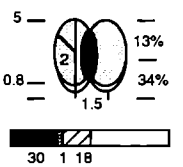
DBH=20 CL=3

BOX 22



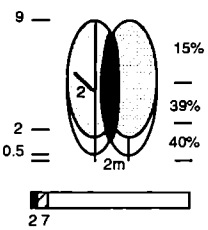
DBH=5 CL=2

BOX 23



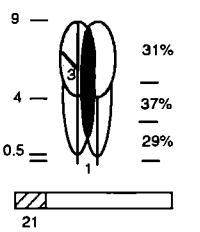
DBH=8 CL=2

BOX 24



DBH=11 CL=2

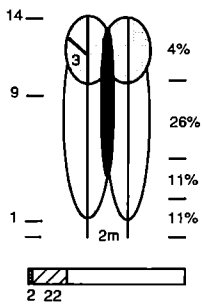
BOX 25



DBH=11 CL=1

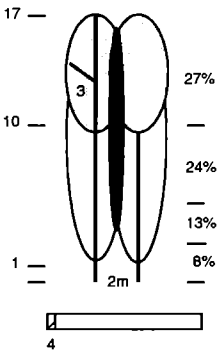
Continued

BOX 19

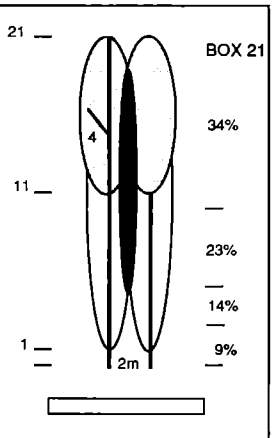


DBH=17 CL=2

BOX 20



DBH=23 CL=2

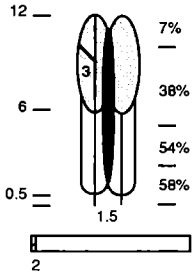


BOX 21

DBH=26 CL=4

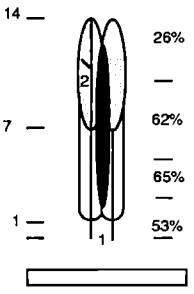
Continued

BOX 26



DBH=16 CL=2

BOX 27



DBH=16 CL=2

BOX 28

Table F Mean values of 14 variables (abbreviations explained in Table 7) for sample plots. These values should be used in conjunction with the key when classifying stands.

Box number	*1*	*2*	*3*	*4*	*5*	*6*	*7*
MH, MD		12, 46	16, 49	20, 39			
MDD, MLV, MB		2, 3, 13	5, 7, 13	10, 11, 7			
MNND, CLUMP		5, 5	5, 3	4, 2			
I1–4		0, 2, 3, 0	0, 0, 6, 3	0, 0, 2, 10			
CV, VM, GR		60, 26, 1	52, 16, 4	39, 25, 6			
Box number	*8*	*9*	*10*	*11*	*12*	*13*	*14*
MH, MD		11, 44	15, 43	14, 30			24, 38
MDD, MLV, MB		1, 2, 12	2, 4, 13	5, 8, 6			2, 13, 4
MNND, CLUMP		4, 5	3, 3	2, 4			3, 2
I1–4		7, 12, 10, 0	1, 7, 18, 9	1, 5, 16, 6			1, 3, 7, 26
CV, VM, GR		30, 23, 6	39, 16, 6	15, 4, 15			0, 0, 0
Box number	*15*	*16*	*17*	*18*	*19*	*20*	*21*
MH, MD	4, 9	6, 9	10, 22	12, 20	14, 17	17, 23	21,26
MDD, MLV, MB	0.2, 0.7, 4	0.5, 0.7, 2	1, 3, 5	2, 6, 4	1, 9, 3	1, 10, 3	1, 11, 4
MNND, CLUMP	2, 3	2, 4	2, 2	2, 3	2, 2	2, 2	2, 4
I1–4	22, 6, 0, 0	4, 9, 4, 0	16, 20, 20, 2	11, 17, 22, 3	11, 11, 26, 4	8, 13, 24, 27	9, 14, 23, 34
CV, VM, GR	76, 3, 1	8, 2, 42	14, 3, 27	2, 4, 42	0, 2, 22	0, 0, 4	0, 0, T
Box number	*22*	*23*	*24*	*25*	*26*	*27*	*28*
MH, MD	3, 5	5, 8	9, 11	9, 11	12, 16	14, 16	
MDD, MLV, MB	0.1, 0.2, 1.6	0.3, 0.8, 2.0	0.5, 2, 2	0.5, 4, 3	0.5, 6, 3	1, 7, 2	
MNND, CLUMP	2, 2	1.5, 2	2, 2	1, 1	1.5, 2	1, 2	
I1–4	15, 2, 0, 0	34, 13, 1, 0	40, 39, 15, 0	29, 37, 31, 0	58, 54, 38, 7	53, 65, 62, 26	
CV, VM, GR	50, 1, 33	30, 1, 18	2, T, 7	0, T, 21	0, 0, 2	0, 0, 0	

