Ecology of Capercaillie within a Managed Pine Forest

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Declaration

I hereby declare that this thesis has been composed by myself.

The work this thesis describes is my own work, except where stated otherwise, and has not been submitted in application for any other degree.

Lois Canham

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Abstract

The capercaillie is a rare species of forest bird which is once again facing extinction in Britain. Working pine forests are thought to represent the future for capercaillie in Scotland. However, few studies have focused on capercaillie within working forests and as a result current management recommendations are based on studies conducted within semi-natural pinewoods. Therefore study of the ecology of capercaillie within working forests is vital for the survival of the species in Scotland. The present study investigated the ecology of capercaillie, based on indirect measures of capercaillie use, within Morangie Forest, a pine plantation managed by the Forestry Commission.

Monthly dropping counts were collected over a 30 month period to gain insight into the capercaillie population at Morangie Forest, and to explore the use of faecal counts as a non-invasive monitoring tool. Habitat analysis, dietary analysis of droppings and genetic analysis of feathers were further conducted to fully explore ecology of capercaillie within Morangie Forest. Results showed that the capercaillie population in Morangie Forest was subject to seasonal movements and that movements were not confined to the bounds of the forest. Substantial mixing occurred with capercaillie from neighbouring Novar Forest. In addition, capercaillie within Morangie Forest selected habitat at a radius of 50m and beyond. The population of capercaillie at Morangie Forest was estimated at around 65 individuals based on measures from dropping counts and genetic determination of individuals from feathers. Results also suggested that winter dropping counts could represent a useful tool for forest managers to monitor the size and

movement of capercaillie populations frequenting their forests. In addition winter dropping counts could be used in conjunction with habitat data to plan management of habitat for capercaillie. The present study contributes towards future management strategies for the conservation of capercaillie within working forests and suggests further research priorities for capercaillie in Scotland, particularly those focused at a landscape scale.

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1.1 General Introduction

In this chapter I provide an introduction to the basic biology and ecology of the capercaillie, summarise the status of the species in Scotland and present reasons for its decline. I introduce commercial forestry in Scotland and its role in the conservation of capercaillie. Finally I introduce the focus of the present study.

1.1.1 The Capercaillie

The capercaillie (*Tetrao urogallus*) is the largest member of the grouse family (Tetranoidae). It is sexually dimorphic, with the male (cock) weighing around 4kg and the hen weighing just under 2 kg (Moss & Picozzi 1994) (Figure 1.1). The world range of the capercaillie lies within the boreal forest zone of northern Europe and Asia, with southern extensions into northern temperate and alpine zones in central and Western Europe (Cramp & Simmons 1980, Johnsgard 1983, Marti & Picozzi 1997, Klauss *et al.* 1989, Petty 2000). The range of the capercaillie is thought largely to coincide with the distribution of Scots pine (*Pinus sylvestris* L.) (Seiskari 1962 *as cited in* Sjöberg 1996), as well as with the eastern limit of bilberry (*Vaccinium myrtillus*) (Klaus *et al.* 1989).

The capercaillie has declined throughout its world range, particularly since the 1960s and is therefore a bird of conservation concern (Batten *et al*. 1990, Moss 1994).

Figure 1. 1 Cock and hen capercaillie

1.1.2 Breeding Biology

The capercaillie is a polygamous lekking species. The term “lek” was first used by Lloyd in 1867 to describe the mating arenas of birds and was named after the Scandinavian word for play, but more or less similar mating aggregations occur in a wide range of taxa (Höglund & Alatalo 1995). A lek can be defined as any aggregation of males that females visit only for the purpose of mating (Höglund & Alatalo 1995).

Three competing hypotheses have been applied to explain the formation of leks: ‘female choice’, ‘black hole’ or ‘hotspot’ and debate focuses on which hypothesis best explains observed behaviour (Davies 1991). The ‘female choice’ hypothesis states that females prefer aggregation of males to facilitate mate choice. Similarly, the 'black hole' hypothesis predicts that leks arise because clusters of male territories retain mobile females. In contrast the 'hotspot' hypothesis is based on the idea that females settle first and then leks form at the maximum point of overlap of female home ranges, i.e. 'hotspots' of female activity.

Irrespective of which hypothesis or combination of hypotheses is most appropriate, all predict that leks should be evenly distributed (Stillman *et al.*1996). Consequently, points where leks are expected but are absent presumably occur because habitat is not suitable (Haysom 2001). This logic can be extended to identify the habitat requirements of a lekking species and can be used to help us understand how to manage forests for species such as capercaillie and black grouse.

Capercaillie cocks gather at leks in spring, where they establish territories and compete for the attention of the hens (Figure 1.2). The peak display period is very short, lasting only around 10 days in late April and early May (Moss & Picozzi 1994). Although males will attend the same lek throughout this time, females will only visit leks for a few days for mating (Wegge *et al.* 2003) and may visit more than one lek before choosing a mate (Hjort 1985).

Figure 1. 2 Capercaillie lek with a male displaying to the females which are crouched low ready to mate (RSPB images)

The dominant or 'alpha' cock will generally mate with the majority of the hens present, although a single male is not necessarily dominant over the whole lekking period (Moss & Picozzi 1994). Cocks will fight for the position of alpha male and it is not unusual for birds to be injured or even die during the lekking season. In continuous forest, leks appear to be spaced at 2km intervals (Wegge & Rolstad 1986, Picozzi *et al*. 1992). The social structure within a lek is known as the "cake wedge theory" (Larsen & Wegge 1985) where between one and twenty cocks may attend, with individual daytime territories typically radiating out approximately 1km from the lek like portions of a cake (Hjörth 1985, Wegge & Rolstad 1986, Picozzi *et al*. 1992, Helle *et al*. 1994) (Figure 1.3).

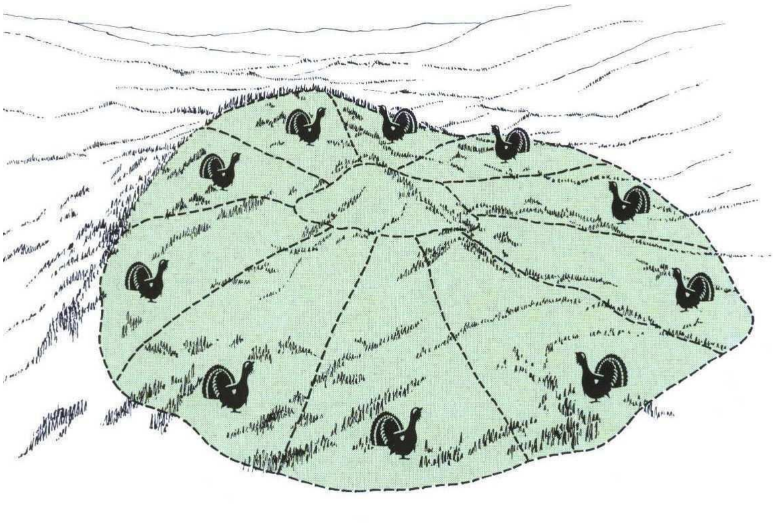

Figure 1. 3 Structure of a lek according to the "cake wedge theory" from Kortland (2006).

Hens are solely responsible for incubating and rearing chicks and when they have finished at a lek, they find a suitable place for their nest. The nest is a scrape on the ground, typically in a hollow under a tree and well concealed by dense ground vegetation or branches (Storaas *et al*. 1982, Jones 1985). However, occasionally nests are found on bare ground in dense woodland, on clear-felled areas or on heather moorland near to woodland (pers. obs., Moss & Picozzi 1994). The hen typically lays up to 11 eggs in early May, taking around 10-20 days to complete a clutch (Cramp & Simmons 1980) (Figure 1.4). Eggs are incubated for 24-26 days (Petty 2000) and chicks hatch synchronously after this period, with most chicks hatching in early June (Moss & Picozzi 1994). When hatched, the chicks will stay in the nest for the first 24 hours and are then led by the hen to suitable brood habitat. The chicks are fully grown when 2-3 months old (Petty 2000).

Figure 1. 4 Capercaillie nest in Meall Mor, Inverness-shire (M. Canham)

1.1.3 Habitat & Diet

The capercaillie is a forest grouse, typically associated with conifer dominated forest types (Storch 2001). Scots pine (*Pinus sylvestris*) is generally preferred (Cramp & Perrins 1994), although larch (Larix sp.), firs (Abies sp.) and spruces (Picea sp.) are also used (Wegge 1985, Moss & Picozzi 1994, Picozzi *et al*. 1996). Occasionally capercaillie are present in more varied forests, such as Cantabrian capercaillie which inhabit forests with high proportions of broadleaved trees such as oak (*Quercus petraea*) and beech (*Fagus sylvatica*) (Castroviejo 1975, Quevedo 2006).

Adult capercaillie are almost entirely herbivorous and during winter months the bulk of the adult diet is conifer needles (Cramp & Perrins 1994, Zwickel 1966), most typically Scots pine (*Pinus sylvestris*) (Seiskari 1962). Conifer needles continue to be an important food source throughout the rest of the year (Jacob 1987). Capercaillie diet is subject to seasonal variations in accordance with the availability of other foods and between early spring and late autumn capercaillie spend most of their time feeding on the ground. Foods such as heather, cotton grass, capsules of moss, sedges, rushes and seeds are all taken when available. However, the most important food plant at this time of year is blaeberry (*Vaccinium myrtillus*) where the shoots, stems, leaves and berries are all eaten (Petty 2000).

Blaeberry is also extremely important for capercaillie chicks which, in contrast to the adults, are insectivorous for the first four weeks of their life (Petty 2000). The invertebrate communities living in the blaeberry field layer are important food sources for capercaillie chicks which specialise on either Formicidae (Spidsø & Stuen 1988) or Lepidoptera larvae (Kastdalen & Wegge 1985, Picozzi *et al*. 1999). Storch (1994) found that capercaillie broods actively select areas rich in *Vaccinium myrtillus*; this is thought to be because these areas support much larger numbers of Lepidoptera larvae than other vegetation types (Summers *et al*. 2004). The dependency on invertebrates provides the protein in their diet required to maintain rapid growth. By seven weeks capercaillie chicks will switch to a mainly vegetarian diet in which leaves and berries of blaeberry are favoured (Spido & Steun 1998). Along with heather, blaeberry also provides cover to capercaillie chicks from predation and weather (Kortland 2006).

1.1.4 Impact of Forest Structure

Forestry influences capercaillie habitat choice in a variety of ways and at different scales. At a stand scale the successional stage and other structural characteristics such as stem density influence the ground vegetation, branching structure and openness of the forest; each of these affect capercaillie habitat choice (Storch 1993, Rolstad *et al.* 1988, Finne *et al.* 2000). At the landscape scale capercaillie require large unfragmented areas of forest, for example an individual cock may have an annual home range over 150ha, and a single lek may require at least 300 ha of suitable habitat to support the birds that attend it (Kortland 2006).

1.2 The Capercaillie in Europe

1.2.1 Distribution

In Europe, the main populations of capercaillie are found in Finland, Norway, Russia and Sweden within the contiguous distribution in the boreal forest from Scandinavia to eastern Siberia (Figure 1.5) (Klaus *et al.* 1989, Marti & Picozzi, 1997). The south-western part of the range in western and central Europe is fragmented primarily due to the patchy distribution of montane conifer forests and secondarily due to habitat loss. In this region, capercaillie are mainly restricted to the Alps, the Pyrénées, the Jura, the Carpathian and Cantabrian mountains (Petty 2000).

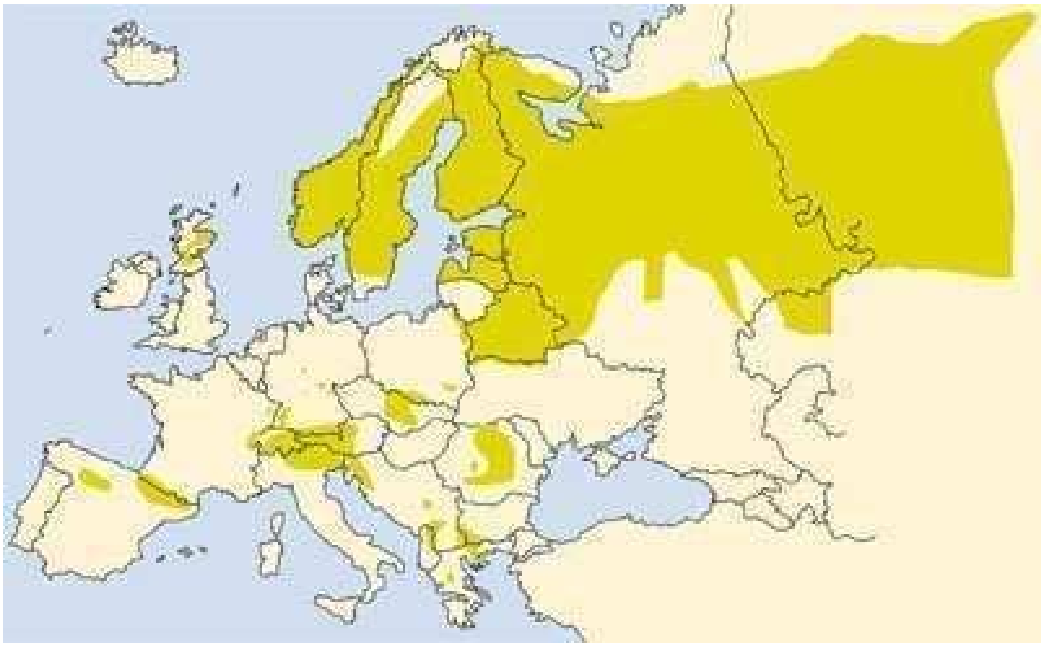

Figure 1.5. Capercaillie distribution in Europe (from www.grouse-tourism.de last accessed 10/07/06)

1.2.2 Population Size and Trend

The capercaillie still occupies most of its original range. However, there has been a contraction in range throughout Europe, with the most severe in the smaller and more isolated central European populations, many of which are now locally extinct (Storch 2000). Consequently, Europe now contains less than half of the global range of capercaillie (Birds in Europe 2004). Nevertheless, there is still an estimated 1,500,000 – 2,000,000 individuals present in Europe and as a result, capercaillie are not a Species of European Conservation Concern (non-SPEC) (Birds in Europe 2004).

1.3 The Capercaillie in Scotland

One of the most spectacular and charismatic of birds, the capercaillie is often thought to be representative of Scotland. The name capercaillie comes from the Gaelic 'capull coille', meaning 'horse of the woods'. It is thought that this name derived either from the bird's huge bulk or from the "clip-clop" noises it makes during lekking (RSPB 2007). The capercaillie is a publicly valued part of Scotland's biodiversity and there is great concern about the current status of capercaillie in Scotland.

1.3.1 Extinction and Reintroduction

Capercaillie fossil evidence from the Wolstonian Glaciation around 150,000 years ago has been found in Britain (BTO 2008), however, capercaillie are not recorded in the literature of Britain until 1527 by Hector Boece (Lever 1979). At that time capercaillie were found throughout Britain, but around 1660-70 the bird became extinct in England (Palmer 1976). Extinction followed in Scotland in 1785 (Pennie 1950) and finally in Ireland in 1790 (Simms 1971). The extinction of capercaillie from Britain was primarily due to large-scale destruction and felling of the birds' natural habitat, native Scots pine (*Pinus sylvestris*) forests (Harvie-Brown 1879). Extensive afforestation in the late eighteenth and nineteenth centuries was probably too late to save the native capercaillie (Moss & Picozzi 1994). The colder, wetter summers of the "Little Ice Age" of the eighteenth century, possibly resulted in reduced survival of capercaillie chicks, which along with continued sports shooting contributed to the reduction in their numbers (Moss & Picozzi 1994).

The capercaillie was the first bird to be successfully reintroduced into the United Kingdom (Marshall & Edward-Jones 1998). In 1837 the introduction of thirteen cocks and nineteen hens from Sweden was made at Taymouth Castle in Perthshire, Scotland. This and subsequent reintroductions resulted in the capercaillie being distributed throughout suitable habitat in central and eastern Scotland by the end of the 19th century (Moss & Picozzi 1994). Twenty-five years later between 1,000 and 2,000 birds were present on Taymouth Estate alone (Palmer 1976). Following a decline in range and numbers during the Second World War, the population increased again to approximately 20,000 individuals (Sharrock 1976). Since the 1970's however, there has been a dramatic decrease in the number of these birds throughout most of Scotland (Catt *et al*. 1998, Marshall & Edward-Jones 1998). Decreases of almost 90% have been recorded between the mid-1970's and mid-1990's.

1.3.2 Current Status and Trends

In addition to the decline in numbers, the capercaillie has declined in range and current surveys show that the distribution is now limited to four distinct zones. Zone 1 includes Easter Ross & Moray, Zone 2 is covered by the forests of Strathspey, Zone 3 comprises of Deeside and Donside with Zone 4 including Tayside and the isolated population on the Loch Lomond islands (Figure 1.6).

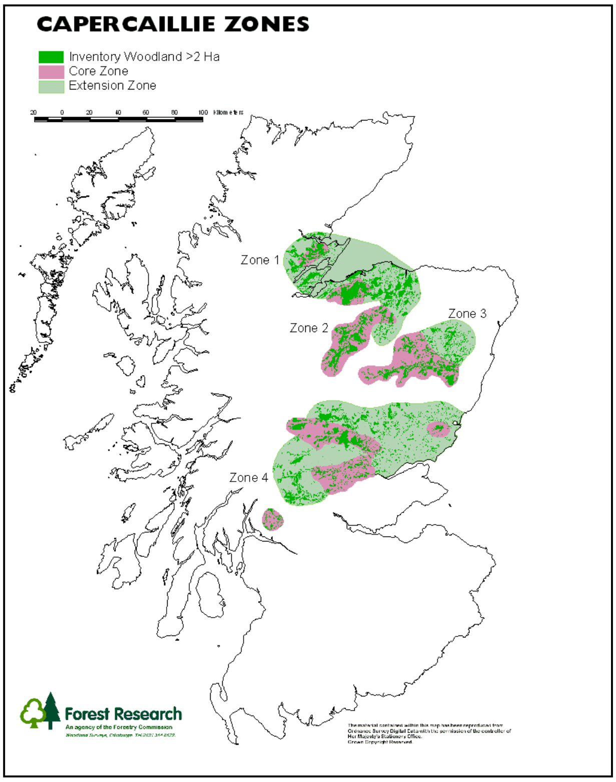

Figure 1. 6 Capercaillie distribution in Scotland (2006)

In 1994 the British population of capercaillie was estimated at 2,200 birds (1500-3200 95% confidence limits) (Catt *et al*. 1998), this declined in 1999 to an estimate of only 1073 (549-2041 95% confidence limits) capercaillie left in Scotland (Wilkinson *et al*. 2002). Predictive modelling had shown that the population of hens could have been as low as 206 by 2003 (Sankey 1996). However, the 2003/2004 survey estimated that capercaillie numbers were around 1980 (1284-2758 95% confidence limits) (Kortland 2004, Eaton 2007). It is worth noting, however, that the confidence intervals for each survey estimate overlap and therefore it cannot be concluded that there has been a statistically significant increase in the population of capercaillie in Scotland between

1994 and 2004. Breeding success is still much lower compared to studies elsewhere within the European range (Baines 2006). During the last five years 60 % of counted hen capercaillie failed to rear a brood and birds are still declining in some areas (Baines 2006). Research conducted by Moss *et al*. (2000) through capercaillie brood counts and radio-tagging found that capercaillie numbers declined in Scottish forests between 1992 and 1997 at a mean rate of 16% per year (1-30% 95% confidence limits). Moss *et al*. (2000) concluded that poor reproduction coupled with fence strikes was the probable cause of decline and further stated that if current trends continue the species could become extinct again in Britain early in the 21st century.

1.3.3 Present Decline

The present decline in Scotland has been attributed to four main factors: predation, fence collisions, weather and disturbance (Capercaillie LIFE Project 2004).

One of the factors thought most crucial to the successful reintroduction of Capercaillie to Britain, was the intense predator control that took place at the time (Moss & Picozzi 1994). The timing of re-establishment coincided with the growing interest in sporting estates and gamebird shooting, which persisted well into the twentieth century. During this period almost the entire predatory guild (mammals, raptors and corvids) was eliminated from some of the largest shooting estates in Scotland (Newton 1972, Newton 1979, Yalden 1999, Petty 2000). Gamekeeper numbers have been steadily falling since the 1900s and only around 15% of the gamekeepers present in the 1900s remain today (Potts 1986, Tapper 2000). Subsequently, increased predation has been proposed as the cause of decline in Scandinavian (Marcström *et al.* 1988, Lindström *et al.* 1994, Kurki *et al.* 1997) and Scottish populations (Moss & Picozzi 1994, Petty 2000). Increased predation may derive from either an increased number of predators (Moss & Picozzi 1994) or from increased predation rate, which can derive from forest fragmentation (Kurki *et al.* 1997). The density and range of foxes and crows has increased over the last 30 years, attributed to changes in land use as well as a decline in gamekeeper numbers. Many potential predators of capercaillie, such as goshawk (*Accipiter gentilis*) and pine marten (*Martes martes*) are now protected by law and have also increased in numbers (Gibbons *et al.* 1993, Petty 2000). Predation is generally limited to nests and broods, as adults have evolved strategies to escape predation and are large (Rolstad *et al.* 1988). There have not been many studies investigating the impact of predation on capercaillie in Scotland, of the few, Baines *et al.* (2004) found that capercaillie reared more young in forests with more blaeberry and fewer predators. However, increasing blaeberry ground cover was found to be far more important than predator abundance in determining capercaillie breeding success.

Fence collisions have been a significant factor in the decline of capercaillie (Petty 2000). Fences are erected to protect young trees and dwarf shrubs that are vulnerable to browsing by domestic stock, rabbits and deer. Fences are also erected in mature forests where browsing by deer is preventing growth and development of natural regeneration, especially in semi-natural pinewoods (Moss & Picozzi 1994). Capercaillie mortality is more frequent in areas where fences pass through mature woodland. The problem with deer fences has been highlighted in an extensive study of bird collision mortality throughout the Highlands of Scotland (Baines & Summers 1997, Catt *et al*. 1994, Summers 1998, Summers 1999). Most recently Moss *et al*. (2000) documented the fate of radio-tagged birds and found that collisions with fences accounted for 38% of the mortality.

Over the last thirty years changes in spring weather, possibly associated with the effects of global warming are thought to have had a major detrimental effect on capercaillie, particularly on breeding success (Moss *et al.* 2001). In spring earlier availability of newly growing plant food to gravid hens improves the quality of their diet, and so increases egg quality and chick viability (Moss *et al*. 2001). The hens need a quick burst of new plant growth in mid April to boost their nutrition, so that they can lay good quality eggs that hatch into viable chicks. Temperature records have shown that early April is now milder than it used to be and that mid April is cooler than before, which means that the burst of new plant growth is too early to benefit breeding capercaillie hens.

Once hatched in early June, the chicks grow very fast and have to gather their own food, with insects being required to supplement the protein in their diet for the first 2-4 weeks (Savory 1989). A number of studies have shown that arthropods can comprise over 50% of chick diet during the first few weeks (Kastdalen & Wegge 1985, Spido & Stuen 1988, Rajala 1959). The timing of capercaillie hatching had previously been shown to roughly coincide with the peak biomass of larvae in Scotland (Baines *et al*.

1996). However, it is suggested that due to the recent changes in the weather resulting in early April being warmer than before, peak larval abundance may occur too early for the chick feeding period (Moss *et al*. 2001).

In addition to this, capercaillie chicks cannot thermo-regulate and have to rely on brooding by the hen to maintain body temperature. The amount of rainfall during June has been found to have a negative effect on capercaillie breeding success due to wet conditions inhibiting foraging by chicks (Moss & Oswald 1985, Moss *et al*. 2001, Summers *et a*l. 2004). Moss *et al*. (2001) concluded that along with deaths from fences, increasingly protracted spring warming seems to have been a major cause of the decline in capercaillie in Scotland.

In the 2001 UK Climate Impacts Programme (UKCIP), Modelling Natural Responses to Climate Change (MONARCH) predicted that capercaillie could be one of the most vulnerable UK species in response to climate change. The bird is already in serious decline and is predicted to lose 99% of its remaining climate space by 2050s under model predictions due to predicted temperature increases of 0.3°C per decade and 6% increase in total annual rainfall (Berry *et al*. 2001).

In Britain, until recently there was little evidence to support the contention that human disturbance had a negative effect on capercaillie. This is in contrast to Europe where several studies had reported the effects of disturbance (Menoni & Bougerol 1993, Ménoni & Magnani 1998, Brenot *et al*. 1996, Zeitler & Glänzer 1998, Palanque 1999, Suàrez-Seoane & García-Rovés 2004). The first study in Scotland to suggest that disturbance had a negative effect on capercaillie was by Summers *et al*. (2004). While investigating habitat selection and diet of capercaillie in Abernethy Forest, Strathspey, Summers *et al*. (2004) found that capercaillie avoided forest tracks. A further study by Summers *et al*. (2007) specifically investigating avoidance of tracks by capercaillie concluded that it was likely that human activity was disturbing capercaillie and that reduced maintenance or removal of tracks would increase suitable woodland available to capercaillie. As a result of this work, track removal is now taking place in certain forests including Abernethy.