This is typical of semi-natural pine forest with scattered, spreading, old 'granny' trees (Steven and Carlisle, 1959) with thick, sweeping branches and rounded crowns. A high PRIN2 score (bad for capercaillie) characterizes tall, closely spaced, mature plantation trees, especially spruces, with a carpet of dead needles. With practice, one soon learns to assign a stand to a box, with only occasional reference to the key. Figure 6 presents in graphic form the main features of each box.

The scoring depends entirely on structural characteristics of a stand and the species of tree is not included in the scoring process. Nonetheless, stands of different species tend to get different scores because they have different structures. The scores for a stand are termed PRIN1 and PRIN2 because they were derived from a statistical technique termed Principal Components Analysis. For this analysis we measured 14 different aspects of a stand thought likely to be important to capercaillie

Table 6 Mean PRIN1 and PRIN2 scores for boxes 1 – 28 (see Figure 5). These are the values used for calculating GRANNY and PLANTATION scores.

BOX	*PRIN1*	*PRIN2*	*BOX*	*PRIN1*	*PRIN2*	*BOX*	*PRIN1*	*PRIN2*	*BOX*	*PRIN1*	*PRIN2*
1	8.5	1.0	8	6.0	1.0	15	3.5	1.0	22	1.0	1.0
2	8.5	2.0	9	6.0	2.0	16	3.5	2.0	23	1.0	2.0
3	8.5	3.0	10	6.0	3.0	17	3.5	3.0	24	1.0	3.0
4	8.5	4.0	11	6.0	4.0	18	3.5	4.0	25	1.0	4.0
5	8.5	5.0	12	6.0	5.0	19	3.5	5.0	26	1.0	5.0
6	8.5	6.0	13	6.0	6.0	20	3.5	6.0	27	1.0	6.0
7	8.5	7.0	14	6.0	7.0	21	3.5	7.0	28	1.0	7.0

(Table 7) in 64 sample plots. The plots contained 10 'main' trees (see Table 7 for definition) in a wide range of forest types. The analysis weighted each of the measurements and grouped them into a number of components. The grouping of variables which explained the greatest amount of variance in the data set formed the first principal component (PRIN1). Each succeeding group (component), explained less. In practice, only the first two components (PRIN1 and PRIN2) were meaningful. When the PRIN1 and PRIN2 scores for each sample plot were graphed, the 64 plots were distributed in fairly distinct clusters. These clusters represent the various developmental stages of a forest upon which the grid of 28 boxes was imposed (Figure 5).

The meaning of most of the variables (Table 7) is obvious from their names but 'canopy closure' and 'clumping' need some explanation. To measure canopy closure, the canopy and branches of a tree were regarded as a cylinder or cone in four height categories (Table 7). The percentage of the circumference that overlapped or touched any neighbour when observed from below defined the amount of interlocking (I1–I4) or touching (T1–T4). These values were summed (CC1–CC4) in the analyses but as branch interlocking was easier to assess than branch touching, only interlocking was used for the key. It was important also to consider how the trees were distributed in the plot, so an index of clumping, independent of tree density, was devised.

Table 7 Measurements taken in sample plots and variables derived from them that were used in the principal components analysis.

Measurements	*Term*	*Qualification*
r	Radius of plot (m)	Area contained 50, 100, 250, 500, 1000, or 2000 m^2
T	Total main trees in plot	Main tree: DBH ≥ 2/3 mean DBH all trees in plot
N	Number of trees measured	Usually 10 main trees
NND	Nearest neighbour distance (m)	Measured to nearest main tree
HEIGHT	Height of tree (m)	Measured with a hypsometer
DBH	Diameter at breast height (cm)	Diameter at *c.* 1.6m above ground level
HTDD	Height to first dead branch (m)	Branch ≥ 50 cm long
HTLV	Height to first live branch (m)	Height to base of crown, i.e. crown height
BRDIAM	Diameter of thickest branch (cm)	25 cm from the trunk usually estimated by eye
I1, T1	% of tree circumference in which	Interlock or touch at 0–2.5 m
I2, T2	branches interlock with (I) or touch (T)	2.5 – 5.0 m
I3, T3	those of any neighbouring trees at	5.0–10.0 m
I4, T4	four height bands	10 + m