1.3.4 Current Conservation

The capercaillie was first included as a UK Red Data Species in 1990 (Batten *et al*. 1990). It was subsequently red-listed in 1996 because of a reduction of over 50% in its breeding range during the past 25 years (Gibbons *et al*. 1996). It is listed under Annex 1 of the EC Birds Directive (as a species whose status is a cause of some concern and identified for special conservation measures), and Appendix II of the Berne Convention (which carries an obligation to protect and conserve endangered or vulnerable species). Britain is a signatory to both the EC Birds Directive and the Berne Convention. Since 1981 the capercaillie has been listed on Schedules 2, 3 and 9 of the Wildlife and Countryside Act which still allowed shooting of the bird but gave some protection with a closed season. However, because of its decline a voluntary shooting ban has been in place on Forestry Commission and privately-owned land since 1990 (Petty 2000). In

2001 the Wildlife and Countryside Act was amended to remove capercaillie from Schedule 2 and 3 and increase its protection to Schedule 1, making it illegal to shoot the species and raising the maximum fine from £1000 to £5000.

In 1994 the capercaillie Biodiversity Action Plan (BAP) steering group was convened. The voluntary group is responsible for implementing the Species Action Plan for capercaillie on behalf of the UK Biodiversity Partnership and the UK Government. Aims of this group included halting the decline of capercaillie in its core range in eastern and northern Scotland by 2000 and expanding the range of capercaillie by 2010. In 2002 the capercaillie LIFE project '*Urgent Conservation for Scottish Capercaillie*' began. The Project secured £2.5m from the European Commission LIFE Nature fund, and a similar amount from a range of partners including Forestry Commission Scotland (FCS), Scottish Natural Heritage (SNH), Royal Society for the Protection of Birds (RSPB), Highland Birchwoods, Forest Research, Scottish Executive and Cairngorms National Park Authority. The main aim of the capercaillie LIFE project was to achieve a population of 5000 by 2010, by implementing a set of measures including: creating and improving condition of existing brood habitat, enhancing current levels of predator control, developing, refining and sharing habitat management techniques, co-ordinating site monitoring and making links with other E.U countries with capercaillie so that information could be shared.

1.4 The Role of Commercial Forestry in Scotland

1.4.1 History of Commercial Forestry in Scotland

Woodland was once the main vegetation type in Scotland, but by the beginning of the 20th century, forest cover had fallen to about 5% of the total land area of Scotland (Gill 1994). Most of the ancient native pinewoods, the preferred habitat of capercaillie, had been cut, burned, overgrazed or receded naturally (Steven & Carlisle 1959, Tipping 1994). The demise of capercaillie in Scotland mirrored the decline of many other woodland species. Their decline was the result of the large-scale deforestation during the fifteenth to eighteenth centuries (Ritchie 1920 *as cited by* Petty 2000).

With the outbreak of World War 1, Britain was no longer able to rely on timber imports and Scotland's woodland cover was dramatically reduced despite substantial tree planting by private owners in the 19th century (Avery & Leslie 1990). Therefore, the Forestry Commission was established in 1919 with the primary objective to re-establish woodland and the requirement to do this as economically as possible was soon added. Rapid conversion of low intensity agricultural ground to commercial forestry followed. The forests that resulted were largely non-native and planted on poor soils (Avery & Leslie 1990). Plantation design was often based on uniform blocks of conifers, with very little consideration of landscape or species choice for conservation (SNH 2002). By the 1970s a greater awareness of the environment developed, and forestry came under increasing pressure from both landscape and nature conservation (Avery & Leslie 1990). This led to rapid change and since the late 1980s, planting has become more sensitive to landscape and wildlife impacts, often using higher proportions of broadleaves and Scots pine (*Pinus sylvestris*) (SNH 2002, Forestry Commission 2004). Although treble the area of woodland in 1919, at 16.4% (Watts 2006) Scotland's woodland cover is still significantly lower than other European countries such as Austria (21%), Czech Republic (27%), Germany (25%) and Hungary (26%) (Iremonger 1997).

1.4.2 Management of Forests for Capercaillie

Capercaillie became so numerous in some areas of Scotland during 1950's-70's that control measures had to be taken to reduce damage to growing trees (Petty 2000). Palmer (1956, 1976) reported that capercaillie could damage the leading bud in young trees causing loss of annual growth and therefore loss of timber production. However, since then there has been a move away from managing Scottish forests solely for timber production and revenue and towards multifunctional forests, and capercaillie are now recognised as key conservation goal.

Forest management and further expansion of woodland area now occurs for a variety of reasons. Timber production is one objective alongside many including enhancing biodiversity, landscape and cultural heritage, developing opportunities for tourism and recreational enjoyment and improving the physical environment (Gill 1994). This change towards multipurpose forestry has undoubtedly improved habitat for capercaillie (Kortland 2006). Capercaillie are now recognised as an “umbrella species”, a species that needs large expanses of habitat and can therefore be used as a surrogate for many other biodiversity components that have similar but less extensive spatial requirements (Shrader-Frechette & McCoy 1993, Suter *et al.* 2002). Therefore managing a forest for capercaillie should favour a significant proportion of the (woodland dependent) biodiversity in need of conservation action.

Over 40% of plantation woodland in Scotland is managed by FCS. The current commitment of FCS is to restore, maintain and enhance Scotland’s biodiversity (Forestry Commission 2006) and this includes replacing exotic tree species with native Scots pine where appropriate, planting broadleaves, and a move to continuous cover systems rather than the current method of clearfelling. Such changes are proposed to benefit capercaillie along with many other woodland species. In important woodlands for capercaillie, a detailed assessment of current use by capercaillie and potential improvements, is undertaken prior to the Forest Design Plan process. FCS owns woodlands within each of the Capercaillie Core Zones (highlighted in Figure 1.6) and within two of the Special Protection Areas (SPA).

FCS is undertaking a wide range of actions to benefit capercaillie across a wide range of sites. These include fence marking, removal and re-routing, predator control, assistance with research projects, recreation management and educational activities (Baptie 2002). In 2001 the Forestry Commission produced a revised guidance note for staff in Scottish conservancies on deer and fencing, which included a framework for assessing the level of risk posed by deer fencing to capercaillie and other woodland grouse. Later in 2001, £700,000 for the removal and marking of deer fences was awarded from the government through a scheme administered by the Forestry Commission (Brankin 2001).

The Scottish BAP group has specific aims for management of forests for capercaillie. These include encouraging sympathetic management of Scots pine, especially extended rotations in commercial plantations, encouraging management of non-Scots pine woodland for capercaillie within, or close to, existing capercaillie ranges and seeking to enhance the continuity of existing isolated woodland fragments within the current range of the species (BAP 1995).

Funding from the European LIFE Project allowed the continuation of important habitat work for capercaillie in Scotland. Much of this work involved stand management within plantation forests to improve habitat for capercaillie. In addition brood habitat was improved and created, predator numbers were reduced and fences removed in forests used by capercaillie.

Through the LIFE project, a guidance booklet titled ‘Forest Management for Capercaillie’ has been published. It is aimed at forest managers in Scotland who want to make their forests more accommodating for capercaillie (Kortland 2006). The guidance is based on extrapolation of findings from European studies and from studies based in semi-natural pinewoods.

1.4.3 Managed Forests - The Future for Capercaillie?

It is thought that the large area of forestry planted in Britain during the 20th Century contributed to the capercaillie's successful reintroduction and re-establishment (Avery & Leslie 1990). Concern was expressed that the composition and structure of these commercial forests would be of limited value to wildlife including capercaillie (Tompkins 1986, Avery & Leslie 1990). However, plantations appear to have benefited capercaillie, providing new feeding grounds and area and hence encouraging further advances in range (Sharrock 1976, Thom 1986). Further to this, capercaillie have apparently adapted to living in forests with a high proportion of exotic conifers (Picozzi *et al*. 1992, Moss & Picozzi 1994). Although research has shown that capercaillie densities are higher in semi-natural woodlands, over 60% of the population are now found in plantation type woodlands (Pottie 1999). This is because the remainder of undisturbed native woodland is now too small to support the majority of capercaillie numbers.

In the past, the majority of literature and guidelines for capercaillie management in Britain have concentrated on capercaillie habitat use in semi-natural pinewoods. It is only more recently that the need for research on capercaillie use in commercial plantations has been identified, with the understanding that these plantations may represent the future for capercaillie. Sympathetic management of these commercial woodlands may be vital to help secure the future for capercaillie. There are various systems of management that can be modified to increase the value of commercial woodlands for capercaillie without undue loss of timber revenue. Some structural changes such as thinning, felling and new planting can be accomplished in a relatively short period of time. With careful planning these structural changes could help counteract some of the factors of decline; for example, reducing predation by creating cover, reducing habitat fragmentation by planting new trees and reducing disturbance by use of screening next to tracks. However, before these structural changes can be recommended, it is necessary to obtain a clear understanding of the habitat preferences of capercaillie within commercial woodlands.

1.5 Aims and Objectives

Management prescriptions based on semi-natural forests may not be economically viable or suitable for plantation forests. In order to manage plantations in a sympathetic way for capercaillie whilst retaining the productive function of the forest, research in working forests is needed. Furthermore, it would be preferable to relate habitat preferences of capercaillie to parameters routinely measured in plantation forests and readily available to forest managers, rather than other habitat measurements, devised in native pinewoods and not easily measured or even found in plantation forests.

1.5.1 Main Aim

The aim of this study is therefore to investigate capercaillie ecology in a managed productive forest and produce management prescriptions with the aim of facilitating direct transfer of scientific knowledge into management action.

1.5.2 Specific Objectives

Specific objectives of the study, which was based in Morangie Forest, Easter Ross, Scotland (Chapter 2) were to:

- Gain insight into the capercaillie population size and distribution in Morangie Forest by testing the use of dropping counts as a monitoring tool. (***Chapter 3***)
- Investigate the distribution of dropping counts as an indicator of capercaillie presence in Morangie Forest in relation to multi-scale habitat factors. (***Chapter 4***)
- Investigate habitat and diet of capercaillie in Morangie Forest in comparison with capercaillie habitat and diet in a semi-natural pinewood. (***Chapter 5***)
- Investigate the genetic structure of the capercaillie population at Morangie Forest. (***Chapter 6***)

1.5.3 Specific Hypotheses

The majority of methods in the present study focus around the use of faecal counts as an indirect measure of the capercaillie population at Morangie Forest. A number of specific hypotheses, relating to the main aims of the study, are introduced within each of the following chapters: 3-6. Methods pertaining to these hypotheses are therefore also contained within the individual chapters.

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Chapter 2. Morangie Forest – A Managed Pine Forest Containing Capercaillie

2.1 Rationale

The study area, Morangie Forest was chosen prior to commencement of this study. Criteria included the need for a capercaillie population in a planted forest; a forest with a range of habitat/management types and a management team sympathetic to the needs of a scientific study, and willing to provide logistic and financial support.

2.2 Description of Forest

The chosen study area is Morangie Forest to the south and west of the town of Tain in Easter Ross, Scotland (57 47 30 N, 04 07 25 W). The forest rises from sea level to 321m at the highest summit (Figure 2.1.) Owned by the Forestry Commission the plantation covers around 6000ha and is part of Dornoch Forest District. Much of the forest is long established woodland of plantation origin with small remnants of woodland planted around the turn of the 20th century. Forestry Commission planting has been almost continuous since it began in the 1950's with the most recent planting being carried out in Strathrory in the 1980's (Leslie 1998). Over the years tree species have been planted in relation to the soil type present, with Scots pine (*Pinus sylvestris*) comprising 48% of the forest and dominating the south and east, in areas such as Lamington (Figure 2.1) on the better drained soil. Sitka spruce (*Picea sitchensis*) (10%) and Lodgepole pine (*Pinus contorta*) (29%) form the major component of the north and west (Leslie 1998). On average 15,000m^3 of timber is harvested from Morangie Forest each year.

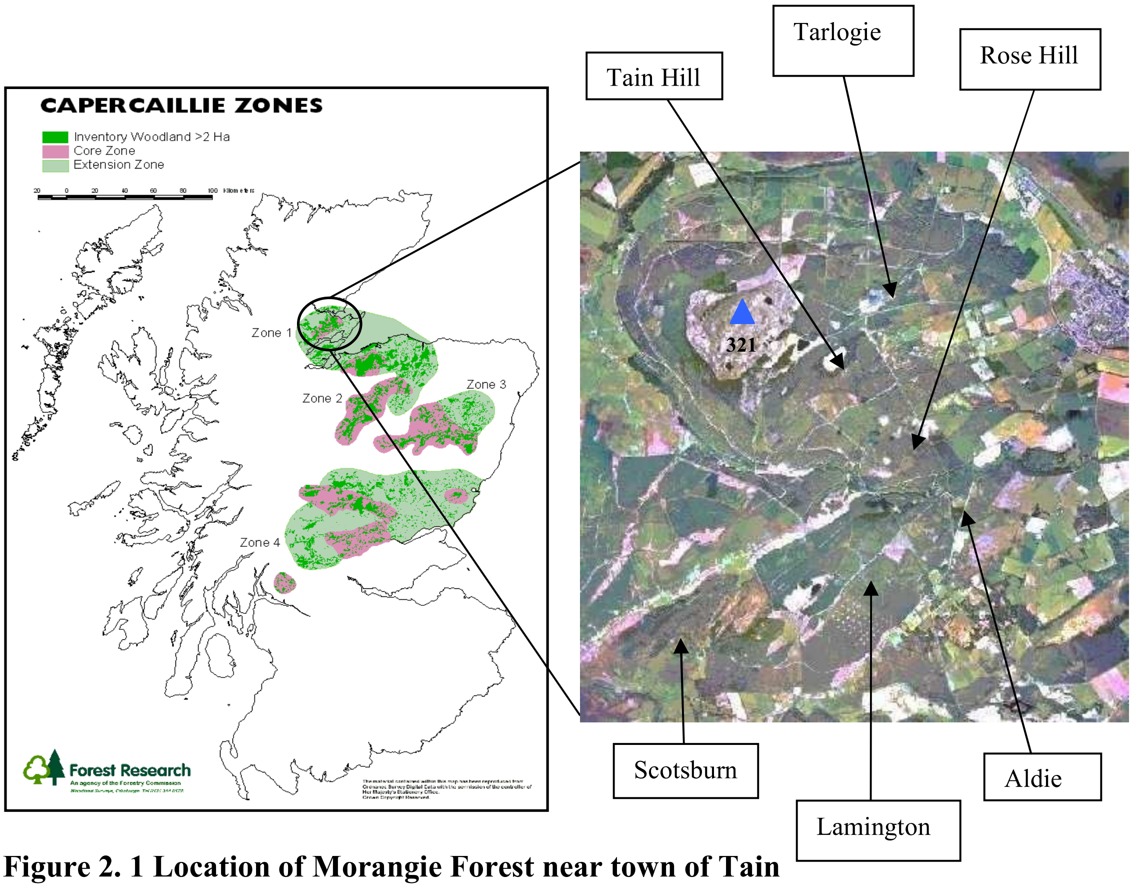

Figure 2. 1 Location of Morangie Forest near town of Tain

Despite the northerly latitude, Morangie Forest experiences average annual temperatures of 8-10ºC, with accumulated temperatures of 1,201 – 1,475 day.degrees above 5ºC (Pyatt *et al*. 2001). The eastern location, the rain shadow effect from the mountains to the west and southwest and warm waters from the Gulf Stream mean that

Morangie Forest receives above average sunshine and below average rainfall (450-700 mm) for the UK. Morangie Forest is located on a hill, and as a result the topography consists of hill, slope, lowland and valley. The soils in Morangie Forest mainly consist of ironpans on the slopes and gleys on the lower ground. Areas of peaty gleys and podzolised soils are found in patches within Morangie Forest, along with small areas of brown earth (Leslie 1998). The vegetation pattern closely follows the soil pattern with *Calluna vulgaris* predominating on the poorer soils and *Vaccinium* sp. on the better soils. There are also areas with a grassier field layer, and in the younger plantings the field layer is mostly moss (pers.obs., Leslie 1998).

2.3 Presence of Capercaillie

Morangie Forest holds the northernmost population of capercaillie in Britain and has been identified by the Capercaillie Biodiversity Action Plan (BAP) group as one of 15 key sites in northern Scotland (Leslie 1998). One of the primary objectives of management of Morangie Forest is to protect and expand the existing population in accordance with the UK BAP for Capercaillie (Leslie 1998). Unlike many other areas the population has remained stable over recent years and was thought to represent around 3% of the British population in 2002 when this study commenced (Leslie 2002).

2.4 Current Management of Morangie Forest for Capercaillie

Morangie Forest was first identified as an important habitat for capercaillie in 1986. As a consequence Wallace Hill (outside the study area, west of Scotsburn) (Figure 2.1), a core area for capercaillie was designated as an FC Capercaillie Reserve, later followed by Tarlogie (Figure 2.1). These early reserves were not successful as the Wallace Hill capercaillie population died or moved out and the Tarlogie population contracted (Leslie 1998). A number of factors were thought to have contributed to the decline of capercaillie in these areas including the small size of the designated areas, at less than 200 ha each, and the presence of deer fences, which were subsequently discovered to cause substantial mortality of woodland grouse (Petty 2000).

A Capercaillie Management Plan (Leslie 1998) was then developed to aid forest managers in capercaillie conservation and formed part of the Forestry Commission Forest Design Plan (FDP). This plan was on a much larger scale than the previous and incorporated the whole of Morangie Forest, maintaining known capercaillie areas as well as improving habitat in other areas to encourage expansion of the capercaillie range. As part of this plan, forestry operations were to be undertaken outwith the breeding season to avoid disturbance, a continuous cover system that avoids large coupes was to be developed, deer fences were to be removed, marked or reduced to stock-fence height, deer control was to be increased and the thinning technique was to be modified to favour ‘capercaillie trees’ (trees with wide crowns and large branches known to be preferred by capercaillie for roosting) (Leslie 2002). Further work involved more fence marking (boundaries), predator control, creation of brood habitat, cattle grazing and mechanical swiping.

Further protection was afforded when Morangie forest was designated as a Special Protection Area (SPA) in 2001. The aim of the SPA designation was to safeguard capercaillie habitat within Morangie Forest and protect the birds from significant disturbance.

Whilst the main management objective for Morangie Forest remains production of timber, constrained by detailed recommendations in the current Capercaillie Management Plan, provision is also made for recreation by local inhabitants and tourists. Formal recreation facilities include Tain Hill forest walk and all-abilities trails through Aldie Burn as well as two long distance cycle routes waymarked through the forest (Figure 2.1). There is a programme of summer events including school visits and themed guided walks. Locals regularly use the forest year around for dog walking, horse riding and cycling.

2.5 Methods

Although management of Morangie Forest already considers capercaillie, it is based largely upon the recommendations of research conducted in semi-natural forests of very different structure and as a result may be misdirected. This study sought in part to improve management by providing knowledge based upon capercaillie ecology in a managed forest. Morangie Forest represented an ideal opportunity to gain information about a population of capercaillie that appeared to thrive in a working forest managed primarily for timber production.

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Chapter 3. The Use of Faecal Counts as an Indirect Measure of the Size and Distribution of Capercaillie in Morangie Forest

Abstract

For forest managers to understand the implications of their management upon target species, an understanding of population size and trend is required. Therefore the size and distribution of capercaillie in Morangie Forest was examined using faecal counts. This was the first study to test the use of avian dropping counts as an indirect monitoring tool. Results showed annual cyclical patterns in dropping counts along with a decline in the number of droppings found over the three year study period. The significant decline in droppings found during summer months could not be fully explained by correcting for digestibility of food items and decomposition of droppings. This suggests that during the summer, capercaillie are using areas of the forest outwith the study area or areas under-sampled within the study area. Winter counts, not subject to the same issues of digestibility and decomposition as summer months, were used to estimate the capercaillie population in Morangie Forest. The capercaillie population was estimated at 63 individuals, comparable with the population estimate made from genetic mark-recapture data (Chapter 6). Results show that using summer capercaillie faecal counts as a monitoring tool has limitations at present. However, winter counts can be used successfully to monitor capercaillie population size and distribution.

Chapter 3. The Use of Faecal Counts as an Indirect Measure of the Size and Distribution of Capercaillie in Morangie Forest

3.1 Introduction

3.1.1 Rationale

For forest managers to understand the implications of their management upon target species, an understanding of population size and trend is required. In addition, an understanding of the spatial distribution of a target species is required in order to identify which habitats are important to the species and which locations need to be managed with particular caution, whether for recreation or for forest operations. Prior to the present study, capercaillie management in Morangie forest was based upon extrapolation from semi-natural woodlands and a collation of casual observations by forest staff. The present study aimed to estimate capercaillie population size and distribution within Morangie Forest as a basis for future management. In addition, due to the endangered state of the current capercaillie population, a key criterion of this project was to devise a method for studying capercaillie use of working forests that created as little disturbance to the bird as possible.

3.1.2 Methods for Estimating Abundance and Distribution

Population abundance is the most sought after measure in wildlife studies. Information on animal population abundances and how they change over space/or time are used to determine if a species is increasing or decreasing in numbers, how it responds to habitat manipulations and which habitats to protect to conserve a species. In short, population abundance is a primary indicator of the health and future well-being of a species under different management actions (Cheng 2007).

The most common methods used to establish population abundance fall into two categories: direct and indirect measurements. Direct measures are direct observations of individuals in a population and usually give estimates of the total number of individuals in a population. The following techniques are commonly utilised to make direct counts of abundance: capture recapture, line transects, point counts and more recently distance sampling (Newey *et al*. 2003). Capture recapture studies have been widely used to estimate animal abundance (Karanth & Nichols 1998, Nichols *et al.* 1984, Schwarz & Dempson 1994), but such studies require considerable investments in time and resources (Newey *et al*. 2003). Line and point transects have also been commonly used to estimate animal abundance (O'Mahony & Montgomery 2006, Teelen 2007) and are often used in surveys of birds (Bibby & Robins 1985, Bibby *et al.* 1992). With the development of more powerful computers and the programme DISTANCE (Thomas *et al.* 2006), distance sampling techniques have become widely used in recent years. Distance sampling involves counting direct sightings along line transects. The distance of a sighting from the line is recorded and using trigonometry a measure of density in an area can be ascertained, accounting for detectability (Buckland *et al.*1993). This method has been used for determining population size and habitat inferences for numerous bird and animal species (Canham 2001, Summers 1999) and has been found to provide reliable estimates for a variety of taxa (Newey *et al.* 2003).

Indirect measures of abundance usually provide an index of the number of individuals present, but not the actual numbers. Indirect measures are based on indirect signs of animal presence such as tracks, calls and song, and faeces. As a result, indirect measurements of population abundance tend to be a less invasive alternative to direct measurements, and can be a more suitable method for assessing population abundances of endangered species. Indirect surveys also prove advantageous where direct surveys of animals may be problematic, for example, species which are secretive in nature, crepuscular in behaviour and frequent areas of cover such as woodlands (Mayle *et al.* 2000).

Using animal tracks to estimate abundance has been most commonly used in areas where there is snow cover, consequently animals leave easily identifiable footprints. This method has been used in studies estimating population levels of wolverines (*Gulo gulo*) and lynx (*Felis lynx*) (Becker 1991) and brown hares (*Lepus europaeus*) (Flux 1967). An index of species abundance using annual snow track counts is commonly used by the Finnish Game and Fisheries Research Institute (FGFRI) to monitor wildlife numbers in Finland. The 2008 snow track census recorded 37,100 snow tracks of mammals from 23 species including pine marten (*Martes martes*), moose (*Alces alces*) and fox (*Vulpes vulpes*) (Helle 2008).

Indices of species' presence or abundance based on auditory cues such as vocal calls are widely used for birds (Lauga & Joachim 1987, Simons *et al*. 2007) and bats (Ahlen 1990, Kapteyn 1993) but less so for terrestrial mammals (Harrington & Mech 1982, Fuller & Sampson 1988) (Reby *et al*. 1998). The use of faecal counts is more commonly used to estimate abundance in terrestrial mammal species.

Faecal counts are an established censusing technique successfully applied to many animal species (Walker *et al*. 2000, Murray *et al*. 2002, Webbon *et al*. 2004) and are becoming a widely used tool to aid management and conservation of a wide range of species (Marques *et al*. 2001). As a result faecal counts are one of the most commonly used indirect methods to estimate population size, and have been found to yield estimates of abundance that are comparable with estimates using direct methods, for a range of species (Barnes 2001). Faecal counts have been used as an indirect estimate of abundance for a range of species including roe (*Capreolus capreolus*) (Mayle *et al*. 2000), red (*Cervus elaphus*) (Laing *et al*. 2003) and sika deer (*Cervus nippon*) (Marques *et al*. 2001), African elephants (*Loxodonta africana*) (Barnes *et al*. 1995, Plumptre & Harris 1995) and western gorillas (*Gorilla gorilla*) (Todd *et al*. 2008). However, faecal counts do not appear to have been used to assess the abundance of bird species. Most faecal counts are made using line transects, and distance sampling using faecal counts is now commonly being used to estimate population size (Marques *et al.* 2001).

In addition to determining the abundance of a population, it is also important to understand their spatial distribution. An understanding of the way a species uses an area has implications for the management of that species. The majority of the methods for assessing abundance, whether direct or indirect, allow a species distribution map to be created. This can be used simply as a tool to locate areas of species presence/absence, on which to focus management, or with further measures can be used to investigate species habitat choice.

3.1.3 Choice of Method for Capercaillie

The most common methods for determining capercaillie abundance are direct observations of the bird including: counts of males and females on lekking sites, counts of females with broods using pointing dogs and counts of birds on line transects (Petty 2000). Lek and brood counts take place annually in Scotland at a site level in key capercaillie areas to estimate productivity and local population size. A national survey of capercaillie in Scotland is conducted every 5-6 years using winter transect counts. The most recent survey (2003/2004) utilised advances in distance sampling techniques to produce a more precise population estimate than those in previous surveys (Eaton *et al*. 2007).

With capercaillie at critically low numbers in Scotland, more studies are now using indirect methods such as faecal or dropping counts to obtain an index of capercaillie presence. However, these observations have been used to derive information about habitat preference (Catt *et al*. 1997, Summers *et al*. 2004), or diet (Picozzi *et al*. 1996, Picozzi *et al*. 1999, Summers *et al*. 2004), rather than determine capercaillie abundance.

After reviewing available techniques, it was decided to test the use of dropping counts as an indirect method of gaining information about capercaillie population size and distribution within Morangie Forest. Direct methods of observation would be impractical as they would create too much disturbance to the capercaillie. Of the indirect methods available, faecal counts represented the most practical and effective method of observation and would be the least invasive for the bird. Faecal counts have not been used to examine population abundance in birds before due to the size and inconspicuousness of most bird droppings. However, the large size of the capercaillie and consequently the large size of their droppings makes them relatively easily found and therefore faecal counts were thought possible at Morangie Forest. As a result, this is the first study to test the use of avian dropping counts as a monitoring tool.

3.2 Aims and Objectives

This chapter investigates the usefulness of capercaillie droppings as a method for assessing abundance and distribution of capercaillie in Morangie Forest. The main aim is to estimate the size, trend and distribution of the capercaillie population at Morangie Forest using dropping counts, with the objective of providing this much needed information to forest managers as a basis for future management.

To meet this aim three specific questions were addressed:

- To what extent does seasonal variability in diet and faecal decomposition rates have an influence on faecal counts in Morangie Forest and can it be corrected for?
- What is the population size and trend of capercaillie at Morangie forest as estimated by faecal counts?
- What is the spatial pattern in distribution of capercaillie in Morangie Forest as estimated by faecal counts?

3.3 Methods

3.3.1 Dropping Counts

Most of the conducted fieldwork was based around faecal counts. The basic assumption is that faeces are produced regularly throughout the day without a particular spatial pattern, as is the case with mammal scats (Ewer 1968). Andreev & Lindén (1994) found that the number of capercaillie droppings produced in a certain area is strictly proportional to the time spent in that area. This means that each collected dropping represents a place where a bird has spent *x* amount of time, where *x* will be a function of the defecation rate (Andreev & Lindén 1994). It was proposed to continue the use of a stratified point sampling framework designed and implemented in 2001 by a research student trialling the use of faecal counts as a method of gaining information about population and habitat use of capercaillie (Scozzafava 2002).

Originally a total of 150 trees had been marked at random within Morangie Forest, with a constraint of being at a distance of no less than 100m from one another (Figure 3.1). Each tree represented the centre of a plot with a 10m radius. One plot tree was subsequently felled between the initial study by Scozzafava (2002) and the present study and therefore 149 plots remained.

Each plot was visited every month for 30 months at roughly similar intervals. A radius of 10 metres around the central plot tree was searched and cleared of droppings in each plot. Using a tree as the centre of each plot ensured that the same area was cleared each month. Due to the density of trees in each plot, the central plot tree was not thought to characterise the plot. The plot was systematically searched for droppings radiating from the central tree out to the 10m radius boundary. The amount of time spent in each plot was related to the detectability of droppings within the vegetation. More time (to a maximum of 30 minutes) was spent in plots where vegetation structure made detectability of droppings more difficult, to ensure that a similar search effort was conducted in all plots. The number of droppings in each plot was recorded and the droppings were removed. Each dropping was defined as a pellet terminating with a white tip of uric acid, resulting from a single defecation act. In the case of broken or weathered droppings, white tips were counted and failing that the number was estimated using the average length of a dropping. The presence of a roost in a plot was also recorded. A roost is where a bird has spent a period of time resting or sleeping. A roost was defined as a group of at least 10 faecal pellets closely clustered (maximum distance less than a droppings length). The heap could be more widespread in the case of a branch roost where the droppings fall from several metres. All droppings were stored in a freezer on same day as collection. Methods closely followed those used by Scozzafava (2002) to allow comparison of data. A shared visit was conducted to familiarise techniques and plot location and also to ensure consistency between observers.

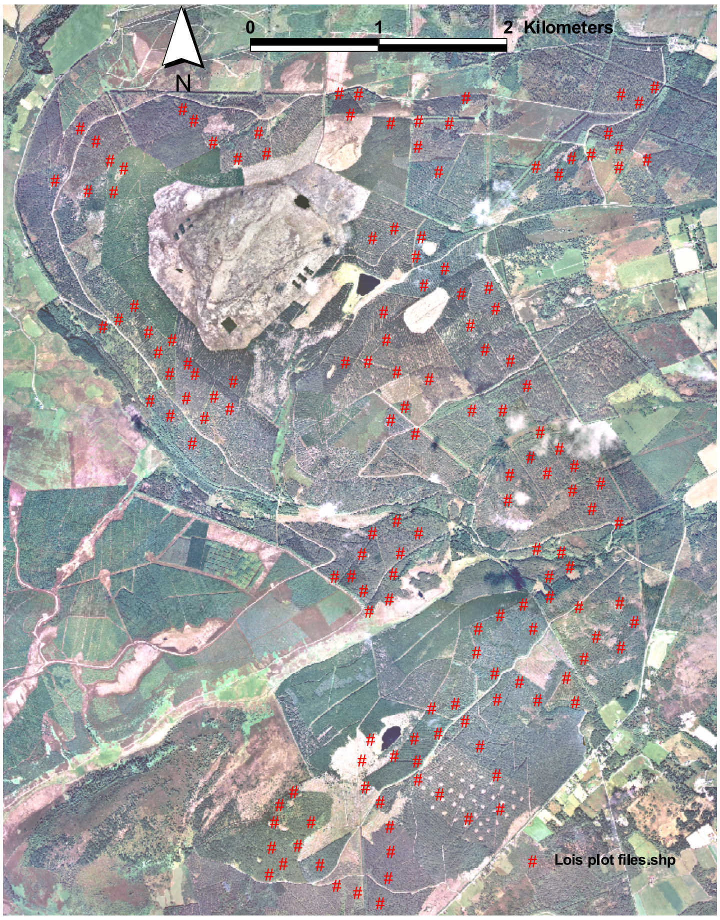

Figure 3. 1 Location of 149 sample plots in Morangie Forest

Due to counts taking around two weeks per month to conduct, and that there was a consistency in findings from month to month, it was decided after a year that the number of study plots should be reduced to allow fieldwork to be completed in a single week per month. The reduction in plot numbers was achieved by removing all plots where droppings were found two months or less out of the 12 months initial study period. This resulted in 87 plots, thought to be achievable in a week survey period. Plots never used were mainly located in the north of Morangie Forest, where capercaillie have never been seen and therefore were thought suitable for removal.

Plots used only one or two months of the year were evenly spaced throughout the forest and therefore acceptable to remove. The percentage of droppings retained when removing these plots counts from the previous dropping counts, resulted in 95.5% of droppings retained in the 87 plots. It was therefore decided that continued counts from the 87 remaining plots would not be compromising count data collected.

Field data consists of location of plots, time and date of droppings counts, total number of droppings in 149 plots over initial 12 month study period, and then total number of droppings in 87 remaining plots over following 18 months. The number of roosts (definition of roost above) in each plot each month was also recorded.

3.3.2 Data Analysis – Summary Count Data

From the total number of droppings collected in each plot every month, a number of summary measures can be ascertained.

Summary measures include:

- *Total number of droppings found each month in plots*. This is a measure of the intensity of use of plots by capercaillie each month.
- *Maximum number of droppings found in a single plot each month*. This represents another measure of intensity of plot use.

- *Number of presence plots each month*. This measure represents the number of plots used by capercaillie each month where use is defined as; the number of plots that contained at least one dropping when surveyed each month.
- *The total number of roosts found each month in plots*. A roost was indicated by the presence of at least 10 droppings closely clustered. This measure represents the time spent in a plot resting or sleeping as opposed to other activities such as feeding.
- *Consistency of use*. This is a measure of plot fidelity and is the number of months capercaillie used sample plots in total.

A further summary measure of count data ascertained was an estimate of the capercaillie population at Morangie Forest. Andreev & Lindén (1994) found that capercaillie during the winter produce on average 177 (95% CI: 142, 212) droppings per day. Therefore, an estimate of the Morangie capercaillie population in December 2002-2004 was made using data from Table 3.1 and the following equation:

$$Cn = (Dtd(Aft/Apt))/Dtm$$

Where: Cn = Estimated number of capercaillie
Dtd = Total number of droppings found in December
Aft = Total area of forest within which plots are located
Apt = Total area of plots
Dtm = Number of droppings produced per month per bird (from Andreev & Lindén 1994)

Table 3.1 Raw data used to estimate capercaillie population size using dropping numbers

Year	Total number of droppings in plots (*Dtd*)	Total area of plots (km^2) (*Apt*)	Total area of forest plots contained within (km^2) (*Aft*)	Number of droppings produced a month (*Dtm*)
2002	1780	0.047	8.85	5310 (±1050)
2003	1110	0.047	8.85	5310 (±1050)
2004	466	0.047	8.85	5310 (±1050)

Estimates from dropping counts were compared to brood and lek count data from GCT & RSPB.

3.3.3 Correction of Counts for Digestibility and Decomposition

The change in digestibility of food items ingested by capercaillie throughout the year, and therefore the change in the number of droppings produced throughout the year means that dropping counts as a measure of use will not be comparable at different times of the year unless correction is made for the change in digestibility of diet.

To account for changes in digestibility, a correction factor was applied to number of droppings collected during August 2003 to make them comparable to the number of droppings collected during December 2003. August and December were the two months where there was the most contrast between summer and winter diets.

Table 3.2 Frequency of dietary items in droppings in December 2003 and August 2003 (Chapter 5) and associated digestibility rates of these dietary items. Digestibility rates from Moss 1983, Moss & Hanssen 1980, Moss & Parkinson 1975, Andreev & Lindén 1994). * average digestibility due to dietary component remaining unidentified

	% Dietary Component		
Diet	December	August	Digestibility %
Pine	100	31.2	30
Blaeberry	0	46.5	65
Seeds	0	17.2	40
Unidentified	0	5.1	45 *
Total no of droppings	1110	258	

The digestibilities of the August dietary components illustrated in Table 3.2, were each entered into the following correctional factor equation:

$$CDi = Dc(Di/Dp)$$

Where: CDi = corrected dietary item
Dc = % dietary component
Di = digestibility of dietary item to be corrected
Dp = digestibility of pine

CDi was then entered into the equation below with actual dropping numbers from August to obtain the corrected number of droppings

$$NDc = (NDa/100)(CDi_1 + CDi_2 + CDi_3 + CDi_4)$$

Where: NDc = number of corrected droppings in August
NDa = number of droppings in August

Unfortunately droppings in other months could not be corrected to winter pine equivalents due to a lack of published digestibility rates for other plant items found in the capercaillie diet during the rest of the year.

In addition to changes in the digestion of the diet of capercaillie during summer months, the decomposition and subsequently the visibility of droppings changes as the diet changes. Changes in digestion and decomposition act synergistically to give significantly higher degradation rates in summer counts than winter counts. It is important to note that for faecal count purposes it is necessary that the droppings remain identifiable as such. During winter months when the majority of the capercaillie diet is pine needles, droppings are recognisable for many months even after heavy rain or snow (pers.obs.) Therefore, decomposition trials were run in Morangie Forest during summer months. Five droppings mainly consisting of each dietary item; pine, blaeberry and leaves/seed mix were placed randomly on the forest floor in Morangie Forest during July and their degradation noted. Trial droppings were checked each day for the first three weeks of the trial then weekly thereafter to a maximum of 13 weeks. When droppings were no longer recognisable as such, the number of days until degradation was recorded.

Because of the constraints involved in calculating digestibility of capercaillie dietary items, the only month where both digestibility and decomposition correctional factors could be applied is August 2003. It therefore means that results of the correction factor can only be used to investigate the cyclical pattern in dropping counts rather than allow a means for correction of all counts. Consequently digestibility and decomposition results are not critical to subsequent analyses of the data.

3.3.4 Spatial Analysis of Count Data

To explore spatial and temporal patterns in dropping counts, and therefore capercaillie, a relatively new method, SADIE (**S**patial **A**nalysis by **D**istance **I**ndic**E**s) was used (Perry 1998). The total number of droppings collected monthly for the 30 month sampling period from May 2002- Dec 2004 was analysed using SADIE.

The SADIE system has been developed for the spatial analysis of count data. Each count is assumed to be spatially-referenced at a specified location in two dimensions; the set of locations may be irregularly spaced and not on a grid (Perry & Dickson 2002). The basis of SADIE is to quantify the spatial pattern in a sampled population by measuring the total effort (in terms of distance moved) that the individuals in the observed sample must expend to move to extreme arrangement, in which the individuals in the samples are either spaced as uniformly (regularly) or are as aggregated (crowded) as possible. In practise, this effort is equated with minimum distance, *D*, required to move to complete regularity; the value of *D* is provided by the Transport algorithm for the linear programming literature (Perry *et al.* 1999, Kennington & Helgason 1980). This algorithm provides a unique solution based on notional 'flows' of individuals and fractions of individuals, from 'donor' sample units, with greater than average abundance, to 'receiver' units, with less than average abundance. The flows may be depicted graphically in a red-blue 'initial-and-final' plot that aids visual interpretation of the major spatial features of the data (Perry 1998).

The spatial pattern is quantified by permuting the observed set of counts among the sample units. This provides data for the null-hypothesis that the counts are arranged randomly with respect to one another, while maintaining precisely the numeric properties of the data, which may be investigated separately. In particular, division of the observed value of D by the mean value from several hundred such randomisations gives an index of aggregation I_a; values of $I_a = 1$ indicate randomly arranged counts, while $I_a > 1$ indicates aggregation of observed counts into clusters (Perry *et al.* 1999).

3.4 Results

3.4.1 Digestibility and Decomposition Correction Factor

Table 3.3. Decomposition time of capercaillie droppings in relation to content

	Decomposition time (days)		
Dropping number	**Pine**	**Blaeberry**	**Leaves and Seeds**
Dropping 1	91+	12	53
Dropping 2	91+	14	35
Dropping 3	91+	13	35
Dropping 4	91+	18	35
Dropping 5	91+	13	42
Average decomposition	91+	14	40

Table 3.3 shows the results of the decomposition trial. Results showed that pine needles and leaves/seed mix were visible for well over the standard month sampling period. However blaeberry droppings were found only to be visible for an average of 14 days. Therefore, assuming that plots were used in a similar manner throughout the month,

A correctional factor of 2.21 was obtained by dividing the number of days in August by the average decomposition time of blaeberry droppings. August 2003 counts were then corrected for decomposition of blaeberry droppings by multiplying the proportion of droppings found in August and comprising blaeberry (Table 3.2) by the calculated correction factor of 2.21. This resulted in a count corrected for decomposition of 419 droppings for August 2003 (Table 3.4).

Using the digestibility equation and values from section 3.3.3 and decomposition results from above, the original August 2003 counts were corrected for both digestibility and decomposition and compared to counts in December 2003 (Table 3.4).

Table 3. 4 Corrected counts for August 2003

	Aug-03	Dec-03
Original dropping count	258	1110
Count corrected for digestibility	419	1110
Count corrected for digestibility and decomposition	684	1110

There still remains a difference between corrected counts and original counts with winter counts remaining higher. Because only August counts could be corrected and compared, all further presentation of dropping counts is based on original counts with the understanding that most probably something other than digestibility and decomposition accounts for the difference in numbers observed.

3.4.2 Summary Measures of Dropping Counts

Using raw count data from the reduced 87 survey plots summary measures each month were plotted (Figure 3.2 & 3.3).

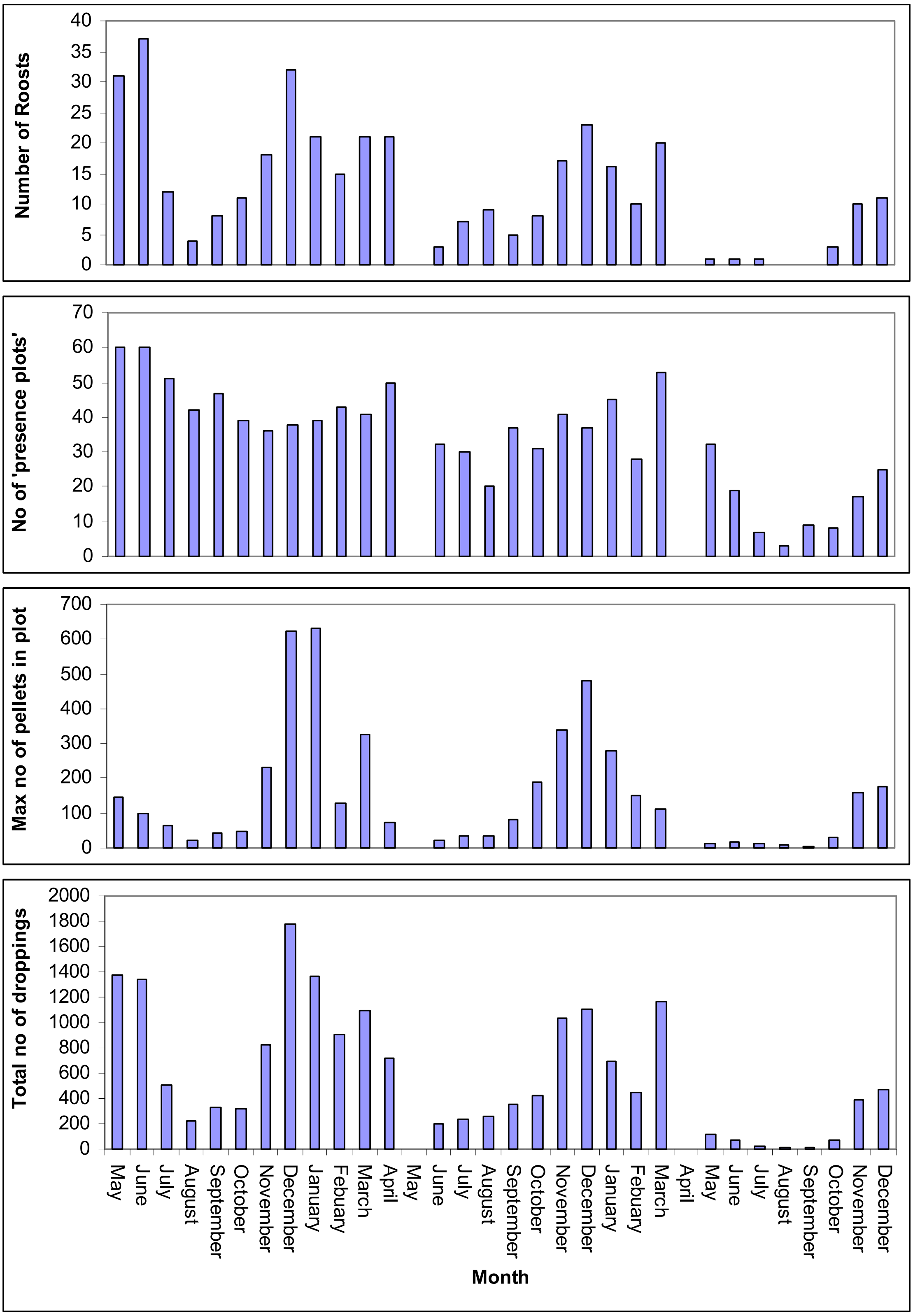

Figure 3.2 Four summary measures of dropping counts each month from May 2002- December 2004 (87 plots)

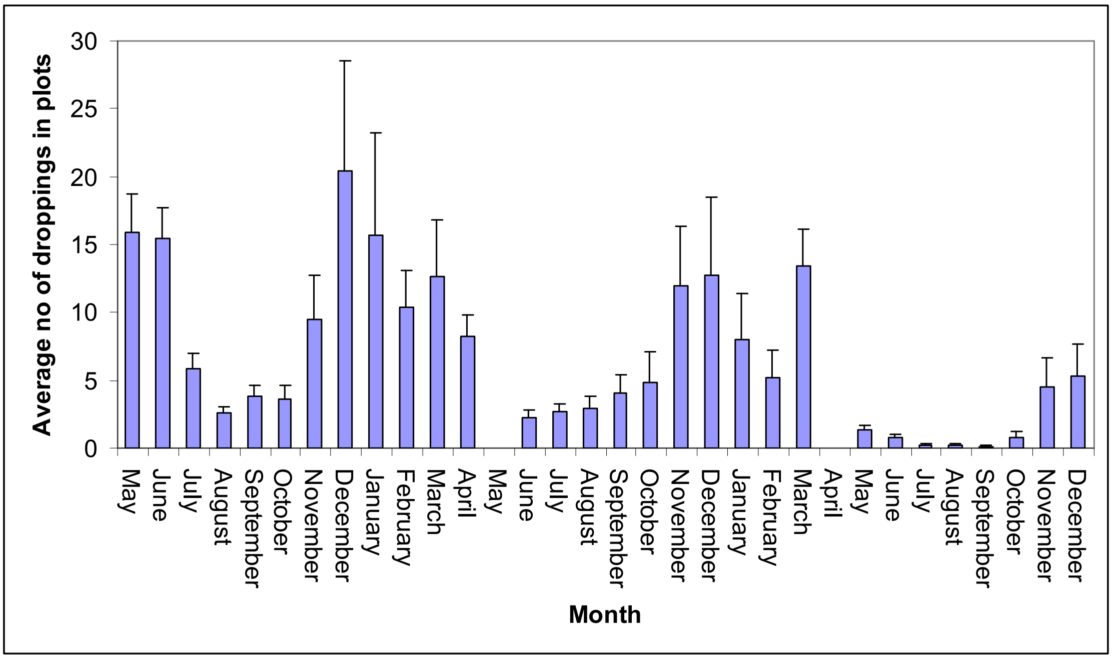

Figure 3.3. Average number of droppings per plot each month from May 2002 – December 2004 (87 plots)

The total number of droppings (Figure 3.2) decreases in summer months then increases again in winter months. This cyclical pattern repeats throughout the remainder of the sampling period and appears to be accompanied with a downward trend in the numbers of droppings counted. The maximum number of droppings found in a plot shows a similar pattern to that of the total number of droppings. The number of 'presence' plots has a less obvious pattern. The number of roosts counted each month appears to mirror the pattern observed with the total number of droppings and the maximum number of droppings found in a plot each month. The average number of droppings per plot (Figure 3.3) also shows a similar pattern with more variation in counts observed during winter months.

Wilcoxon matched pairs tests were conducted to test for difference in annual trends in dropping count data. Winter dropping counts (December, January & February) were used to test for significant annual change in dropping numbers (Table 3.5).

Table 3.5. Results of Wilcoxon matched pairs test on annual trends in dropping count data

Trend in Dropping Counts	Dropping Data	Test Statistic	Sample Size	Probability
Annual Decline	Dec 02 - Dec 03	614.5	54	0.325
	Dec 03 - Dec 04	258.5	41	0.030
	Dec 02 - Dec 04	742.5	67	0.019
	Jan 03 - Jan 04	473.5	51	0.167
	Feb 03 - Feb 04	399	51	0.012

Results show that between December 2002 and December 2003 the change in dropping numbers was not significantly different. The same result was found in January 2003 to January 2004. However, there was a significant decline in the number of droppings from February 2003 to February 2004 ($p<0.012$). In addition, dropping counts from December 2002 to December 2004 also showed a significant decline ($p<0.019$).

Another useful measure to determine capercaillie use of plots is the number of months in a year that plots are used by capercaillie. This gives a measure of the consistency of use of a plot or plot fidelity. Figure 3.4 highlights the mean number of months a year capercaillie used plots from 2002-2004. The mean number of months plots are used in a year falls from 2002 to 2004.