Variables used in principal components analysis

CLUMP	Clumping index, independent of tree density in plot	$\pi r^2 . N/\Sigma NND^2 . T$
MH	Means for each measurement taken on *N* sample trees in the plot	Σ HEIGHT/*N*
MD		Σ DBH/*N*
MDD		Σ HTDD/*N*
MLV		Σ HTLV/*N*
MB		Σ BRDIAM/*N*
MNND	Mean nearest neighbour distance	Σ NND/*N*
CC1	Canopy closure index for sum of interlocking and touching branches for *N* trees in plot	Σ I1 + Σ T1
CC2		Σ I2 + Σ T2
CC3		Σ I3 + Σ T3
CC4		Σ I4 + Σ T4
CV	Sum of % cover of each ground layer species separately over four 1 m^2 quadrats	Heather *Calluna vulgaris*
VM		Blaeberry *Vaccinium myrtillus*
GR		Grass

Evenly spaced trees would have an index of 1, highly clumped ones an index of 5 or more.

It is possible from the key to decide fairly quickly and with no, or very few, measurements, which box would best describe any plot of 10 main trees chosen at random as representative of a forest compartment. The PRIN1 and PRIN2 coordinates for the centre of each box are given in Table 6; when a stand shares the characteristics of adjacent boxes, the average scores should be used to describe the stand.

Describing the structure of a forest

Each pair of box scores for PRIN1 and PRIN2 (Table 6) describes the structure of a stand or compartment, but a forest usually includes many compartments. Scores for the forest in the 1 km around the lek were calculated from weighted averages of the PRIN1 and PRIN2 scores for all the compartments in the forest. This was done according to the following equations to produce first, a GRANNY score, based on the PRIN1 values for all compartments and second, a PLANTATION score, based on PRIN2 values (see Table 8 for step-by-step guide):

$$\text{GRANNY} = \sum_{i=1}^{i=n} \left[\frac{\text{area of compartment } i}{\text{area of forest}} \times \text{PRIN } 1i \right]$$

$$\text{PLANTATION} = \sum_{i=1}^{i=n} \left[\frac{\text{area of compartment } i}{\text{area of forest}} \times \text{PRIN } 2i \right]$$

The greater the GRANNY score (maximum 8), the more a forest displays characteristics in common with a semi-natural pine forest. This score is related to the number of cock capercaillie attending a lek. Within the birds' range, it may be used to predict the number of cocks at a lek for any block of forest of 300 ha or more with at least a 65 % ground cover of trees > 2 m.

The greater the PLANTATION score, the more a forest reflects attributes of a dense plantation with tall, closely spaced trees with little or no ground vegetation. A value of 6 is the worst that could be obtained for capercaillie and forest management should aim to reduce it. However, the PLANTATION score is only weakly, negatively correlated with numbers of cocks attending a lek. While it may prove important in other contexts, it is not the best predictor of potential capercaillie abundance and so it is not considered further here, or in the main text (but see Picozzi *et al.*, 1992).

Table 8 How to calculate a GRANNY score

Step 1	Measure on a map the area of each compartment in a forest block with trees taller than 2 m. If it is intended to apply the score to a known lek site the block should cover the ground within a 1 km radius (314 ha) of the lek centre.
Step 2	Choose a sample plot to represent each compartment. One plot can represent more than one compartment if there are several similar compartments. Use Tables A–F to find the box number for each sample plot.
Step 3	Read the PRIN1 score for each sample plot's box number from Table 6.
Step 4	Multiply the PRIN1 score for a sample plot by the area (ha) it represents and divide by the summed area of all the compartments with trees taller than 2 m (Step 1).
Step 5	Add the values obtained in Step 4 for all compartments to give an overall GRANNY score for the forest.
Step 6	If the score is being applied to a known lek, substitute the GRANNY score in the equation: Expected number of cock capercaillie = 2 × GRANNY score – 4.3. (This will only apply if the total area of trees > 2 m tall covers at least 65 % of the ground within 1 km of the lek. If the area is less, there may be fewer cocks.)
Step 7	Steps 1–5 may be repeated using PRIN2 to obtain a PLANTATION score (see text).

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