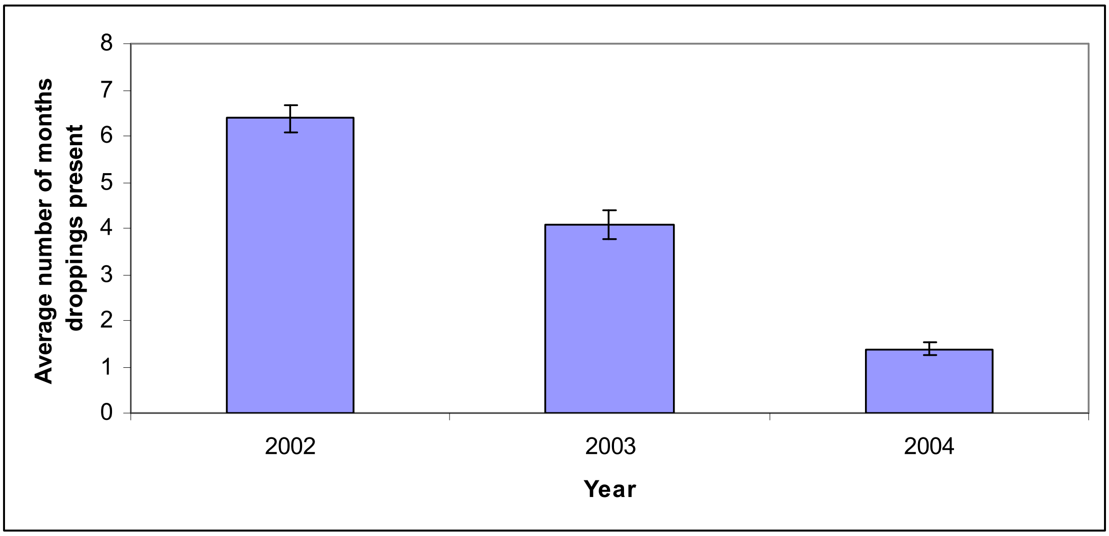

Figure 3.4 Graph to show the average number of months plots used by capercaillie in 2002-2004

Using the equation given in 3.3.2, an estimate of capercaillie population size in December 2002-2004 was made at Morangie Forest. Table 3.6 compares these population estimates, obtained indirectly from dropping counts, with estimates obtained from direct methods. Estimates from dropping counts were obtained during winter months and are therefore not directly comparable with lek counts made during April and brood counts made during July and August. Nonetheless, it is interesting that all counts are 'in the same ballpark'.

Table 3. 6 Estimate of capercaillie population at Morangie Forest based on December dropping counts in comparison with other population estimates. * Intervals for population estimate based around confidence intervals given by Andreev & Lindén (1994) for average number of droppings produced per day.

Year	Estimate of population size from dropping counts	Estimate from lek counts (assuming 1:1 sex ratio)	Estimate from brood counts (male, female & juveniles)
2002	63 (53, 79)*	30	42
2003	39 (33, 49)*	30	39
2004	17 (14, 21)*	42	32

With reference to Table 3.6, the estimate from dropping counts clearly shows a decline. A decline is also observed in brood count numbers. A decline is however, not mirrored by the lek counts, which show an increase in numbers between 2002-2004.

3.4.3 Spatial Analysis of Count Data

The spatial pattern of presence or absence of capercaillie from 87 plots for the sampling period of 30 months was analysed. Red stars represent donor plots in which plots are used more than expected if used randomly, blue stars represent receiver plots, plots that are used less than expected by random chance, red lines represent the flow of droppings required to redistribute counts to uniformity, open circles represent the original 149 plots and hats above stars represent plots that contained a roost in that month.

Visual interpretation of the data shows that capercaillie droppings are not randomly distributed throughout plots. An Initial-and-Final plot from November 2002 is used as an example of dropping distribution in winter months (Figure 3.5). The Initial-and-Final plot shows that a small proportion of plots, distributed throughout the study area, are used more heavily by capercaillie in comparison to the rest of the study plots. These are illustrated as a red donor plots. Plots appear to be used less heavily in the north of the forest. This is illustrated as the directional movement of droppings from red donor plots to blue receiver plots. In addition, more heavily used plots tend to be roosting plots during November 2002.

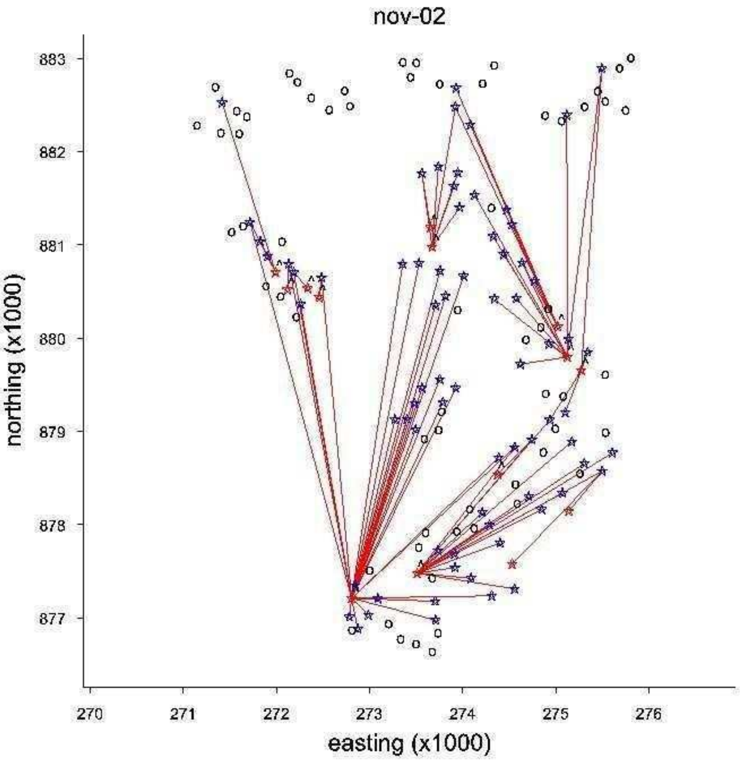

Figure 3. 5 Initial-and-Final Plots for November 2002. Red stars represent donor plots, blue stars represent receiver plots, red lines represent the flow of droppings required to redistribute counts to uniformity, open circles represent the original 149 plots and hats above stars represent plots that contained a roost.

An Initial-and-Final plot from July 2002 is used as an example of dropping distribution in summer months (Figure 3.6). The Initial-and-Final plot shows that during July 2002 there is a larger proportion of donating plots than in November 2002. However, in order to achieve regularity, donating plots in July 2002 are donating fewer droppings to fewer plots than those in November 2002. In addition, the directional movement calculated by SADIE required to rearrange counts into complete regularity, is more random and does not show the directional movement observed in November 2002.

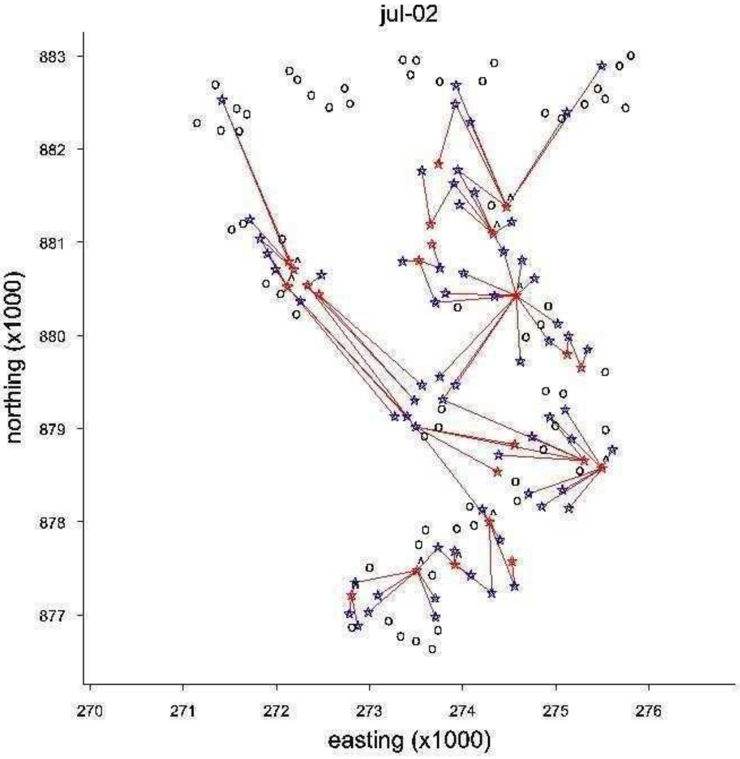

Figure 3. 6 Initial-and-Final Plots for July 2002. Red stars represent donor plots, blue stars represent receiver plots, red lines represent the flow of droppings required to redistribute counts to uniformity, open circles represent the original 149 plots and hats above stars represent plots that contained a roost.

Using Initial-and-Final plots for December 2002-2004 and August 2002-2004 (Figure 3.7) further highlights the directional movement calculated by SADIE required to redistribute droppings to complete regularity. During December, a small number of plots are donating droppings to a large number of plots, and these donations are in a northerly direction. However, in August the movement becomes less linear and it tends to be plots in the North donating to other plots.

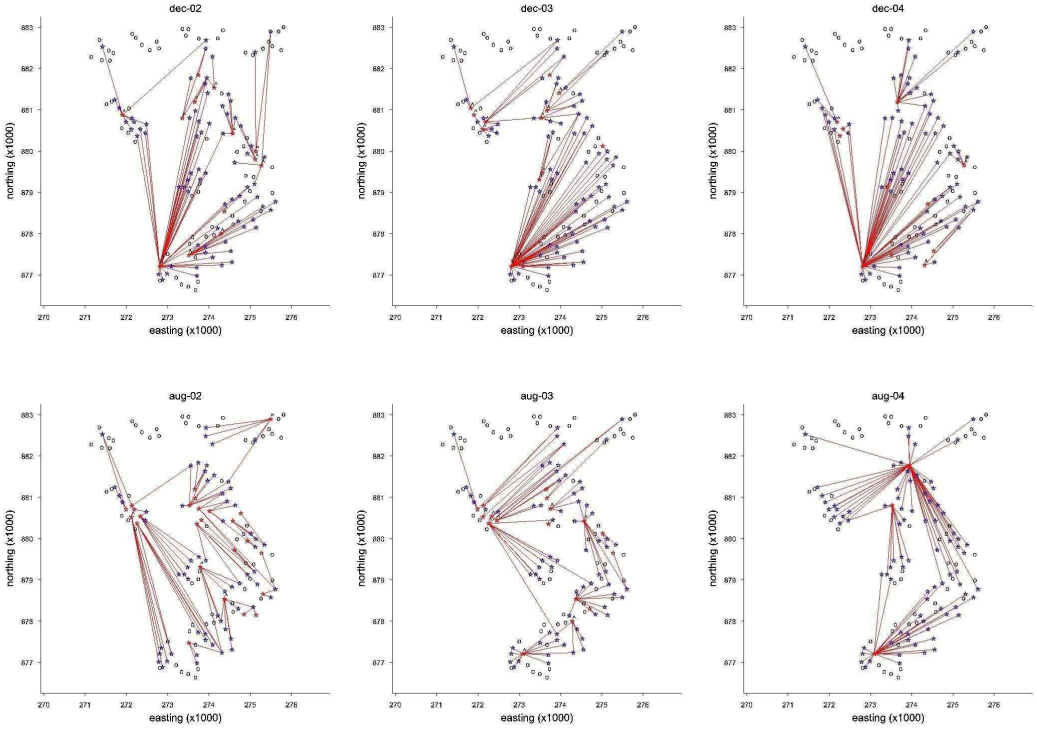

Figure 3. 7 Initial-and-Final Plots for Dec 2002-2004 and August 2002-2004. Red stars represent donor plots, blue stars represent receiver plots, red lines represent the flow of droppings required to redistribute counts to uniformity, open circles represent the original 149 plots and hats above stars represent plots that contained a roost.

In biological terms, results from the spatial analysis equate to capercaillie using plots in the south of the forest more frequently during winter months, typically as roosting plots and using plots in the north of the forest more frequently during summer months.

Index of Aggregation

Ia, a measure of Index of Aggregation determines whether dropping counts between plots are random or aggregated. Figure 3.8 shows Ia for the 30 months sample period from May 2002 – December 2004 and for the total monthly counts (Month 31).

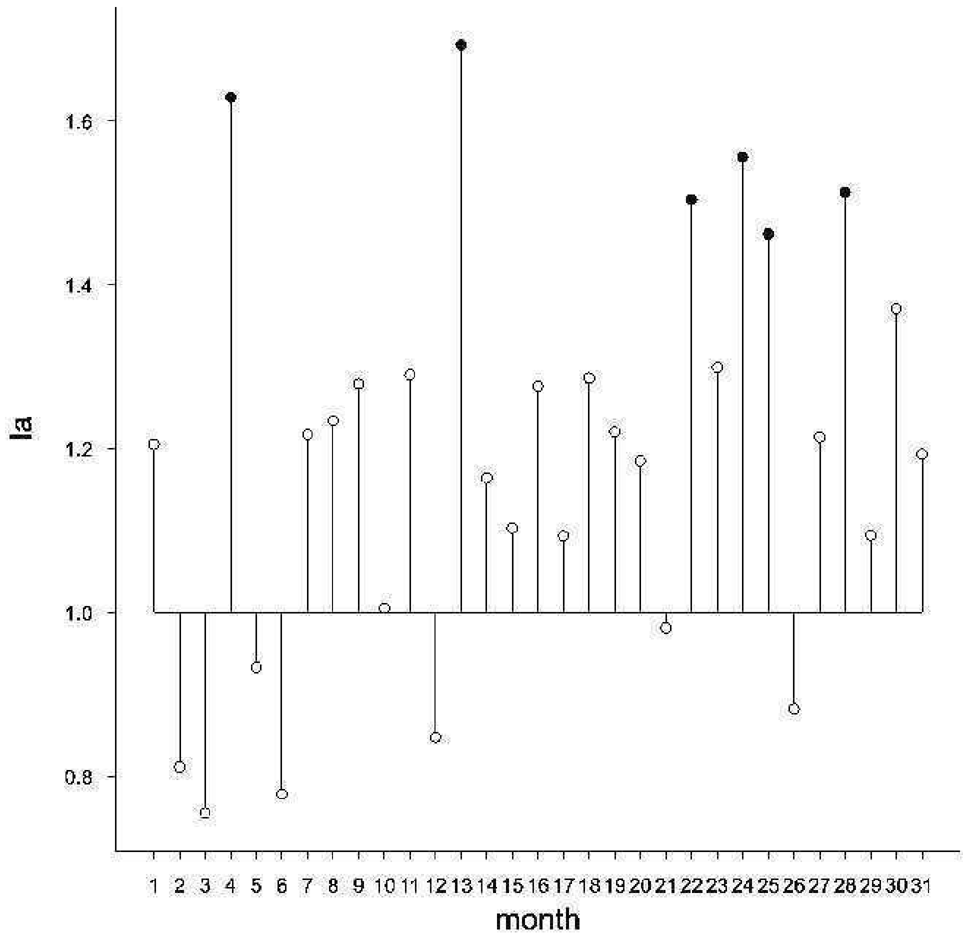

Figure 3. 8 Ia, Index of aggregation for 30 month sampling period and for total counts (Month 31). Filled circles represent months where dropping counts are significantly aggregated.

Dropping counts in plots with a value of Ia > 1 show signs of aggregation, dropping counts with a value of Ia<1 show signs of uniformity and dropping counts with values of Ia = 1 show random distribution. For any of these Ia values, $p<0.001$ to be significant. Filled circles represent months where dropping counts are significantly aggregated. Twenty-five from the total 31 months show signs of aggregation; however the aggregation is only significant in six of the study months. Months showing signs of aggregated plot use are: August 2002, June 2003, March 2004, June 2004, July 2004 and October 2004.

Nearest Used Neighbour Distance

Figure 3.9 shows the nearest used neighbour distance, that is the nearest distance between two plots used by capercaillie in the same month. Over the study period May 2002-December 2004, the average used 1st neighbour distance per month increases.

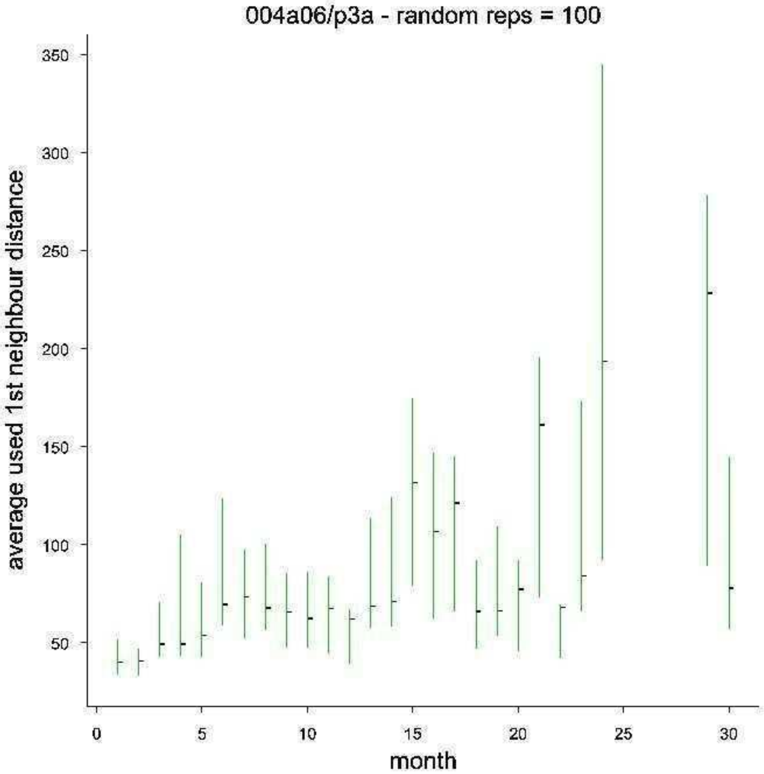

Figure 3. 9 Average used 1st neighbour distance over 30 month sampling period

3.5 Discussion

3.5.1 Digestibility and Decomposition

From the August 2002 counts corrected for digestibility and decomposition it would appear that there is a clear effect from digestibility and decomposition on the number of droppings produced. Unfortunately annual dropping counts could not be corrected for digestibility due to a lack of published data on digestibility rates for many dietary items of capercaillie. However, digestibility and decomposition only account for around half of the variation between December and August counts and therefore other factors must be driving differing dropping numbers between winter and summer counts.

3.5.2 Size and Trend of Dropping counts

Results of capercaillie dropping counts show a cyclical pattern of use of plots throughout the year and a decline in use over the three year study period, which was statistically significant. Taking into account digestibility and decomposition effects, summer counts are still much lower than winter counts. It also appears that the frequency a plot is used during summer months decreases along with number of plots used. This was also reported in a pilot study at Morangie Forest in the summer of 2001 (Scozzafava 2002). Roosting data mirrors the pattern observed in the maximum number of droppings, suggesting that the cyclical patterns in counts are largely driven by roosting behaviour. These seasonal changes in the number of droppings found in plots are suggestive of capercaillie using plots less during summer months. During spring and summer, capercaillie will be visiting leks to breed and other areas for nesting and moulting. Therefore, it would appear that capercaillie summer habitat is under-sampled in the study plots. For example, areas such as thickets used for moulting by males unable to fly and bog areas used by hens with broods were not sampled in study plots.

The significant downward trend observed in dropping counts from 2002-2004 was also observed in the number of months plots were used each year, which fell from an average of around 6 months use per year in 2002 to less than 2 months use in 2004. It is important to note that this observed downwards trend over the three year study period is indicative of fewer capercaillie using study plots rather than fewer capercaillie being present in the three year study period. This decline in use could be an effect of observer disturbance in plots. Although the present study aimed to reduce disturbance by using indirect methods to determine capercaillie presence, it may have inadvertently caused disturbance by the continued monitoring of plots. The capercaillie is a species where human disturbance associated with recreation has been partly implicated in the declines in Western Europe (Mueller 1981, Leclercq 1985, Menomi 1994, Brenot *et al.* 1996, Palanque 1999). Recent studies in Scotland have highlighted capercaillie avoidance of areas even with low levels of human use (Summers *et al.* 2007). In addition, results from the present study investigating capercaillie habitat use in Morangie Forest (Chapter 4) found that capercaillie avoid areas close to tracks.

Therefore capercaillie may have shifted their distribution to avoid areas continually monitored. If observer disturbance was responsible for the decline in droppings within plots in Morangie Forest it reduces the ability to make inferences about Morangie Forest as a whole from a number of plots, and therefore the efficacy of monthly dropping counts as a monitoring tool.

3.5.3 Estimate of Capercaillie Population Numbers

An estimate of the size of the Morangie Forest capercaillie population in 2002 from dropping counts was 63 birds. This is supported by the results of the genetic analysis of the capercaillie population at Morangie Forest in 2002 (Chapter 6), which estimates the population at 60-70 individuals.

Capercaillie numbers estimated from dropping counts show a decline from 63 to 17 birds in 2002-2004. Because the population estimates using dropping counts were made using winter dropping counts, they are not directly comparable to spring and summer indexes of abundance made from brood and lek counts. However, they do allow comparison with the overall trend in estimates over 2002-2004. Estimates from brood counts show a decline in the number of individuals observed. Capercaillie lek counts, conversely, show an overall increase in individuals from 2002-2004. This may be due to the unusual lek structure at Morangie Forest, where males rarely gather in distinct groups to display (C.Leslie pers. comm.). This has been observed in at least one other capercaillie population (Hjorth 1985). Solitary display means that some males might easily go undetected as there is no “traditional” display ground to visit. Since the beginning of the study there has been increased effort during lek counts so that less obvious lekking males can be counted (pers. obs.), and this may account for increases in lek counts observed from 2002-2004.

The decline in numbers between 2002-2004, estimated using dropping counts, is an effect of declining counts in plots over the study period, and as mentioned above does not necessarily indicate that capercaillie are declining from Morangie Forest, only from the study plots. The capercaillie population estimate from dropping counts made in December 2002 represents the most reliable estimate of the three as this was made before any decline in use of plots was observed and has been substantiated by the genetic estimate of capercaillie numbers made in 2002.

3.5.4 Spatial Analysis of Dropping Count Data

The spatial pattern in the distribution of capercaillie droppings was analysed using SADIE. Results showed that within months generally a small number of plots were used heavily and between months recipient and donor plots were constantly changing. This would suggest that capercaillie are continually using different plots. In winter, SADIE results show southern plots acting as recipients donating to plots in the north. This would suggest that during winter, plots in the south of the forest are used more heavily by capercaillie than those in the north of the forest. However, in summer months the movement becomes less linear and it tends to be plots in the north donating to other plots. In addition, during summer months fewer droppings are required to be donated in order to reach uniformity suggesting that fewer capercaillie are using plots during summer months. These results are in accordance with the seasonal trends in dropping counts, and additionally show that there is spatial movement of capercaillie within and between seasons. Results of the genetic analysis of feathers also showed movement of capercaillie throughout the forest during different months (Chapter 6). The index of aggregation for plots over the 30 month study period suggests that the majority of dropping counts in plots are aggregated, although this is only significant in 20% of the months in the study period. This is indicative of capercaillie using certain areas more than others. The majority of months, where plots were significantly aggregated, were found towards the end of the study period, implying that capercaillie use of plots declined to core areas rather than randomly throughout the forest. When the average used 1st neighbour distance is plotted, the average distance that you would have to go from a presence plot to the next nearest presence plot increases over the 30 month study period. This would suggest that capercaillie are declining to a number of core areas.

3.5.5 Feasibility of Faecal Counts as a Monitoring Tool

Faecal counts are commonly used as an indirect method of determining population size, especially for deer populations (Staines & Ratcliffe 1987, Ratcliffe & Mayle 1992) and as a result there have been many studies testing their efficacy as a monitoring tool

(Walker *et al*. 2000, Webbon *et al*. 2004, Wiegand 2005). However, although dropping count methodologies are beginning to be applied to capercaillie studies (Catt *et al*. 1997, Finne *et al*. 2000, Summers *et al*. 2004), no study has specifically evaluated the use of dropping counts as a monitoring tool for capercaillie, or indeed for birds in general. Therefore various issues concerning this study are discussed below.

The use of dropping counts as a monitoring tool for capercaillie at Morangie Forest was only partly successful. Not being able to successfully correct for digestibility and decomposition of droppings throughout most of the year and not being able to account for the reduction in dropping numbers over the study period reduces the efficacy of dropping counts as a monitoring tool for capercaillie. In addition, formal detectability tests with 'dummy' droppings should have been conducted before the start of the study to correct for the differing vegetation structure on dung detection rates. However, with some modifications the use of faecal counts as a monitoring tool for capercaillie could be worthwhile.

The current estimation of capercaillie abundance successfully minimised the effects of dietary changes, weather and vegetation structure by basing population estimates on counts from capercaillie during the winter, when the capercaillie are known to have an almost 100% pine based diet. From decomposition trials in the study area, pine droppings are still visible after two months, therefore comfortably within the sampling period. In addition, dropping detectability rates were more similar during winter months due to the less concealing ground vegetation. Using a population estimate based on winter counts also reduced any further error in detection rates as the pine droppings had a distinctive colour, structure and shape and were easily observed.

The plot location for the present study was determined during an initial trial study at Morangie Forest in 2001 (Scozzafava 2002). Plots were allocated at random (subject to a constraint of being over 100m apart) within Morangie Forest during a trial dropping count study in 2001 (Scozzafava 2002). However, plot distribution does not appear to be completely random over the study area, with some habitats being under-sampled i.e. thickets. In hindsight, plots would have been better positioned systematically in a grid fashion. This would allow the whole study area to be covered equally and in turn would give greater confidence in counts.

When inferring capercaillie presence in an area from dropping counts in a few plots, it has to be considered that at low dropping densities, plots may not be representative of actual capercaillie use. For example, the greater the number of droppings in a plot, the longer a capercaillie has frequented it, and in turn probably frequented the surrounding area in a radius of unknown size. On the other hand, plots with zero droppings do not necessarily mean that capercaillie have not visited the area at all, it only means that droppings were not found in that specific place. There have been many instances, in areas of low to moderate use where sample plots were found to contain no droppings, but just outside the plot boundary a roost was observed (pers. obs.).

3.5.6 Application of Capercaillie Dropping Counts for Forest Managers

There are various issues concerning the application of faecal counts as a population monitoring tool including differing decay rates, age/sex differences in defecation rate, and dietary effects (Takenoshita & Yamigiwa 2008). However, the results of the present study suggest that with modification, dropping counts could be a worthwhile tool to ascertain information about capercaillie populations.

Due to the problems with digestibility and decomposition dropping counts should be limited to winter only. Formal dropping detectibility trials should be run to correct for differing vegetation structure on dropping detection rates. A two month sampling period (one to clear plots of droppings and another to count droppings) would allow a simple estimate of population numbers every year, and would reduce any effects from disturbance of continually monitored plots. This method would also reduce the effort in terms of conducting counts. Counts could also be conducted by existing forestry staff, removing the need to subcontract. Using a systematic grid should also remove any bias in plot positioning.

If winter dropping counts were used in combination with habitat data, then dropping counts could represent a viable option for forest managers wanting to gain further information about how capercaillie are using their forests. Forest managers have varying amounts of habitat data available to them as part of the forest compartment database, which could be used, in conjunction with dropping counts to plan management of habitat for capercaillie (Chapter 4).

Since the start of this study, there have been significant developments in the extraction of DNA from feathers and faeces (Regnaut 2004). To date, only genetic analysis of moulting feathers has been used to derive information about capercaillie population and movement (Chapter 6). Because feathers are only found in summer months, information about individual movement is restricted to these months. Methods now allow droppings to be identified pertaining to individual birds and therefore genetic analysis of droppings from winter months could add a further dimension to counts.

3.6 Conclusions

The present study was the first to test the use of avian dropping counts as an indirect monitoring tool. Results of the study show that capercaillie faecal counts as a censusing tool are limited to winter months. This is due to changes in the digestibility of the capercaillie diet and decomposition of capercaillie droppings during summer months. For dropping counts to be considered as a monitoring tool during summer months, further investigation of digestibility and decomposition would have to be conducted. However, capercaillie winter dropping counts did allow population estimation and could easily be implemented by forest managers as a monitoring tool for capercaillie.

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Chapter 4. What Habitats are Used by Capercaillie? Results using Faecal Counts and Other Indirect Measures.

Abstract

Habitat choice of capercaillie within Morangie Forest was determined using presence and absence of capercaillie droppings. The importance of habitat data scale and source was examined within logistic regression models. Results from this study show that capercaillie within Morangie Forest appear to be selecting habitat at a radius of 50m and beyond. Results also show that using data derived from the Forestry Commission compartmental database or from geo-orthorectified aerial photographs produce better predictions of capercaillie habitat use than using variables collected from the field. These findings emphasise the importance of adopting a large-scale management approach for capercaillie. Habitat variables included in models explain capercaillie winter presence and absence to a greater degree than capercaillie presence and absence in other seasons. Habitat models that successfully predicted capercaillie presence and absence in Morangie Forest have the potential to be used as a basis for predicting capercaillie habitat use in other commercial forests. The importance of rides and thinning racks for capercaillie roosting was also reported along with differential habitat use between capercaillie sexes.

Chapter 4. What Habitats are Used by Capercaillie? Results using Faecal Counts and Other Indirect Measures.

4.1 Introduction

Availability of suitable habitat is essential for the survival of any individual, population or species. The definition of habitat is the physical environment in which an animal of a certain species can survive and reproduce, or more simply, any place where the species occurs (Storch 2003). Habitat studies attempt to explore which aspects of the environment the individual, population or species require or prefer in order to survive. However, in many studies the spatial dimensions of the habitat are overlooked, with many describing habitat as simply one or more vegetation types (Storch 2003). In practice defining a habitat is an issue of spatial awareness and scale that is dependent upon the perception of any given observer, or species. Therefore the definition of a habitat is not unique but depends upon the species (or phenomenon) under study; the constituent makeup of the habitat as perceived by the species and the interaction between the constituent elements of the habitat and species itself (Stewart 2000). Scale is a fundamental conceptual problem in ecology, if not science (Levin 1992, Keppie & Kierstead 2003). However, ecologists did not start formally addressing the issues of scale until the 1980s (Schneider 2001) and some wildlife biologists still act if scale does not matter (Bissonette 1997). Some would respond to this by arguing that biologists simply do not yet know the scale(s) that an organism uses to measure its environment or for which critical processes occur (Keppie & Kierstead 2003). But to not measure or analyse habitat at multiple scales would mean that the opportunity is missed to detect possible domains over which environmental characteristics and animal behaviour are associated uniformly and to search for scales at which potentially important (sharp) changes in these associations occur (Weins 1989). Species habitat relationships often exist at several hierarchically structured spatial scales, ranging from a species' geographical range, to the spatial structure of populations, to the home range of individuals and the distributions of specific resources therein. At each scale, a different set of habitat relationships are likely to exist (Storch 2003).

In the case of capercaillie, past descriptions of capercaillie habitat needs have almost exclusively addressed vegetation structure at the forest stand level, and accordingly, habitat management measures for capercaillie have primarily focussed on stand structure (Picozzi *et al.* 1992, Storch 1995). Even if a habitat model can correctly reflect a species' smaller scale habitat preferences, its potential to predict population abundance at larger scales may remain limited (Storch 2002). Both small scale and landscape scale characteristics of the habitat should be included in models explaining and predicting the distribution and abundance of vertebrate species (Mazerole & Villard 1999, Storch 2002). Even though Wiens *et al.* (1993) used capercaillie to help promote a new research framework based on spatial patterns and scale there has been little use of this in the design of grouse research (Keppie & Kierstead 2003). According to Storch (2003) for capercaillie populations to persist, their habitat requirements must be met on all scales. A minimum of three scales are therefore necessary to describe habitat relevant to capercaillie: vegetation in the forest stands, stands in the forest, and forests within the landscape (Storch 1997).

There are two main but contrasting types of conifer woodland in Scotland, ancient native pinewood or semi-natural pinewood composed almost entirely of Scots pine and birch, and plantations composed of single or mixed conifer species, including non-native conifers (Summers *et al*. 1999). The characteristics of managed plantations differ dramatically to those of native pinewoods and semi-natural pinewoods. Native and semi-natural pine forests are recognised as predominantly native species with irregularly spaced trees, including large deep-crowned trees with thick trunks, commonly known as "granny pines" inter-dispersed with birch, rowan and juniper. They are also characterised by a range of age structures with the presence of *Calluna*, *Erica* and *Vaccinium* species as a ground vegetation layer.

In contrast, managed plantations in Scotland are composed of closely-spaced trees of similar size and thin branches, and comprise a mixture of conifers including mainly Scots pine, Lodgepole pine *Pinus contorta* and Sitka spruce *Picea sitchensis* (Summers *et al*. 1999). Due to their dense cover, deep shade and subsequent poor ground vegetation, plantations are thought to be less biologically rich than ancient native pinewoods (Ratcliffe & Thompson 1989, Summers *et al.* 1999). This has however, been challenged in recent years. Results of a study aimed at understanding the levels and types of biodiversity currently found in plantations, found surprisingly that in most cases plantations were as species rich as native woodland, with the exception of vascular plants and lichens, and therefore should be viewed as making a positive contribution to biodiversity conservation in the UK (Humphrey *et al*. 2001, Humphrey *et al*. 2003).

In the past, capercaillie habitat research in Scotland has mainly focused on describing capercaillie habitat in ancient native or semi-natural pinewoods, the capercaillies' historical habitat in Scotland. In 1992, Picozzi *et al*. devised a new method of describing forest structure. It was based around performing structural analysis on a set of measurements taken from various forests in Scotland and interpreted in relation to capercaillie numbers using principal component analysis. Forests ranged from semi-natural pinewoods to plantations of pine and introduced conifers. A numerical method based on principal component analysis was devised for describing the structure of a forest. The first principal component (PRIN1) grouped attributes tending towards a semi-natural pine forest with scattered, spreading, old 'granny' trees (Steven & Carlisle 1959) with thick sweeping branches, rounded crowns and an open canopy with a good field layer of dwarf shrubs (Picozzi *et al*. 1992, Moss & Picozzi 1994). In contrast the second principal component (PRIN2) characterises tall, closely spaced, mature plantation trees, especially spruces, devoid of vegetation (Picozzi *et al*. 1992). Principal component scores were used to calculate a GRANNY score (based on PRIN1) and a PLANTATION score (PRIN2) for forests where capercaillie were counted. Results of the study found that densities of capercaillie were strongly associated with GRANNY scores and weakly negatively associated with PLANTATION scores. It was concluded that managing for a higher GRANNY score was beneficial for capercaillie, although mention was made that plantation forests, even with a high level of introduced conifers, could provide habitat suitable for capercaillie (Picozzi *et al*. 1992).

Since this study, there has been further acceptance that managed plantations can provide suitable habitat for capercaillie. Although ancient native pinewoods have the highest densities of capercaillie, the majority of the population occurs at low densities in plantations (Catt *et al*. 1998, Summers *et al*. 2004). Therefore it is important that the habitat requirements of capercaillie in managed forests are ascertained so that effective management strategies can be put in place. Using habitat models that select against plantation characteristics for capercaillie such as the one devised by Picozzi *et al*. (1992), are thought to be less suited to determining habitat use within plantations. Extrapolating habitat study results from semi-natural pinewoods and using them to predict habitat use of capercaillie in managed plantations is not viable, for example, one might assume that because managed plantations lack the large branching structure of granny pines (typical roosting trees for capercaillie in semi-natural woods) that there would be no roosting in managed plantations. In addition, present recommendations for management of plantations involves changing the plantation to more like that of semi-natural woodlands, and in the majority of cases this is not a feasible option for a commercially run forest. However, relatively minor actions can significantly improve plantations for capercaillie (Kortland 2006) and therefore management recommendations that incorporate capercaillie conservation within a working economic forest are required.

Therefore in this chapter, capercaillie habitat data will be collected from Morangie Forest, an already recognised example of a commercially viable forest, managed primarily for timber, but with sympathetic management for capercaillie.

4.2 Aims and Objectives

The main aim of this chapter is to measure habitat at different scales (10m, 50m & 100m) and from varying sources, obtained by intensive field surveying (Field) and obtained remotely (Digital Elevation Model (DEM), Forestry Commission Compartmental Database & Aerial Photographs) and then relate these habitat measurements to capercaillie use of plots. It was outwith the remit of the present study to measure capercaillie habitat at the landscape scale in terms of over many forests, however measurements of habitat variables at Morangie Forest were made ranging from the single tree to the forest stand.

To meet this aim the following questions were asked:

- What habitat variables determine capercaillie presence or absence?
- What habitat variables are capercaillie selecting for when choosing roosting sites?
- What habitat variables are capercaillie selecting at different times of the year?
- What scale of habitat measurements best explain capercaillie presence?

- How well does habitat data available to forest managers, through the compartmental database, explain capercaillie habitat use and how does it compare to habitat data from other sources?
- Do other signs of capercaillie presence give further information about how they use habitat at Morangie Forest?

4.3 Methods

4.3.1 Data Collection – Dropping Counts

Data collection for dropping counts follows methods explained in Chapter 3. Only dropping count data from May 2002 – April 2003 was used to explore habitat use. After April 2003 the 149 study plots were reduced to 87 and these only included plots that had been used in the previous year by capercaillie. Therefore, to investigate capercaillie habitat use by means of presence and absence of capercaillie droppings the count data from the original 149 plots was used. A plot was considered a 'presence' plot in a given month if at least one dropping was found. The presence of capercaillie roosts (pile of 10 or more droppings, less than a droppings length apart) was also used as a measure of habitat usage. In addition capercaillie presence and absence was determined by season. Dropping count data were divided into spring (March, April & May), summer (June, July & August), autumn (September, October & November) and winter (December, January & February) to give capercaillie presence and absence each season.

4.3.2 Data Collection – Scale and Source of Data

To investigate what scale of habitat measurements best explain capercaillie presence at Morangie Forest, various habitat data sources were utilised. Habitat measurements were made in the field, from the Forestry Commission (FC) compartmental database, from a Digital Elevation Model (DEM) and from geo-rectified aerial photographs of Morangie Forest from 2000.

Using the data sources listed above allowed habitat measurements to be made on three distinct scales: 10m radius of study plots, 50m radius of study plots and 100m + radius of study plots. Plots were at least 100m apart from each other and as such data collected from each plot was considered independent.

Table 4.1 lists all variables measured, along with the scale they were measured on and the data source they were obtained from.

Table 4.1 Habitat variables collected, the data source they were obtained from and scale they were measured on

VARIABLE	DATA SOURCE	SCALE OF MEASUREMENT
MAIN TREE SPECIES IN PLOT	Field	10m
NO OF TREES	Field	10m
NO OF SPECIES	Field	10m
TOP HEIGHT (M)	Field	10m
TREE MAX DBH	Field	10m
TREE AVERAGE DBH	Field	10m
TREES/HA	Field	10m
BA/HA	Field	10m
NO OF GROUND VEGETATION SPECIES	Field	10m
HEATHER %	Field	10m
HEATHER TOPHEIGHT	Field	10m
BLAEBERRY %	Field	10m
BLAEBERRY TOPHEIGHT	Field	10m
GRASS %	Field	10m
GRASS TOPHEIGHT	Field	10m
MOSS %	Field	10m
MOSS TOPHEIGHT	Field	10m
TOTAL TOPHEIGHT	Field	10m
NO OF GROUND VEGETATION SPECIES	Field	50m
TOTAL TOPHEIGHT	Field	50m
HEATHER %	Field	50m
HEATHER TOPHEIGHT	Field	50m
BLAEBERRY %	Field	50m
BLAEBERRY TOPHEIGHT	Field	50m
GRASS %	Field	50m
GRASS TOPHEIGHT	Field	50m
MOSS %	Field	50m
MOSS TOPHEIGHT	Field	50m
ELEVATION - ANNE KATHERINE	Compartment	0m
ALTITUDE FC DATABASE	Compartment	0m
YEILD CLASS FROM FC DATABASE	Compartment	10m
TREE SPECIES FROM FC DATABASE	Compartment	10m
TREE SPACING FROM FC DATABASE	Compartment	10m
SPRUCE % AREA	Compartment	50m
SP (OTHER) % AREA	Compartment	50m
ROTATION	Compartment	50m
OPEN GROUND % AREA	Compartment	50m
NO OF SPECIES	Compartment	50m
NO OF POLYGONS	Compartment	50m
NO OF BOUNDARY LINES	Compartment	50m
MAIN TREE SPECIES	Compartment	50m
LP % AREA	Compartment	50m
LARCH % AREA	Compartment	50m
BROADLEAVES % AREA	Compartment	50m
AV ERAGE YIELD CLASS 50M	Compartment	50m
ALL OTHER SPECIES % AREA	Compartment	50m
AGE IN 50M, WEIGHTED BY % COVER	Compartment	50m
TREE SPECIES 50M sp (old) % AREA	Compartment	50m
SIZE OF COMPARTMENT	Compartment	100m
NO OF POLYGONS 100M	Compartment	100m
LENGTH OF BOUNDARY LINES (M) 100M	Compartment	100m
AGE IN PLOT COMPARTMENT	Compartment	100m
ACCUMULATED TEMPERATURE	DEM	0m
MOISTURE DEFICIT	DEM	0m
ELEVATION	DEM	0m
SLOPE	DEM	0m
ASPECT	DEM	0m
HILLSHADE	DEM	0m
PRESENCE OF OLD PINE	Aerial Photos	10m
PRESENCE OF OLD PINE	Aerial Photos	50m
NO OF ROADS	Aerial Photos	50m
NO OF RIDES	Aerial Photos	50m
DISTANCE TO ROAD MEASURING TOOL	Aerial Photos	100m
DISTANCE TO ROADS ANNE KATHERINE	Aerial Photos	100m
DISTANCE TO OLD PINE	Aerial Photos	100m
% RIDE COVER	Aerial Photos	100m
RIDE LENGTH	Aerial Photos	100m
% OPEN SPACE	Aerial Photos	100m
% FOREST	Aerial Photos	100m
% FOREST COMPLETE	Aerial Photos	100m
% FOREST SCATTERED	Aerial Photos	100m
% FOREST OPEN	Aerial Photos	100m
DIVERSITY IN LAND USE	Aerial Photos	100m
WOODLAND TYPES	Aerial Photos	100m
NEIGHBOURING HABITAT	Aerial Photos	100m

4.3.3 Data Collection - Habitat Data

Habitat data was collected for each of the 149 sample plots. Habitat features from the field were measured in September 2003. A total of 75 variables were measured including raw and derived variables. Habitat features measured included those associated with:

- Habitat structure
- Fragmentation
- Landscape features
- Disturbance

4.3.3.1 Habitat Structure

Being able to determine the preferred habitat structure of plantation forests used by capercaillie can give forest management information on how best to provide for capercaillie in new and existing plantations. Therefore habitat components relating to individual trees, ground vegetation and stand structure were measured.

Tree Species

In Scotland, while usually associated with semi-natural and planted Scots pine, capercaillie also occur in mixtures of pine and non-native conifers (Moss & Picozzi

1994). Choice of tree species was examined for capercaillie in Morangie forest. Tree species was recorded in the field for all trees within a 10m radius of the study plot.

In addition, tree species listed in the Forestry Commission sub-compartmental database in a 10m radius and the percentage area of each tree species in a 50m radius of study plots was also calculated. Tree species in the compartment each sample plots was located in was found by use of "spatial join" function in ArcView 3.2. The "intersect two themes" function was then used to determine tree species for each 10m radius plot and % of each tree species in a 50m radius of the study plot.

Tree Density

Number of trees per ha is also considered an important habitat variable for capercaillie. Many varying density levels have been proposed to be most suitable for capercaillie, some relating to densities for leks (Wegge & Rolstad 1986), others giving densities for optimum blaeberry growth and others giving densities for winter feeding (Moss & Picozzi 1994). Therefore the number of trees in a 10m radius of each study plot was counted in the field to give tree density figures.

Tree Height

Tree height can affect underlying vegetation and canopy cover, both thought to be important variables for capercaillie. Therefore, the average height of trees was measured in 10m radius of study plots using a laser height finder (Jasumback & Carr 1991).

Tree Diameter at Breast Height (1.3m) Dbh

Dbh of trees is thought to be an important habitat factor for capercaillie (Picozzi *et al.* 1992). It follows that the greater the dbh the heavier the branching structure and therefore the more appealing to capercaillie, which are thought to like thicker branches on which to perch and roost. Therefore dbh was recorded for each tree in a 10m radius of the study plots. Dbh for all trees in a 10m radius of study plots was obtained by use of digital tree callipers and the resulting data were used to calculate basal area (ba) using the formula (Larsen 1999) below.

$$BA = (\pi/4*144)DBH^2$$

$$BA = 0.00545414*DBH^2$$

Planting Year

It is important for future planning to determine at what tree age capercaillie will start using areas of forestry. Therefore tree age was ascertained from the FC compartmental database using the same method for tree species. Two values of age were found, the age of trees contained within the 10m plot, and age of trees in a 50m radius of the plot.

Where the plots contained different stands of trees of different ages, age has been weighted by area to give an average figure per plot.

Rotation

Rotation is an important factor to include as it differentiates between trees planted on previously open/non-woodland sites or trees planted on previous woodland sites. The classifications are as follows:

1: Formerly open/non-woodland
2: 2nd and subsequent rotations
5: Ancient semi-natural woodland
9: Woodland (to include new planting on old woodland sites)

Rotation was determined from the FC compartmental database. Rotation was derived using 'intersect two themes' in ArcView 3.2, described above for tree species. Generally only one rotation class was represented at the 50m plot level, but where crops with different rotation classes were present, a single figure for rotation was derived by selecting the rotation category most representative of the buffer area.

Yield Class

Yield class is a measure of how trees are growing, it allows foresters to see whether trees are growing at their expected rate (for given species, site location and conditions) and if not what rate they are growing. Results have consequences for thinning and timber production. Yield class is measured in cubic metres per hectare. A compartment that is said to belong to yield class 12, for example has a mean annual timber increment of $12m^3$ per hectare. Yield class will be analysed as it will give an idea if capercaillie prefer trees that grow more quickly or those that under perform. Yield class was derived from the FC compartmental database in a 10m and 50m radius of the plot using ‘intersect two themes in ArcView 3.2 as described for tree species. An average yield class weighted by area was taken when more than one yield class was present in plot buffer areas.

Old Growth Pine

Capercaillie are typically associated with semi-natural pinewoods. The structure of these woodlands is preferable as trees have large crowns with heavy branches ideal for roosting and perching upon (Moss & Picozzi 1994). Morangie forest has remnants of old growth pine originating from before 1900. Therefore the presence of this old growth will be analysed to see whether capercaillie actively seek these type of trees in their habitat if available.

The difference in the structure of old growth pine in comparison with the planted trees was clearly visible from aerial photographs (Figure 4.1) therefore the distance from plots to old growth Scots pine was measured using the "distance measure" tool in ArcView 3.2. The presence or absence of old growth pine in a radius of 10m and 50m from a plot was also calculated.

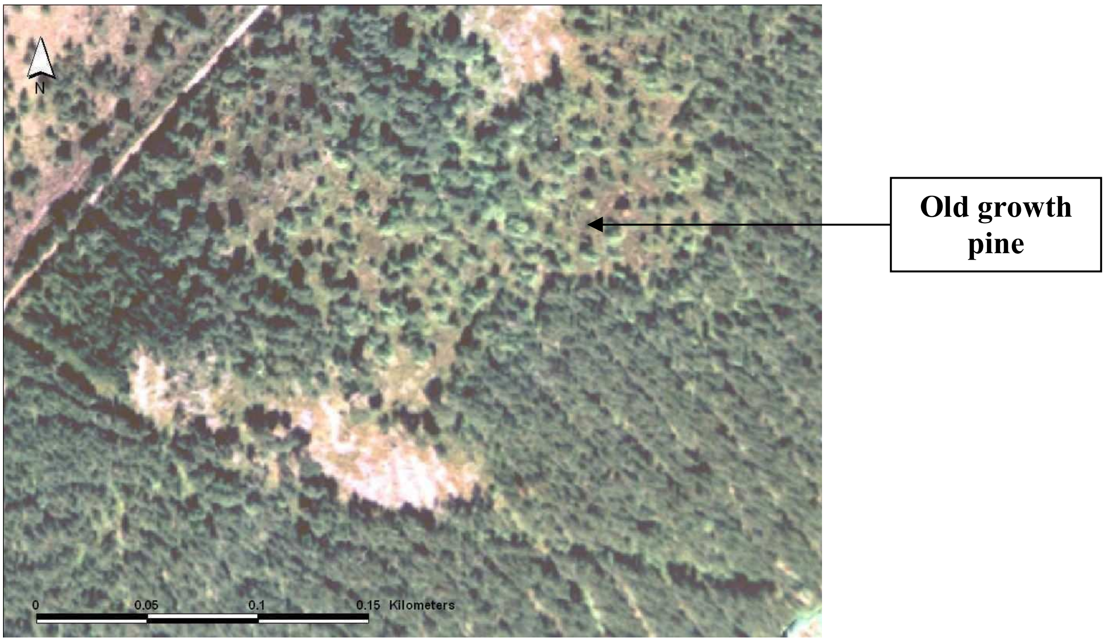

Figure 4. 1. Difference in structure of old growth pine in comparison with planted trees

Vegetation Data

Frequency and spatial distribution of ground vegetation data were assessed in the field. Data were collected in a radius of 10m and 50m from each of the study plots. Vegetation data within a 10m radius reflected characteristics of the central plot tree. Transects following each of the 8 compass directions radiating from the central plot tree were walked. Every 5 metres maximum vegetation height was measured using a sliding polystyrene disk (24cm in diameter) on a graduated stick. The most dominant vegetation type every 5 metres was also recorded. Vegetation was classified in to four main ground vegetation species groups: heather, blaeberry, grass and moss. This built up a ground vegetation map for each plot (Figure 4.2).

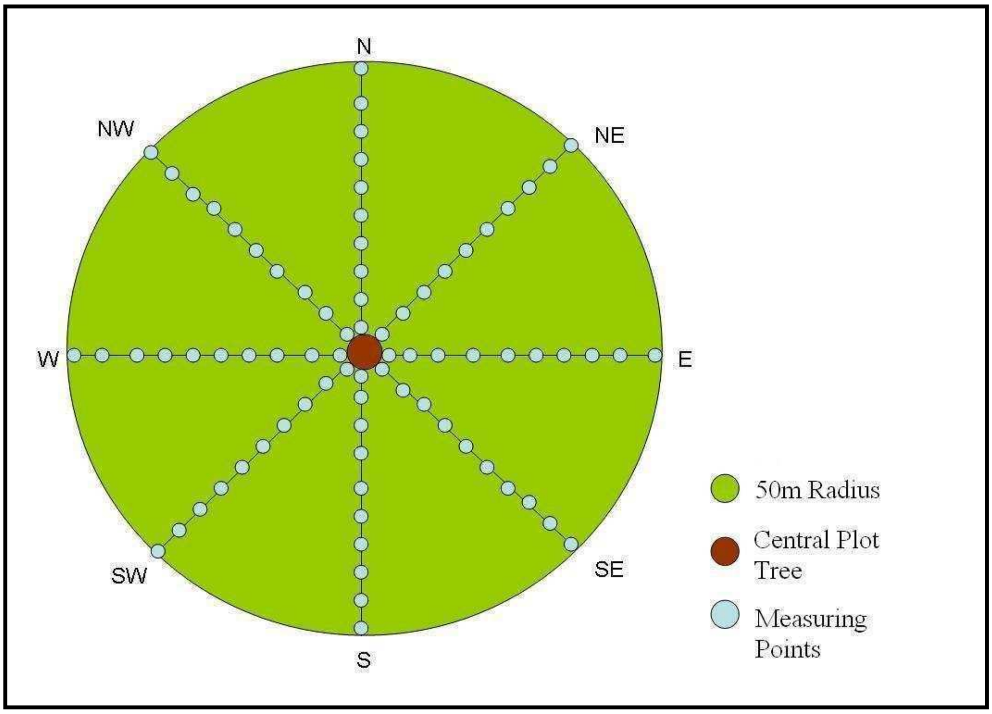

Figure 4. 2 Diagram to show vegetation data collection

Degree of Open Space to Forested Area

Degree of open space was estimated by eye from aerial photographs in ArcView 3.2 as a percentage of the area in 100m radius of the study plot that was open; it included visible ground within the forest as well as roads/rides (Scharling 2003).

Forest Density

Forest density was measured by eye using aerial photographs in ArcView 3.2. Forest density was estimated within a 100m radius of study plots and was based on an "openness parameter" estimated as a percentage and categorised into three following groups: dense/compact forest (no ground visible), scattered forest (single trees visible), and open forest (forest ground is visible – typically a thinning rack).

Habitat Diversity

Habitat diversity was ascertained from aerial photographs of Morangie Forest imported into ArcView 3.2. Habitat diversity within a 100m radius of study plots was described as two variables - woodland diversity and land use diversity.

A: Woodland diversity- the number of different woodland types present, solely on the basis of colour differences, density differences and planting directions (maximum score possible 5).

B: Land use diversity – the amount of the following features present with a score of 1 point per attribute present: roads, rides, forest, soil (white), single trees, grass, hedges, bare ground (brown), water, visible thinning racks and the amount of forest types (maximum score possible 11).

4.3.3.2 Fragmentation

The consequences of habitat fragmentation are multiple and include edge effect, habitat change and lack of continuity in the landscape. On a smaller scale, and for larger animals, it can however also be of advantage in an otherwise uniform landscape pattern, such as managed forests (Scharling 2003). In order to examine the effect of fragmentation on capercaillie at Morangie Forest the following habitat variables were calculated: compartment area, number of polygons, length of boundaries and thinning intensity.

Compartment Area

Compartment area was analysed in order to establish whether capercaillie prefer larger areas of continuous forest as quoted in the literature (Quevedo *et al*. 2006). Compartment data was taken from the FC compartmental database and manipulated in ArcView 3.2. The area of the compartment that each plot was located in was found by using ‘spatial join’ within ArcView 3.2.

Number of Polygons

The FC compartmental database was imported into ArcView 3.2. Number of polygons was ascertained by buffering plots by 50m and 100m and using the "intersect two themes" function in the GeoProcessing wizard in ArcView 3.2 to produce an overlay. The overlay contained only the polygons within buffered zones around plots (Figure 4.3). This therefore allowed the number of polygons to be counted.

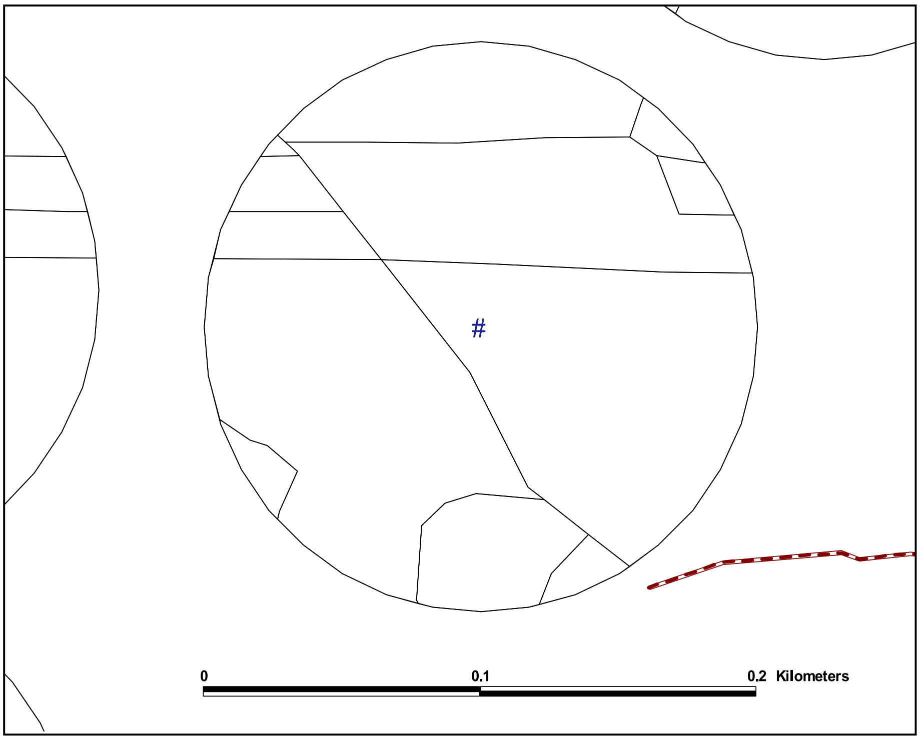

Figure 4. 3 Example of a buffered plot showing the polygons that comprise the FC compartmental database intersected by the 100m buffer

Length of Boundaries

The number of boundary lines present within a 100m radius of a plot was determined using the same method as above. The length of boundary lines was then calculated by use of the "measure tool".

Thinning Intensity

Thinning racks are linear 'tracks' through the forest created and used infrequently by machinery to access areas for thinning. These racks occur at regular intervals throughout compartments that have been thinned. Thinning racks are not suitable for vehicular or pedestrian access due to the brash that is laid across these racks as thinning occurs, and as a result have little human disturbance. Thinning racks have been classified as a measure of fragmentation as they counteract the uniformity of a forest, however, they do not necessarily represent negative aspects, more so features of the forest. Thinning intensity was estimated by eye using aerial photographs of Morangie Forest within ArcView 3.2. Thinning intensity was classified as "percentage of habitat area characterised with visible thinning racks" in a 100m radius of the study plots. Length of thinning racks was also calculated in a 100m radius of the study plots using the "distance measure" tool (Scharling 2003).

4.3.3.3 Landscape Features

Underlying landscape features such as climate and topography are known to influence capercaillie habitat choice (Storch 1993). Therefore the following landscape variables were measured: elevation, slope, aspect, hillshade, accumulated temperature and moisture deficit. In addition, neighbour effect as a measure of the number of other habitat boundaries which intersected the study plots was measured.

Neighbour Effect

Neighbour effect was determined using aerial photographs in ArcView 3.2. The effect from adjoining habitats was analysed by counting the amount of other habitat boundaries within a 100m radius of each of the study plots.

Elevation, Aspect & Slope

Underlying habitat quality factors such as elevation, aspect and slope are generally difficult to assess in the field. These factors can however be derived from a Digital Elevation Model (DEM) 10m resolution (Ordnance Survey data used under Forestry Commission Licence No 100025498 (2007)).

Elevation, aspect and slope were analysed as a raster grid in ArcView 3.2 using the Spatial Analyst Extension. The elevation model was loaded and from this, slope and aspect were derived from the surface option in Spatial Analyst. Using the co-ordinates of the central plot tree and the use of "summarise zones" options in Spatial Analyst the number of presence and absence plots within each category were extracted.

Hillshade

The amount of sunshine (conversely known as hillshade) that the study plots within Morangie Forest receive, is also an important habitat variable to consider. Capercaillie are thought to prefer southern sunny slopes (Storch 1993). Hillshade was attained under the "compute hillshade" option in the surface menu of Spatial Analyst in ArcView 3.2. "Compute hillshade" creates a grid theme as an output where each cell represents the illumination at that location on the surface, based on the direction of the sun (azimuth) and its height in the sky (altitude). The Digital Elevation Model (DEM) shape file was first converted into a grid with a cell size of 20m, the hillshade grid was then computed monthly using sun azimuth and altitude values from the US Naval Observatory website (US Naval Observatory 2006). This website allowed a table to be computed of sun azimuth and altitude values at certain grid references over the month and year selected. Finally using the co-ordinates of the central plot tree and the "summarise zones" option in Spatial Analyst the number of presence and absence plots within each hillshade category per month were extracted. Monthly hillshade averages were then separated into an average for the year and averages per season.

Accumulated Temperature and Moisture Deficit

The climatic variables of accumulated temperature (number of day degrees above 5 deg. Celsius) and moisture deficit (mm) provide an estimate of climatic warmth and climatic wetness, respectively. Accumulated Temperature (AT) is an index of warmth that has been calculated from monthly mean temperatures for the 30 year period 1961-1990 (Pyatt *et al*. 2001).

Moisture Deficit (MD) is an index of climatic droughtiness/wetness. It reflects the balance between potential evaporation and rainfall and emphasises the dryness of the growing season. It is calculated by subtracting monthly rainfall from monthly evaporation and keeping a running balance throughout the summer (Pyatt *et al*. 2001). Pyatt *et al*. (2001) interpolated these indices from a 20X20 km grid using a multiple regression model based on elevation, easting and northing. The number of presence and absence plots in each category was calculated using the same method as slope and elevation above.

4.3.3.4 Disturbance

Disturbance from forest roads and walking trails has been shown to have an adverse effect on capercaillie (Summers *et al*. 2004). The major roads and to some extent the larger rides in Morangie forest are where vehicles drive and walking trails are routed. In addition many dog walkers neglect to keep their dogs on a lead despite the provision of information boards explaining the need to minimise disturbance (Scozzafava 2002, Scharling 2003, pers. obs.). Free running dogs are known to be a disturbance to wildlife (Ballegaard 1994). The recent move to multipurpose forests incorporating timber production, conservation and recreation means that investigating disturbance is vital so that future planning can incorporate both recreation and conservation.

The effect from disturbance was analysed by examining:

- Distance to nearest road or track from sample plot called "distance to roads".
- Density of roads or track within a 50m radius of study plot called "number of roads".

Density of roads was calculated by counting number of roads in a 50m radius of the study plots from aerial photographs. Distance to roads was ascertained by use of the "distance measure" tool in ArcView 3.2.

4.3.3.5 Other Data

Other data including capercaillie sightings, feathers and location of roosts within the forest were also collected. Any sightings of capercaillie or feathers found were recorded along with the date, grid-reference and sex if known. In November 2002, while walking between plots, the location of roosts observed was recorded. A compass bearing was followed between plots to reduce bias from following rides or thinning racks. Roosts on or less than a metre from a ride or thinning rack were noted as 'roosts on a ride'. Roosts more that a metre from a ride were recorded as 'roosts within the forest'. Roost sites are easily observed and therefore the probability of observing a roost on a ride or within the forest was thought to be similar.

4.3.4 Data Analysis

4.3.4.1 Logistic Regression

A logistic regression analysis was used to model the relationship between capercaillie droppings and the habitat factors. Regression analysis has been widely used to investigate the influence of environmental variables on the presence and absence of a species (Perrin *et al*. 2003, Bollmann *et al*. 2005) and has been further evaluated by Guisan & Zimmerman (2000). Logistic regression is a form of regression analysis that uses the proportions of the two possibilities of the single binary 'dependent', or 'effect', variable (p and (1-p)), converted to a logit scale, log(p/(1-p)). The linear relationship between the logit response and the 'independent' or 'predictor' variables is calculated. It is particularly useful when there are proportions near 0 or 1 (Dytham 2003). Besides providing a simplified view of the relationship between the variables, it also provides a way of evaluating the importance of the variables and the correctness of the derived model (Rogerson 2001). A full review of logistic regression analysis can be found in Kleinbaum & Klein (2005).

4.3.4.2 Logistic Models

A number of logistic models were created using different scales and data sources (Table 4.2). Independent predictor variables at different scales (10m, 50m and 100m +) and different data sources (field, FC compartment database, DEM and aerial photographs) were entered into models with response variables annual presence/absence of droppings, seasonal presence/absence of droppings and annual presence/absence of roosts. Finally, a model was run using all habitat variables as predictor variables along with the same response variables used in previous models. A list of all variables and the models they were entered into can be found in Appendix 8.1.

Table 4.2 Summary table of logistic regression models and corresponding predictor variables

Model	Source of Habitat Variables	Availability of Habitat Data
10m	Field, Compartmental Database	Variable
50m	Field, Compartmental Database, Aerial Photographs	Variable
100m	Compartmental Database, Aerial Photographs	Variable
Field	Field measurements	Least available
DEM	Extracted from DEM	Most available
Compartmental Database	Extracted from Compartmental Database	Most available
Aerial Photographs	Extracted from Aerial Photographs	Fairly available
All Variables	From all the above	Variable

4.3.4.3 Application of Logistic Regression

The plot records, containing the dropping presence/absence data and the habitat variables, were imported into SAS/STAT software and logistic regression models fitted using PROC LOGISTIC procedure. The habitat variables were treated as independent predictors and a stepwise selection was used, with a significance level of 0.05 required to allow a variable to enter or leave a model. For each habitat variable retained in the final model, the parameter estimate, with the associated Wald statistic and *p*-value, was retained.

The model thus built was used in the computation of the predicted probability that the binary response variable was 1, as opposed to 0. For example, for the presence/absence response, this would be considered a prediction of the probability that a plot was occupied. A threshold value had to be chosen above which the predicted probability was accepted. The best threshold value was assessed by looking at the classification table in the SAS/STAT output. Five measures were used to quantify the efficacy of the proposed model: correct, which measures the ability of the model to correctly predict all responses; sensitivity, which measures the ability of the model to correctly predict positive responses; specificity, which measures the ability of the mode to correctly predict negative responses; false positives, which are the proportion of true negative responders that had a positive result; and false negatives, which are the proportion of true positive responders that had a negative result. The best threshold value is one that maximises the sum of sensitivity and specificity (Fielding & Bell 1997). Once the threshold was found, the predicted values were classified into predicted presence and absence according to it.

Another approach to data analysis that could have been considered in this study is multimodel inferencing see Burnham & Anderson (2002) and Whittingham *et al.*

(2006) for further information. While multimodel inferencing was not used in the present study it could be a fruitful avenue for further research.

4.4 Results

4.4.1 Logistic Regression Analysis

4.4.1.1 Overview of Logistic Models

The results of the logistic regression analysis are shown in Table 4.3. Models and response variables are given on the left of the table, with predictor variables found significant within models at the top of the table. Predictor variables that had a negative effect on response variables are represented by '-', predictor variables that had a positive effect on response variables are represented by '+', all predictor variables considered are marked grey and predictor variables not considered for inclusion are blank. Predictor variables were all continuous except for factors (with labels highlighted in grey).

Table 4.3 Results of the logistic regression analysis summarising models, response variables and predictor variables significant in the analysis. '-' represents negative predictor variables, '+' represents positive predictor variables. Blank squares = not considered, grey squares = predictor not significant. All predictor variables are continuous except highlighted variables which are factors

Model	Response Variables	Accumulated temperature 0m	Altitude 0m	Average age of trees 50m	Average yield class 50m	Blaeberry height (cm) 50m	Distance to road from plot (m)	Diversity in land use 100m	Elevation 0m	Grass % cover 10m	Grass % cover 50m	Grass height (cm) 50m	Heather height 50m (cm)	Hillshade 0m	Hillshade season average 0m	Length of boundary lines 100m	Moisture deficit 0m	Moss % cover 10m	Moss % cover 50m	Moss height 10m (cm)	Moss height 50m (cm)	Neighbouring habitat 100m	No of ground veg spp 50m	No of polygons 100m	N0 or roads 50m	No of trees 10m	No of tree species 10m	% Area scots pine 50m	% Forest 100m	% Forest complete 100m	% Forest open 100m	% Forest scattered 100m	% Old scots pine 50m	% Open ground 50m	% Ride cover 100m	Absence of old pine 10m	Absence of old pine 50m	Ride length 100m	Rotation 1 50m	Woodland types 100m
Field	*Presence/Absence*					▨				▨	▨	▨	▨					▨	▨	▨	▨		-			▨	▨													
	Roost/Non Roost					▨				▨	▨	▨	-					▨	▨	▨	▨		▨			-	▨													
	Season: Spring					▨				▨	▨	▨	▨					▨	+	▨	▨		▨			▨	▨													
	Season: Summer					▨				▨	-	▨	▨					▨	▨	▨	+		▨			▨	▨													
	Season: Autumn					▨				▨	▨	▨	▨					▨	▨	▨	▨		▨			▨	▨													
	Season: Winter					-				▨	▨	-	▨					▨	▨	▨	▨		▨			-	▨													
Compartment	*Presence/Absence*		+	▨	▨											▨								▨				▨					▨	-					-	
	Roost/Non Roost		▨	▨	▨											▨								▨				+					▨	▨					▨	
	Season: Spring		▨	▨	▨											▨								▨				▨					▨	▨					▨	
	Season: Summer		▨	▨	▨											-								▨				▨					▨	▨					-	
	Season: Autumn		▨	▨	▨											▨								▨				▨					▨	-					▨	
	Season: Winter		+	▨	-											-								▨				▨					▨	▨					▨	
DEM	*Presence/Absence*	▨							+					+	▨		▨																							
	Roost/Non Roost	▨							▨					▨	▨		▨																							
	Season: Spring	▨							+					▨	+		+																							
	Season: Summer	▨							▨					▨	+		▨																							
	Season: Autumn	▨							▨					▨	+		▨																							
	Season: Winter	-							▨					▨	+		▨																							
Aerial Photos	*Presence/Absence*						▨	▨														-			-				▨	▨	▨	▨			+	▨	-	▨		▨
	Roost/Non Roost						▨	-														▨			▨				▨	-	▨	▨			▨	▨	-	▨		▨
	Season: Spring						▨	▨														▨			-				+	▨	▨	▨			▨	▨	-	▨		▨
	Season: Summer						▨	▨														▨			-				▨	▨	▨	▨			▨	▨	-	+		▨
	Season: Autumn						▨	▨														▨			▨				+	▨	▨	▨			▨	-	▨	▨		-
	Season: Winter						+	▨														▨			▨				+	-	▨	▨			▨	▨	▨	▨		▨
10m Radius	*Presence/Absence*									▨								▨		▨						▨	▨									▨				
	Roost/Non Roost									▨								▨		▨						-	▨									▨				
	Season: Spring									▨								+		▨						▨	▨									-				
	Season: Summer									-								▨		▨						▨	▨									▨				
	Season: Autumn									▨								+		▨						▨	▨									-				
	Season: Winter									▨								▨		▨						▨	▨									▨				
50m Radius	*Presence/Absence*			▨	▨	▨					▨	▨	▨						+		▨		-		-			▨					▨	-			▨		-	
	Roost/Non Roost			▨	▨	▨					▨	▨	-						▨		▨		▨		▨			+					▨	▨			-		▨	
	Season: Spring			▨	▨	▨					▨	▨	▨						+		▨		▨		-			+					▨	▨			-		-	
	Season: Summer			▨	▨	▨					-	▨	▨						▨		▨		▨		-			▨					▨	▨			-		▨	
	Season: Autumn			▨	▨	▨					▨	▨	▨						▨		▨		▨		▨			▨					▨	-			▨		▨	
	Season: Winter			-	▨	-					▨	-	▨						▨		▨		▨		-			+					+	▨			▨		▨	
100m + Radius	*Presence/Absence*						+	▨								▨						-		▨					+	▨	▨	▨			▨			▨		▨
	Roost/Non Roost						▨	-								▨						▨		▨					▨	-	▨	▨			▨			▨		▨
	Season: Spring						▨	▨								▨						▨		▨					+	▨	▨	▨			▨			▨		▨
	Season: Summer						+	▨								▨						▨		▨					▨	▨	▨	▨			▨			+		▨
	Season: Autumn						▨	▨								▨						▨		-					▨	▨	▨	▨			▨			▨		▨
	Season: Winter						+	▨								▨						▨		-					▨	▨	+	+			▨			▨		▨
All Variables	*Presence/Absence*	▨	▨	▨	▨	▨	▨	▨	+	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	-	▨	-	▨	▨	▨	▨	▨	▨	▨	▨	-	▨	▨	▨	▨	-	▨
	Roost/Non Roost	▨	▨	▨	▨	▨	▨	-	▨	▨	▨	▨	▨	▨	▨	▨	▨	+	▨	-	▨	▨	▨	▨	▨	-	+	+	▨	-	▨	▨	▨	▨	▨	▨	-	▨	▨	▨
	Season: Spring	▨	▨	▨	▨	▨	▨	▨	+	▨	▨	▨	▨	▨	+	▨	▨	▨	+	▨	▨	▨	▨	▨	-	▨	▨	+	▨	▨	▨	+	▨	▨	▨	▨	-	▨	-	▨
	Season: Summer	▨	▨	▨	▨	▨	▨	▨	▨	▨	-	▨	▨	▨	+	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Season: Autumn	▨	▨	▨	▨	▨	+	▨	▨	-	▨	▨	▨	▨	+	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	-	▨	▨	▨	▨	▨	▨
	Season: Winter	-	▨	▨	▨	▨	+	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	-	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

A total of 39 habitat variables (from the original 75 habitat variables) entered at least one of the 48 models (Table 4.3). Stepwise selection allowed for variable reduction. For five models no significant predictors were found. Key habitat variables significant within many of the models include ‘distance to roads’ (+ve effect) or ‘number of roads’ in proximity to a plot (-ve effect) along with ‘absence of old pine’ in a plot (-ve effect). Other variables such as ‘average yield class’ in a 50m radius of study plots (-ve effect) and ‘number of tree species’ within a 10m radius of study plots (+ve effect) were only used in one model, although they were entered into 18 different models. Models constructed using habitat variables recorded on a larger scale (50m and above) have a greater number of significant habitat variables. All variables used within models to predict capercaillie habitat use had a constant negative or positive effect within models.

To determine the predictive power of each model the threshold values were chosen from corresponding sensitivity and specificity values (Table 4.4). The model predictive powers presented within this study are based on predicting capercaillie absence as well as capercaillie presence. This is the case even when there is a low incidence of absence habitat. An overall probability of the model to predict of 0.7 to 0.9 indicates that the model has ‘average’ accuracy (Manel *et al*. 2001). Thirteen models had average accuracy, with the remaining 35 models being of poor accuracy. Models with average accuracy had predictive powers ranging from 70% to 78%.

Table 4.4. Table showing the probability threshold at which a predicted value was taken to indicate presence and predictive power of models produced in logistic regression analysis (blank spaces = no model, highlighted models = models with average accuracy)

Model	Response Variables	Probability level	Predictive Power
Field	*Presence/Absence*	0.82	54%
	Roost/Non Roost	0.64	60%
	Season: Spring	0.60	64%
	Season: Summer	0.70	61%
	Season: Autumn		
	Season: Winter	0.44	71%
Compartment	*Presence/Absence*	0.86	73%
	Roost/Non Roost	0.66	64%
	Season: Spring		
	Season: Summer	0.66	64%
	Season: Autumn	0.54	59%
	Season: Winter	0.40	64%
DTM	*Presence/Absence*	0.84	64%
	Roost/Non Roost		
	Season: Spring	0.64	70%
	Season: Summer	0.68	59%
	Season: Autumn	0.52	54%
	Season: Winter	0.44	64%
Aerial Photos	*Presence/Absence*	0.82	77%
	Roost/Non Roost	0.62	66%
	Season: Spring	0.66	68%
	Season: Summer	0.72	68%
	Season: Autumn	0.54	62%
	Season: Winter	0.44	71%
10m Radius	*Presence/Absence*		
	Roost/Non Roost	0.64	58%
	Season: Spring	0.58	64%
	Season: Summer	0.72	55%
	Season: Autumn	0.50	64%
	Season: Winter		
50m Radius	*Presence/Absence*	0.86	74%
	Roost/Non Roost	0.62	65%
	Season: Spring	0.62	69%
	Season: Summer	0.70	62%
	Season: Autumn	0.56	59%
	Season: Winter	0.40	78%
100m + Radius	*Presence/Absence*	0.84	72%
	Roost/Non Roost	0.60	67%
	Season: Spring	0.66	58%
	Season: Summer	0.66	64%
	Season: Autumn	0.56	61%
	Season: Winter	0.44	73%
All Variables	*Presence/Absence*	0.90	75%
	Roost/Non Roost	0.66	74%
	Season: Spring	0.70	71%
	Season: Summer	0.72	69%
	Season: Autumn	0.56	64%
	Season: Winter	0.40	75%

Annual presence/absence of dropping models and winter presence/absence of dropping models had higher average predictive powers than models using annual presence/absence of roosts or presence/absence of droppings in spring, summer or autumn as response variables. In addition models based on habitat variables measured on a smaller scale had lower average predictive powers than those based on habitat variables measured on a larger scale.

4.4.1.2 Examples of High Predictive Power Models

The four models that had the highest predictive powers to successfully classify capercaillie presence or absence are presented below.

Aerial photograph model with annual presence/absence as response variable

Table 4.5 Parameter estimates for the aerial photograph model using annual presence/absence as the response variable

Variable	Direction of Association	Parameter	Standard Error	Wald Statistic	*P*	Point Estimate	95 % Wald Confidence Limits	
Intercept		2.597	0.608	18.276	<.0001			
Absence of old pine 50m	-ve	-0.879	0.353	6.203	0.012	0.172	0.043	0.688
Number of roads in a 50m radius of plots	-ve	-1.997	0.726	7.567	0.001	0.136	0.033	0.563
Percentage ride cover in 100m radius of plots	+ve	0.018	0.008	5.142	0.023	1.018	1.002	1.034
Neighbouring Habitat	-ve	-0.922	0.326	8.013	0.005	0.398	0.210	0.753

The results of the annual presence/absence based logistic regression with aerial photograph predictor variables resulted in a model with absence of old pine 50m, number of roads in a 50m radius of plots, % ride cover in a 100m radius of plots and neighbouring habitat in a 100m radius of plots as significant predictor variables (Table 4.5). The effect size of significant variables is shown using odds ratio estimates (Table 4.5).

A threshold probability level of 0.82 was selected which produced a model predictive power of 77% (Table 4.4). The resulting equation to predict capercaillie presence is:

$$Z = 2.597 - 0.879a - 1.997b + 0.018c - 0.922d$$

Where: Z: predicted logit score
a: absence of old pine in 50m radius of plots
b: number of roads 50m
c: % ride cover 100m
d: neighbouring habitat 100m

50m radius model with winter presence/absence as response variable

The results of the winter presence/absence based logistic regression with 50m predictor variables resulted in a model with % old Scots pine, % area of Scots pine, age of trees, blaeberry height, grass height and number of roads as significant predictor variables (Table 4.6). The effect size of significant variables is shown using odds ratio estimates (Table 4.6).

Table 4.6 Parameter estimates for the 50m radius model using winter presence/absence of droppings as the response variable.

Variable	Direction of Association	Parameter	Standard Error	Wald Statistic	*P*	Point Estimate	95 % Wald Confidence Limits	
Intercept		8.912	2.267	15.456	<.0001			
% old Scots pine 50m	+ve	0.237	0.054	19.561	<.0001	1.267	1.141	1.408
% area of Scots pine 50m	+ve	0.038	0.009	17.905	<.0001	1.039	1.021	1.057
Age of trees 50m	-ve	-0.198	0.052	14.816	0.0001	0.820	0.742	0.907
Blaeberry height 50m	-ve	-0.095	0.023	17.376	<.0001	0.909	0.870	0.951
Grass height 50m	-ve	-0.076	0.022	12.242	0.0005	0.927	0.888	0.967
Number of roads 50m	-ve	-2.669	1.170	5.208	0.0225	0.069	0.007	0.686

A threshold probability level of 0.40 was selected which produced a model predictive power of 78% (Table 4.4). The resulting equation to predict capercaillie presence is:

$$Z = 8.912 + 0.237a + 0.038b - 0.198c - 0.095d - 0.076e - 2.669f$$

Where: Z: predicted logit score
a: % old Scots pine 50m
b: % area of Scots pine 50m
c: age of trees 50m
d: blaeberry height 50m
e: grass height 50m
f: number of roads 50m

All habitat variables model using annual presence/absence as response variable

Table 4.7 Parameter estimates for the all variables model using annual presence/absence of droppings as the response variable.

Variable	Direction of Association	Parameter	Standard Error	Wald Statistic	*P*	Point Estimate	95 % Wald Confidence Limits	
Intercept		2.192	1.785	1.507	0.220			
% open ground 50m	-ve	-0.067	0.020	10.909	0.001	0.936	0.899	0.973
No of ground vegetation species 50m	-ve	-1.100	0.368	8.953	0.003	0.333	0.162	0.684
Rotation 1 50m	-ve	-1.896	0.468	16.432	<.0001	0.023	0.004	0.141
Number of roads 50m	-ve	-1.925	0.791	5.929	0.015	0.146	0.031	0.687
Elevation	+ve	2.600×10^{-5}	7.738×10^{-6}	11.072	0.001	1.000	1.000	1.000

The annual presence/absence based logistic regression including all predictor variables resulted in a model with % open ground in 50m radius of plots, number of ground vegetation species in 50m radius of plots, rotation 1 in 50m radius of plots, number of roads in 50m radius of plots and elevation as significant predictor variables (Table 4.7). The effect size of significant variables is shown using odds ratio estimates (Table 4.7).

A threshold probability level of 0.90 was selected which produced a model predictive power of 75% (Table 4.4). The resulting equation to predict capercaillie presence is:

$$Z = 2.190 - 0.067a - 1.100b - 1.896c – 1.925d + 0.000e$$

Where: Z: predicted logit score
a: % open ground 50m
b: number of ground vegetation species 50m
c: rotation 1 50m
d: number of roads 50m

e: elevation (m)

All habitat variables model using winter presence/absence as response variable

The winter presence/absence based logistic regression with all habitat predictor variables resulted in a model with number of trees 10m, distance to roads and accumulated temperature as significant predictor variables (Table 4.8). The effect size of significant variables is shown using odds ratio estimates (Table 4.8).

Table 4.8 Parameter estimates for the all variables model using winter presence/absence of droppings as the response variable.

Variable	**Direction of Association**	**Parameter**	**Standard Error**	**Wald Statistic**	***P***	**Point Estimate**	**95 % Wald Confidence Limits**	
Intercept		24.997	5.096	24.059	<.0001			
Number of trees 10m	-ve	-0.141	0.038	13.784	0.0002	0.868	0.806	0.936
Distance to roads	+ve	0.004	0.001	8.178	0.0042	1.004	1.001	1.007
Accumulated temperature	-ve	-0.024	0.005	25.123	<.0001	0.977	0.968	0.986

A threshold probability level of 0.40 was selected which produced a model predictive power of 75% (Table 4.4). The resulting equation to predict capercaillie presence is:

$$Z = 24.997 - 0.141a + 0.004b - 0.024c$$

Where: Z: predicted logit score
a: number of trees 10m
b: distance to roads
c: accumulated temperature

4.4.2 Other data

4.4.2.1 Use of rides for roosting

Using the results of roost data collected during November 2002, capercaillie show preference to rides and thinning racks for roosting ($X^2 = 11.36$, d.f. = 1, $P<0.01$). Three times the quantity of roosts were found on rides or thinning racks than found within the forest. This result is even more prominent when the ratio of forest to rides is calculated. Using ride length data from the habitat variables collected and an average ride/thinning rack width of 4m, the percentage ride/thinning rack to forest was calculated at 11% to 89%. Compass directions were followed between plots therefore the time spent on either rides/thinning racks or forest is thought to be proportional to the percentages present.

4.4.2.2 Capercaillie sightings

Sightings of capercaillie were recorded along with location and sex. A total of 200 sightings were recorded between April 2002 and February 2004. Determination of sex from droppings was found to be inaccurate (Chapter 5) and therefore habitat requirement according to sex could not be determined from droppings. However, using capercaillie sightings, some measures of capercaillie habitat use according to the sexes can be ascertained. The only habitat information available for these sightings is that derived from the FC compartmental Database. Using the compartment variables altitude, age, compartment area, yield class and rotation (further described in 4.3.3), Mann-Whitney U tests were conducted to explore any significant habitat use differences between the sexes and between seasons.

Table 4.9 Differences in habitat use between capercaillie sexes during winter months.

Winter	**Sex**				
	Male		**Female**		
Habitat Variables	Median	Interquartile	Median	Interquartile	P-value
Altitude	180	165 - 230	260	170 - 270	0.0074
Area of compartment km^2	0.15	0.07 - .035	0.30	0.24 - 0.33	0.0368
Age of trees	51	42 - 53	46	36 - 50	0.0139
Yield Class	8	6 - 8	8	6 - 8	1.0000
Rotation	9	1 - 9	1	1 - 9	0.0034

Habitat use was only significantly different between the sexes during winter months (December, January, and February) (Table 4.9). During winter months, female capercaillie were found at significantly higher altitudes than males, in larger compartments with younger trees than males and in woodland planted on formerly open ground rather than woodland planted on old woodland sites; which is preferred by males.

4.4.2.3 Capercaillie feathers

Capercaillie feathers were collected and recorded with feather location and sex of feathers. 284 feathers were collected between May 2001 and September 2003. Using habitat variables from the FC compartmental database, difference between male and female habitat use was explored (Table 4.10).

Table 4.10 Differences in habitat use between capercaillie sexes using feather locations

Feathers	Sex				
	Male		Female		
Habitat Variables	Median	Interquartile	Median	Interquartile	P-value
Altitude	180	150 - 230	210	150 - 252.5	0.0026
Area of compartment km^2	0.15	0.08 - 0.35	0.26	0.14 - 0.33	0.1629
Age of trees	51	50.5 - 53	50	45 - 53	0.0152
Yield Class	8	6 - 8	8	6 - 8	0.5493
Rotation	9	1 - 9	9	1 - 9	0.5329

Altitude and age of trees were the only habitat variables that significantly varied between the sexes using collected feathers as an indication of capercaillie habitat choice.

4.5 Discussion

4.5.1 Importance of Multiple Scales and Data Sources in Capercaillie Habitat Study

Because organisms interact with their environments at multiple scales, habitat models need to address these relationships at different spatial scales in order to adequately capture an organisms requirements. Multi-scale approaches in habitat studies have been encouraged to further acknowledge influences of spatial variation on species behaviour (Levin 1992, Luck 2002, Sergio *et al.* 2003, Graf *et al.* 2005, Manzer & Hannon 2005, Michel *et al.* 2008).

The importance of scale in species-habitat studies was highlighted by Storch in 2002 when investigating the effects of spatial resolution on the performance and applicability of habitat models for capercaillie. Since then several studies have investigated capercaillie habitat in relation to scale (Lande *et al*. 2004, Graf *et al*. 2005, Graf *et al*. 2007). Results of these studies confirm that habitat variables should be included at different spatial scales when species-habitat relationships are investigated.

This is the first study in Scotland that specifically addresses capercaillie habitat use on a number of scales from individual trees to forest level. Results from the logistic regression analysis of habitat variables collected at varying scales suggest that habitat variables measured on a larger scale successfully predict capercaillie presence better than those measured on a smaller scale. Graf *et al*. (2007) also found that small-scale forest structure had limited power to predict capercaillie occurrence and including landscape variables improves predictions at the forest stand scale. In addition, within the present study, combining habitat variables at different scales in predictive models of capercaillie presence resulted in a stronger models than using variables within one scale alone. Graf *et al*. (2005) also found that multi-scale models used to predict capercaillie presence performed better than single-scale models. The scale at which habitat variables could be measured was limited at Morangie Forest. It was outwith the scope of the present study to measure habitat variables beyond the scale of the forest. Recent work, mostly in Scandinavia has shown that capercaillie populations are substantially driven by landscape-scale processes (Kurki & Linden 1995, Kurki *et al*. 2000). This is supported by the results of Graf *et al*. (2005) who found that course grained habitat models at the landscape scale perform better for capercaillie in the Swiss Alps. Quevedo *et al*. (2006) also found that the importance of capercaillie response to landscape configurations extends further than that from local habitat units. It is therefore vital that future capercaillie studies in Scotland consider even broader scales of habitat measurement, so that measures can be implemented to manage capercaillie over the whole of Scotland. National survey data along with habitat variables measured at a landscape scale could be used to examine the probability of forest patches being used by capercaillie.

The source of data used in habitat models within the present study is also an important consideration and as such models were constructed on the basis of data origin. Forest managers have a certain amount of habitat information readily available to them through compartmental databases, which are commonly digitised in the form of Geographical Information Systems (GIS). Aerial photographs are now commonly digitised and available through GIS. In addition, Digital Elevation Models (DEMs) containing environmental variables are now readily available for forest managers to use. Habitat variables collected in the field, such as vegetation structure represent the least readily available source of habitat information for forest managers and are probably the most time consuming to collect. Results from the present study found that habitat variables measured from aerial photographs and forest parameters from the FC compartmental database produced better models than variables collected from the field. Other studies have also utilised aerial photographs and forest parameters in order to derive information about capercaillie habitat use. Graf *et al*. (2005) and Lande *et al*.

(2004) used aerial photographs and GIS to analyse capercaillie habitat at the landscape scale and Gossow *et al*. (1984) specifically investigated capercaillie habitat use in relation to forest parameters in order to give forest managers information on how to improve their plantations for capercaillie, using terminology understandable to forest managers. Results of this study show that information already available to forest managers can successfully predict capercaillie presence.

4.5.2 Results of Logistic Models

4.5.2.1 Significant Habitat Predictors

Habitat predictor variables found significant in logistic regression models are discussed below.

Habitat structure variables significant within models

A number of habitat structure predictor variables were found significant within logistic regression models including percentage area of Scots pine, presence of old Scots pine, rotation, number of ground vegetation species, percentage cover and height of moss. Forest density measurements such as percentage forest, percentage open ground and percentage forest complete, scattered or open were also found to be significant predictors of capercaillie presence within models. Finally habitat diversity measurements; diversity in land use and woodland types were also found significant within models.

Capercaillie are more likely to be present in areas with a higher percentage of Scots pine, and in addition, are more likely to avoid areas where old Scots pine is not present. Capercaillie association with Scots pine is well documented (Rolstad & Wegge 1989, Moss & Picozzi 1994, Petty 2000, Summers *et al*. 2004). Small isolated areas of relic Scots pine planting from the turn of the 20th century are interspersed throughout Morangie Forest. The structure of these trees and the associated ground vegetation is more like that of the preferred habitat of capercaillie; semi-natural pinewoods and therefore capercaillie are more likely to be present in areas that are in proximity to areas of old Scots pine.

Presence of woodland on areas that were previously open or non-woodland sites was found to negatively influence capercaillie habitat choice. Capercaillie were more likely to be absent from areas of this woodland type. This may be due to differences in the vegetation species composition and structure between historical woodland sites and sites that used to be heathland before being planted, which was the case at Morangie Forest or related to the presence of old pine on previously planted woodland sites.

Vegetation diversity is indicated as a negative term in many of the present models. Storch (1993) also found that capercaillie prefer stands with lower vegetation diversity. However this was a reflection of the overwhelming preference by capercaillie for blaeberry within the study area. No preference was found for blaeberry within the present study and in fact, blaeberry height along with heather and grass height was found to be negatively associated with capercaillie presence, when entered into a model using capercaillie presence/absence during winter months. Percentage moss cover, however, was found to be a positive predictor of capercaillie presence. Capercaillie are more likely to be present in plots that have a higher percentage ground cover of moss. This could suggest a preference for areas with lower vegetation height. Storch (1993) found that capercaillie rarely used vegetation taller than 40cm and cock capercaillie rely on concealing cover less than hens, and therefore use sites with shorter ground vegetation.

Capercaillie are more likely to avoid areas with a higher percentage of open ground. This is consistent with capercaillie preferring areas of continuous forest and supports previous findings that have shown that capercaillie prefer continuous areas of forestry (Helle *et al*. 1994, Rolstad & Andersen 2003). In addition, percentage forest also has a significant effect on capercaillie presence, plots are more likely to be occupied if the percentage forest is higher. This is synonymous with capercaillie preferring less fragmented areas. However, within areas of continuous forest capercaillie were more likely to be present within areas of forest with a more open structure, with scattered trees and open spaces. This is indicative of capercaillie preference for irregular spaced trees, more similar to the spacing found in semi-natural pinewoods; the preferred habitat of the capercaillie (Picozzi *et al*. 1992, Wilkinson *et al*. 2002).

Finally diversity of land use and woodland types were also found to be negative predictors of capercaillie presence within models. This is suggestive of capercaillie preference for more continuous uniform areas of habitat.

Fragmentation variables significant within models

A number of fragmentation predictor variables were found significant within logistic regression models including number of polygons, length of boundary lines, percentage ride cover and ride length.

Capercaillie were more likely to be absent from plots that had a higher number of polygons and longer boundary line lengths. This would suggest that capercaillie avoid more fragmented areas within Morangie Forest. Reasons for this may be due to an increased predation risk in areas where there are more boundaries to the forest. Storch (1990) stated that habitat fragmentation creates spatial variations in predation risk, with a tendency for higher losses near edges than inside areas of homogeneous habitat. Numerous studies have reported the negative effect of forest fragmentation on capercaillie presence (Henttonen 1989, Wegge *et al*. 1992, Menoni *et al*. 1997, Segelbacher *et al*. 2003).

The effects of fragmentation, characterised by the length and percentage ride cover were found to have a positive effect on the presence of capercaillie. Capercaillie were more likely to use an area of forest where thinning racks or rides were present, therefore this measure of fragmentation appears to be a positive feature for capercaillie. Capercaillie were often seen roosting on the edge of thinning racks, flying along thinning racks and in the case of more dense forest, feeding from the more developed ground vegetation present on thinning racks (pers. obs.). The role of thinning racks and rides has been recognised in other studies as providing flight lines through dense forest (Jones 1982, Gossow *et al.* 1984) and providing more developed ground vegetation (McGowan 2002). Jones (1982) stated that capercaillie appeared to make the greatest use of trees associated with flightways; such flightways were commonly provided by thinning racks in more uniform compartments. In uniform stands capercaillie were often flushed from trees beside the intersection of thinning strips where a choice of clear flight paths was possible (Jones 1982).

Landscape feature variables significant within models

A number of landscape predictor variables were found significant within logistic regression models including accumulated temperature, elevation, hillshade, moisture deficit and neighbour effect.

Accumulated temperature had a negative effect on capercaillie presence during winter months suggesting that capercaillie avoid areas during the winter where higher accumulated temperature values are found. It is not clear what is driving this behaviour in capercaillie.

Capercaillie presence is positively associated with higher elevations, which may be a result of lower elevations being closer to edges with bordering farmland and moorland, which is known to increase the rate of predation (Angelstam 1986, Storch 1990). Klaus *et al*. (1986) and Storch (1993) both reported the preference of capercaillie for elevated terrain. Storch (1993) commented that altitude-related differences in resource abundance and possibly predation risk may explain the preference of capercaillie for higher elevations.

Hillshade of plots, or conversely the amount of light a plot receives, was found to significantly influence capercaillie presence within a number of models including seasonal presence/absence models using all habitat variables as predictor variables. This suggests that capercaillie prefer habitat located on sunny hillsides on Morangie Forest. This is in accordance with Storch (1993) who found that capercaillie prefer southern sunny slopes.

Moisture deficit as a predictor variable has a positive effect on capercaillie presence. Capercaillie prefer areas that are dryer than surrounding areas. The results of the present study are in agreement with Moss (1985) who found that capercaillie in Scotland had shifted their distribution to less rainy areas.

Neighbouring habitats had a negative predictive effect on capercaillie presence, further suggesting that capercaillie prefer continuous areas of forestry with less fragmentation.

Disturbance variables significant within models

Capercaillie are more likely to be present in areas further away from roads and with a fewer number of roads in proximity. These results support a study by Summers *et al*. (2007) which showed that trees used by capercaillie were further from tracks than those not used. Evidence from Chapter 3, suggests that continual observer presence at study plots may have caused capercaillie to avoid these areas over time. However, whether capercaillie avoidance of plots near roads in Morangie Forest is caused by disturbance from human recreation or is an artefact of habitat edge or microclimate is unclear. Summers *et al*. (2007) concluded that human recreation accounted for the absence of capercaillie close to tracks, however they also mentioned that capercaillie avoided tracks even at low levels of disturbance. Therefore disturbance may not be the only factor limiting capercaillie use near roads. Many of the forest tracks in Morangie Forest have little or no recreational use and therefore it is unlikely that disturbance alone would create such a strong result. Anecdotal evidence found that three capercaillie nests, from a total of eight, observed during the study period were found less than 50m from a road. Direct sightings, dust baths and droppings were also regularly observed on tracks during the study period (pers. obs). Therefore, in the case of Morangie Forest capercaillie do not seem to avoid tracks, just plots within the vicinity of tracks. None of the habitat variables collected were correlated with distance from tracks and therefore investigation, including a survey of track use, would have to be conducted before any conclusions could be made about the effects of human disturbance on capercaillie in Morangie Forest.

4.5.2.2 Effect of Response Variables

Models using annual capercaillie dropping presence/absence and winter presence/absence as response variables consistently produced models with higher predictive powers than those using spring, summer and autumn presence/absence of droppings or presence/absence of roosts. This would suggest that the habitat variables collected within the present study are measuring overall or winter capercaillie habitat use rather than specific habitat use such as roosting or feeding, or seasonal habitat use such as nesting or moulting. It therefore appears that habitat variables collected, especially those in the field failed to measure capercaillie habitat use outwith winter months.

4.5.2.3 Logistic Models

The logistic models presented had predictive powers of between 75-78% and are discussed below.

Aerial photograph model with annual presence/absence as response variable

Results of the logistic regression analysis using annual presence/absence of droppings along with predictor variables measured from aerial photographs resulted in a model with a predictive power of 77%. This model had a higher predictive power than models using all habitat variables and highlights the importance of using different data sources when constructing habitat models. Habitat variables found significant within the aerial photograph model include absence of old pine 50m (-ve), number of roads in a 50m radius of plots (-ve), % ride cover in a 100m radius of plots (+ve) and neighbouring habitat in a 100m radius of plots (-ve). Very similar results were found by Braunisch & Suchant (2007) when evaluating the 'habitat potential' of a landscape for capercaillie. Their final predictive model of capercaillie presence included three land use variables namely; proportion of forest (+ve), distance to roads (+ve) and forest-agricultural borders (-ve) which they found explained a high degree of capercaillie habitat selection.

50m radius model with winter presence/absence as response variable

The results of the winter presence/absence based logistic regression with 50m predictor variables resulted in a model with % old Scots pine (+ve), % area of Scots pine (+ve), age of trees (-ve), blaeberry height (-ve), grass height (-ve) and number of roads (-ve) as significant predictor variables. This model had a predictive power of 78%, higher than any other model, suggesting that measured habitat variables are successfully predicting winter habitat choice of capercaillie. Interestingly, vegetation height was found to negatively influence the probability of capercaillie using a plot, this would support the findings of Storch (1993), who found that capercaillie avoided areas with tall vegetation during winter months.

All habitat variables model using winter presence/absence as response variable

The results of the winter presence/absence based logistic regression with all habitat predictor variables resulted in a model with number of trees 10m (-ve), distance to roads (+ve) and accumulated temperature (-ve) as significant predictor variables. Results of this model suggest that during the winter capercaillie prefer areas of forest with fewer trees. This is probably a reflection of their roosting requirements and is supported by number of trees being one of only two habitat variables significant in a model predicting capercaillie presence of roosts. Summers *et al*. (2004) also found that capercaillie preferred areas of woodland with a lower density of trees.

All habitat variables model using annual presence/absence as response variable

Results of the logistic regression using annual presence/absence of droppings along with all predictor variables resulted in a model with percentage open ground in 50m radius of plots (-ve), number of ground vegetation species in 50m radius of plots (-ve), rotation 1 in 50m radius of plots (-ve), number of roads in 50m radius of plots (-ve) and elevation (+ve) as significant predictor variables. This model had a predictive power of 75% and again highlights the preference of capercaillie for areas of continuous forest at higher elevations with fewer roads.

The improved predictive power of models with all variables entered as predictor variables, compared to the majority of other models run, emphasises that capercaillie habitat choice depends upon many different habitat factors all acting upon various scales within the forest. It also re-highlights the need to consider capercaillie habitat variables on varying scales.

4.5.3 Roosting Behaviour of Capercaillie

Results from roosting data collected within Morangie Forest demonstrate that capercaillie show significant preference for rides and thinning racks for roosting. This is in accordance with Jones (1982) who found that within a commercial plantation, capercaillie used a significantly higher number of pines with projecting branches growing on rides or thinning rack edges, than control pines within the forest interior. In addition, Thiel *et al*. (2007) found that one of the most important factors discriminating roost trees from random trees was the number of forest aisles leading away from the roost tree. This is an important finding for forest managers, who should aim to create a network of access corridors for capercaillie, which in turn will act as roosting sites and escape routes for capercaillie. Care should be taken not to make rides or racks over 10m wide as this has been found to increase the edge effect of the forest and encourage predation (Storch 1990).

Habitat variables significant within logistic models specifically using roost/non roost as a response variable include diversity in land use (-ve), number of trees (-ve), area of Scots pine (+ve) and percentage of complete forest (-ve). This is suggestive of capercaillie preferring roost sites that are in areas of continuous lower density woodland, predominantly of Scots pine. This is reflective of the structure of semi-natural pine forests, the preferred habitat for capercaillie.

4.5.4 Differential Habitat Use by Sexes

There have been many studies published that highlight the differences between male and female capercaillie habitat use over the seasons (Rolstad 1988, Gjerde 1991, Storch 1993, Saniga 2004). However, no habitat variables collected from the FC compartmental database were significant when compared to capercaillie sighted during spring, summer and autumn. Only during winter months were habitat characteristics significantly different between the sexes. During winter months female capercaillie were found at higher altitudes than males, in larger compartments with younger trees than males and in areas of woodland planted on ground that was previously open, whereas males were located in areas of woodland that had previously been planted on. Jones (1982) and Rolstad *et al.* (1988) also found that female capercaillie select younger plantations than males. Female capercaillie were also located in larger compartments than males. Results of genetic analysis of feathers (Chapter 6) showed that females had larger home ranges than males, perhaps explaining why they preferred more sizeable compartments than males. Storch (1993) stated that selection of larger patches relates to predator avoidance. Therefore larger areas of forest may be selected by females, which are more likely to be depredated when nesting. In addition, female capercaillie were found at higher elevations than male capercaillie. Elevation was a significant predictor variable in explaining capercaillie presence in logistic regression models; capercaillie were more likely to be present at higher elevations. Storch (1993) also found that both male and female capercaillie had a marked preference for higher elevations during winter months. However, there is no evidence in the literature to support female capercaillie specifically preferring higher elevations to males during winter months. These present observations may be reflective of female use of younger areas of plantation in the north of the forest which happen to be planted at higher elevations than the rest of the forest and were previously areas of heather moorland (pers. obs.).

4.5.5 Observations and Suggestions for Further Study

The habitat data collected during this study appears to be predicting capercaillie habitat use in winter more effectively than in other seasons. This is supported by the poor predictive powers of logistic regression models constructed using presence/absence of droppings with spring, summer and autumn as response variables. Typical capercaillie summer habitats such as thickets and boggy areas appear to have been under-represented in the current study. Therefore, in order to investigate summer habitat use of capercaillie in Morangie Forest, survey plots would have to be positioned within these under-represented habitats.

No preference was found for blaeberry cover within the present study and blaeberry height was actually found to be a negative predictor of capercaillie presence. This is in contrast to published data that states that blaeberry is important for capercaillie (Storch

1993, Moss & Picozzi 1994, Petty 2000, Perrin *et al*. 2003). In addition, other habitat studies which were conducted in winter months still found a positive association between capercaillie and blaeberry, showing that habitat requirements at other times of the year influence winter habitat choice (Storch 1993, Wilkinson *et al*. 2002). The average percentage cover of blaeberry in Morangie Forest is 16%. Baines *et al*. (2004) found that capercaillie breeding success increased with increasing blaeberry *Vaccinium myrtillus* ground cover, but did not improve further above 15-20% cover. Therefore, it may be that there is sufficient blaeberry within habitats in Morangie Forest and as a result capercaillie are not having to actively select habitats on the basis of it. Bollman *et al*. (2005) studied capercaillie habitat use at the stand scale within a managed alpine forest in the central Alps, and reported that they could not confirm a direct response of capercaillie to blaeberry present within the study area. Results of the dietary analysis of droppings (Chapter 5), however, suggest that although capercaillie in Morangie Forest do not choose habitat on the basis of blaeberry cover they actively select for it in their diet.

Image analysis of aerial photographs was conducted by eye rather than using textural analysis software. There are therefore errors associated with observer bias from habitat measurements made from these photographs. An improvement to the study could be made by using a number of people to make habitat measures from aerial photographs, in order to calculate an estimate of error. Textural analysis software also represents a more effective method of making habitat measurements from aerial photographs.

In general, the present study successfully generated a number of habitat variables found significant in capercaillie habitat choice and produced models that could be used to predict habitat suitability for capercaillie in commercial plantations. However, results could be improved by including measures of habitat used by capercaillie during summer months and conducting more formal image analysis on aerial photographs.

4.6 Conclusions

This study has investigated habitat features that are important to capercaillie within working forests. Almost all previous studies in Scotland of capercaillie habitat have focused on preferences within semi-natural or ancient pinewoods. Therefore results of this study have helped provide much needed information about capercaillie habitat preferences within commercial forests.

The importance of the scale at which capercaillie habitat measurements are made has also been illustrated. This has been illustrated for a range of species including the rufous treecreeper (Luck 2002), South Island saddleback (Michel 2006) and caribou (Mayor *et al*. 2008). In addition to the scales studied in the present study, future capercaillie studies should consider even broader scales, so that measures can be implemented to manage capercaillie over the whole of Scotland.

As well as the scale that habitat measurements are made on, the source of the data used to describe capercaillie habitat choice has been shown to be important. Habitat models have been successfully constructed for a range of species using habitat variables from forest databases linked to GIS including red squirrel (Gurnell *et al*. 2002), brown bear (Kobler & Adamic 2000) and golden-winged warbler (Martin *et al.* 2007). Results of this study show that information already available to forest managers, or easily extractable from available data sources, can be used to successfully predict capercaillie presence and absence within an area and could therefore aid management of working forests for capercaillie.

The power of a model to correctly predict presence and absence of a species is an important factor when considering the efficacy of habitat models. The logistic models created within this habitat study produced predictive powers that correctly classified capercaillie presence and absence to a higher degree than those found in some published studies (Bollman *et al*. 2005: 68.5%) and to a comparable degree with other similar habitat studies (Storch 2002: 76%, Graf *et al*. 2009: 71-77%). The logistic regression models created in this present study can therefore provide a suitable support tool for forest managers when planning forest operations or future planting.

The logistic regression models created in this study have produced plausible, biologically consistent outcomes that fit quite well with other habitat association studies of capercaillie, suggesting that dropping count data are a reasonably good index of capercaillie distribution, at least outwith the breeding season.

The present habitat study at Morangie Forest demonstrates that capercaillie can successfully adapt to habitat within working forests and has identified the types of habitat that capercaillie prefer within a working forest. It is hoped that the present results will contribute to management planning of capercaillie within these working forests.

4.7 Bibliography

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Chapter 5. A Comparison of Habitat and Diet of Capercaillie in a Working Forest and a Semi-Natural Pinewood

Abstract

Habitat and diet of capercaillie within Morangie Forest was determined and compared to the habitat and diet of capercaillie in Abernethy Forest (Summers *et al*. 2004), a semi-natural pinewood. Similar dietary analysis techniques were used to aid comparison. Results showed that capercaillie in Morangie Forest and Abernethy Forest had largely similar diets. However, capercaillie in Morangie Forest had higher percentages of pine in their diet throughout the year in comparison with capercaillie in Abernethy Forest. In addition, capercaillie in Morangie Forest selected for blaeberry in their diet more frequently than those in Abernethy Forest. Results of the capercaillie habitat analysis highlight the differences in structure between Morangie Forest and Abernethy Forest. Capercaillie in Morangie Forest were using areas of forestry that had thinner higher trees, more closely spaced, with a higher percentage moss and grass cover, and a lower percentage blaeberry cover than capercaillie in Abernethy Forest. Results suggest that although significantly different in structure from semi-natural pinewoods, commercial forests can provide suitable habitat for capercaillie, albeit at lower densities.

Chapter 5. A Comparison of Habitat and Diet of Capercaillie in a Working Forest and a Semi-Natural Pinewood

5.1 Introduction

In the present chapter I investigate the habitat and diet of adult capercaillie in a working forest and compare it to a similar study conducted in a semi-natural pinewood. A review of habitat studies has already been given in Chapter 4. Therefore, in this introduction I concentrate on a review of dietary studies, and in particular, faecal analysis.

There are various methods used to examine the diet of individuals including direct observation, examination of gut and crop contents in animals and birds, and analysis of faeces or pellets (Jordan 2005). Direct observation is difficult in most cases due to the elusive nature of many wild species and is usually confined to birds in nests (Redpath *et al.* 2001, Tornberg & Reif 2007) and grazing herbivores (Bugalho *et al.* 2001, Parker & Bernard 2005). Gut or crop analysis was routinely used in dietary studies in the past (Zwickel 1966, Moss & Parkinson 1972, Puglisi *et al.*1978), however, is less commonly used nowadays as many individuals need to be sacrificed in order to establish the full range of dietary items. Dietary analysis of faeces therefore, represents a non-invasive method of establishing information about diet and as a result has been a commonly used method over the past 60 years (Baumgartner & Martin 1939, Marti 1982, Breuer 2005). However, faecal analysis is not without problems, objections persist that it does not allow quantitative measurement of diet and that often resulting lists of food items are incomplete (Marti 1982). Most notable biases include the differential digestibility of plant parts and variation in particle size (Starling-Westerberg 2001). For example, in order to achieve a random distribution and have an equal chance of being selected during examination, particles need to be of uniform size (Sparks & Malechek 1968). Faecal analysis, nevertheless, does allow a non-invasive opportunity to study diet and can provide good qualitative and quantitative information on diet (Marti 1982). It is therefore thought suitable for use in studies of endangered animals if results are interpreted with care.

The general diet of the capercaillie has been well documented (see Petty 2000 for a complete review). However, few studies have investigated the capercaillie diet in Scotland in detail. Zwickel (1966) investigated the winter food habits of capercaillie through crop analysis, concluding that Scots pine (*Pinus sylvestris*) forms the major winter food of capercaillie in the North-East of Scotland. Jones (1982) assessed winter diet of capercaillie in Scots pine plantations through crop analysis, and annual diet using direct observations. Results showed that Scots pine was eaten throughout the year, with dwarf shrubs additionally consumed during summer months. Diet of capercaillie in a Scottish plantation forest was examined by Picozzi *et al*. in 1996. Results showed that unusually spruce comprised the main constituent of capercaillie diet during winter months, replaced by sedges and rushes in summer months. Most recently Summers *et al*. (2004) studied the diet of capercaillie throughout the year in a Scottish semi-natural pinewood using faecal analysis, concluding that capercaillie switch from a diet largely consisting of pine needles in the winter to one of mostly blaeberry leaves and berries during summer months.

In addition to studying capercaillie diet, Summers *et al*. (2004) also studied habitat use of capercaillie in a Scottish semi-natural pinewood. Summers *et al*. (2004) commented that although there have been a number of studies investigating the habitats of capercaillie, most often habitat descriptions have not been quantified or conclusions have been general. Therefore, one of the aims of the Summers *et al*. (2004) study was to provide more detailed descriptions and measurements of semi-natural pinewood habitat in order to recommend management prescriptions. The present study shared the same aim; to provide a more detailed description and measurement of capercaillie habitat but in a commercial plantation rather than a semi-natural pinewood (see Chapter 4).

This similar study by Summers *et al*. (2004) represented an ideal opportunity to conduct a direct comparison between capercaillie habitat and diet in a semi-natural pinewood and a commercial plantation. In addition, although commercial Scots pine plantations probably represent the future for capercaillie in Scotland; due to their extent in comparison with semi-natural pinewoods (the preferred habitat of capercaillie), no detailed study has investigated annual capercaillie diet in commercial pine plantations. Therefore, droppings collected as part of the study investigating size and distribution of the capercaillie population at Morangie Forest (Chapter 3) were used to conduct dietary faecal analysis and habitat data collected as part of the study investigating habitat use of capercaillie at Morangie Forest (Chapter 4) were compared to habitat data collected in a semi-natural pinewood (Summers *et al*. 2004).

5.2 Aims and Objectives

The main aim of this chapter is to investigate capercaillie diet in a working forest through analysis of droppings and compare it to capercaillie diet in a semi-natural pinewood determined using the same methodology. A further aim is to compare habitat features used by capercaillie in a commercial forest and those used by capercaillie in a semi-natural pinewood.

To meet these aims three specific questions were addressed:

- What do adult capercaillie eat throughout the year in Morangie Forest?
- How does adult capercaillie diet in Morangie Forest compare to that in a semi-natural pinewood?
- How does capercaillie habitat choice in Morangie Forest compare with that in a semi-natural pinewood?

5.3 Methods

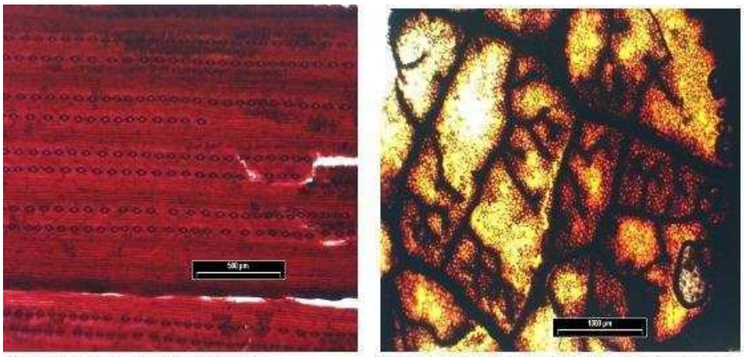
5.3.1 Collection of Capercaillie Droppings for Dietary Analysis

All droppings from January 2003 to December 2003, collected as part of the main study investigating size and distribution of the capercaillie population at Morangie Forest (Chapter 3), were broadly categorised on collection according to whether they comprised mostly of pine needles or other material. From this, the percentage of droppings comprising mostly pine needles and the percentage of droppings containing all other food items each month could be ascertained. In addition, 20 fresh droppings were randomly selected from around Morangie Forest each month so that fine scale analysis of dietary constituents could be performed. 'Freshness' of droppings was identified by the colour and moisture content. Droppings were frozen until analysis.

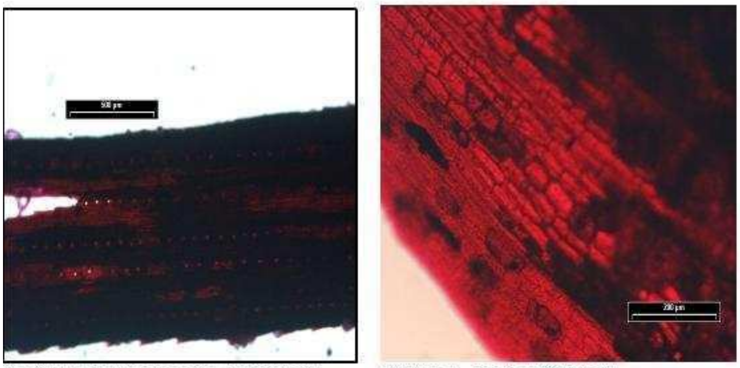
5.3.2 Development of a Capercaillie Dietary Reference Collection

Specimen capercaillie diet constituents were collected from Morangie Forest during 2001-2002 and used to develop a capercaillie dietary reference collection. Samples containing all parts of the plant such as leaves, berries, stem and flowers were cut and placed in labelled plastic bags, then frozen until mounting. Samples were prepared for mounting by boiling in acid, staining and dehydrating. Specimens were then embedded in epoxy resin, mounted on a glass slide and digital images taken. For an overview of the methods used to create the reference collection see Cameron (2002).

Dietary reference items included: Scots pine (*Pinus sylvestris*), Lodgepole pine (*Pinus contorta*), Larch (*Larix sp*.), Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziesii*) Blaeberry (*Vaccinium myrtillus*), Heather (*Calluna vulgaris* & *Erica cinerea*), Cowberry (*Vaccinium vitis-idaea*), Crowberry (*Empetrum nigrum*), Birch (*Betula* sp.), Rowan (*Sorbus aucuparia*), Sedges (*Carex* sp.), Cotton grass (*Eriophorum* sp.), Rushes (*Juncus* sp.) and Bracken (*Pteridum aquilinum*) (see Figure 5.1) (for all images see Appendix 8.2).



Scots pine needle epidermis *Vaccinium myrtillus* berry epidermis



Lodgepole pine needle epidermis *Carex* sp. seed epidermis

Figure 5. 1 Selection of digital images of capercaillie dietary reference collection. Notice the similarity between epidermal cells of Scots pine and Lodgepole pine

5.3.3 Dietary Analysis of Capercaillie Droppings

In order to quantify the proportions of food items in the droppings, a subsample was taken from each dropping of the 20 droppings collected monthly and placed in a gridded petri dish, and observed under a binocular microscope. At each of the 100 intersections on the grid, the nearest food fragment was identified. Frequencies of each food type were averaged for all droppings collected in a given month. This resulted in the percent frequency of occurrence for each food type per month. Methods closely followed those of Summers *et al.* (2004) to allow comparison of results.

Dietary items were identified using a combination of digital images from the dietary reference collection and drawings used to identify diet components in the Summers *et al.* (2004) study. Some items remained unidentified and due to the similarity in shape and arrangement of the stomata in Scots pine and Lodgepole pine, species of pine was not identified.

5.3.4 Comparison of Capercaillie Habitat

The study by Summers *et al.* (2004) used the presence of capercaillie droppings to infer information about capercaillie habitat use in Abernethy Forest in Scotland. Therefore, habitat variables collected in the present study and those collected by Summers *et al.* (2004) could be compared to investigate differences in capercaillie habitat choice between commercial forests and semi-natural pinewoods.

A total of nine habitat variables collected at Morangie Forest were directly comparable with those collected at Abernethy Forest by Summers *et al*. (2004). These included; diameter at breast height (DBH), tree height, tree density, nearest neighbour, heather % cover, blaeberry % cover, grass % cover, moss % cover and distance to nearest road/track. Methods pertaining to collection of habitat variables from Morangie Forest can be found in Chapter 4. Methods for habitat data collection at Abernethy Forest can be found in Summers *et al*. (2004).

To test for differences in forest characteristics between habitats used by capercaillie in Morangie Forest and those used by capercaillie in Abernethy Forest, a Mann-Whitney U test for non-parametric data was conducted. A 95% confidence level was chosen as a threshold for significance.

5.4 Results

5.4.1 Percentage Dietary Component of Capercaillie Droppings

From the broad-scale determination of diet, using all droppings counted in the period January 2003-December 2003, it can be seen that capercaillie predominantly feed on pine needles during winter and spring months (Figure 5.2). During summer months pine needles only comprise less than half of the diet of capercaillie. It also appears that capercaillie switch their diet abruptly from summer to winter months.

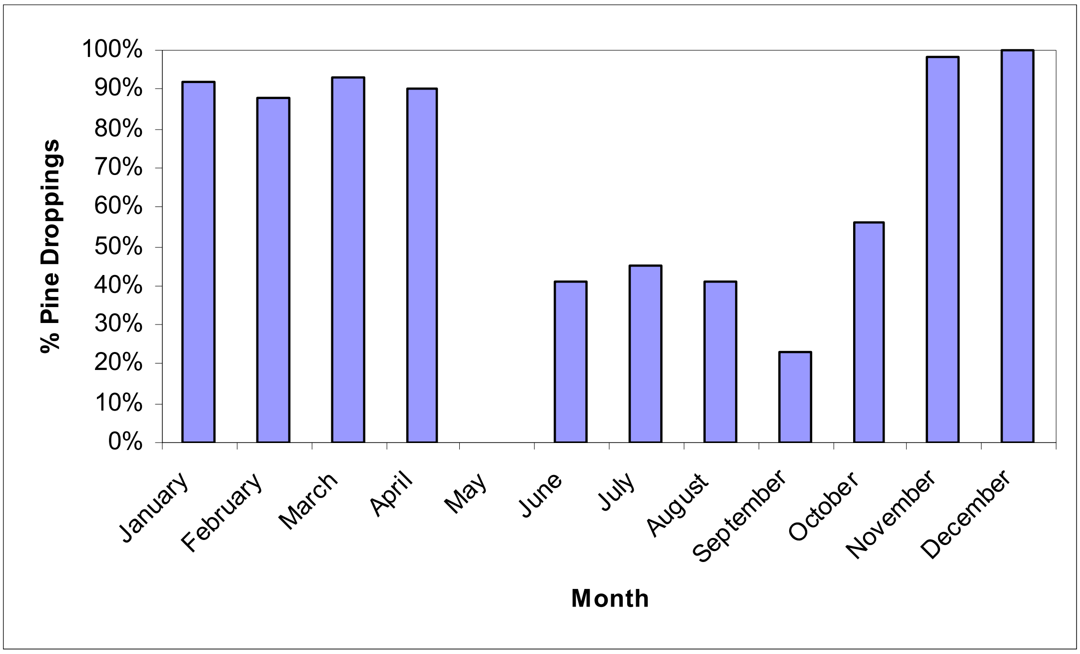


Figure 5. 2 Graph of percentage droppings comprising mostly pine each month between January 2003-December 2003. May 2003: missing data.

Results of the fine-scale analysis of capercaillie droppings monthly from January 2003 to December 2003 are shown in Table 5.1a and 5.1b. Within Table 5.1a, the percentage of droppings that contain each dietary item per month are displayed along with the average percentage of dietary item when present in droppings each month. Table 5.1b gives the 95% confidence intervals for the median % content of 20 samples per month, based on 10,000 bootstrap resamples following the method of Efron and Tibshrani (1986).

Table 5. 1a Percentage frequency of occurrence of dietary components of capercaillie droppings per month in Morangie Forest

	Percentage Frequency of Dietary Components															
	Pine Needles		Pine pollen cones		*V.myrtillus* leaves		*V.myrtillus* berries		*Calluna vulgaris* leaves		*Eriophorum* spp. flowers		*Carex* seeds		Unidentified vegetation	
Month	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present	% droppings containing	Average % where present
January	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
February	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	100	99.8	0	0	0	0	0	0	5	4	0	0	0	0	0	0
April	100	99.6	0	0	0	0	0	0	10	4	0	0	0	0	0	0
May	75	56.7	60	51.7	25	53.2	0	0	20	46.5	0	0	0	0	10	4
June	70	55	40	89.3	25	58	0	0	10	46	10	49	0	0	5	36
July	65	68.9	10	77	55	36	5	54	20	48	0	0	15	80	35	9.7
August	60	52	0	0	75	26.7	55	48.2	0	0	0	0	30	57.3	45	11.3
September	75	71.1	0	0	40	23.8	55	41.5	35	41.1	0	0	0	0	0	0
October	100	88.4	0	0	0	0	0	0	50	22	0	0	0	0	5	12
November	100	97.9	0	0	15	14	0	0	0	0	0	0	0	0	0	0
December	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.1b 95% intervals for the median % content of 20 samples per month, based on 10,000 bootstrap resamples following the method of Efron and Tibshrani (1986). With l=lower, middle value=median u=upper limits.

Month	l	Pine needles	u	L	Pine pollen cones	u	l	*Vaccinium myrtillus* leaves	u	l	*Vaccinium myrtillus* berries	u	l	*Calluna vulgaris* leaves	u	l	*Eriophorum* spp. flowers	u	l	*Carex* seeds	u	l	Unidentified vegetation	u
January	*	100.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*
February	*	100.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*
March	100.00	100.00	100.00	*	0.00	*	*	0.00	*	*	0.00	*	0.00	0.00	0.00	*	0.00	*	*	0.00	*	*	0.00	*
April	100.00	100.00	100.00	*	0.00	*	*	0.00	*	*	0.00	*	0.00	0.00	0.00	*	0.00	*	*	0.00	*	*	0.00	*
May	2.50	29.00	73.50	0.00	21.00	51.00	0.00	0.00	0.00	*	0.00	*	0.00	0.00	0.00	0.00	0.00	0.00	*	0.00	*	0.00	0.00	0.00
June	0.50	23.50	62.50	0.00	0.00	76.50	0.00	0.00	0.00	*	0.00	*	0.00	0.00	0.00	0.00	0.00	0.00	*	0.00	*	0.00	0.00	0.00
July	0.00	46.00	85.00	0.00	0.00	0.00	0.00	5.50	17.50	0.00	0.00	0.00	0.00	0.00	0.00	*	0.00	*	0.00	0.00	0.00	0.00	0.00	3.00
August	0.00	18.00	37.00	*	0.00	*	4.00	12.00	30.50	0.00	14.00	41.50	*	0.00	*	*	0.00	*	0.00	0.00	12.50	0.00	0.00	9.00
September	28.50	65.50	83.50	*	0.00	*	0.00	0.00	13.50	0.00	15.00	36.00	0.00	0.00	5.00	*	0.00	*	*	0.00	*	*	0.00	*
October	93.00	99.50	100.00	*	0.00	*	*	0.00	*	*	0.00	*	0.00	0.50	7.00	*	0.00	*	*	0.00	*	0.00	0.00	0.00
November	100.00	100.00	100.00	*	0.00	*	0.00	0.00	0.00	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*
December	*	100.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*	*	0.00	*

Table 5.1a shows that pine needles comprise the majority of the diet through winter months, with other dietary items becoming more prominent in summer months. During summer months the percentage of droppings that contain pine along with the percentage of pine within droppings falls. By October all droppings sampled contained pine needles, and by December the whole diet once again comprised 100% pine needles.

5.4.2 Comparison of Capercaillie Diet

In order to compare the capercaillie diet at Morangie Forest with that of Abernethy Forest (Summers *et al*. 2004), the average percentage of dietary items found in droppings each month was calculated. Figure 5.3 highlights the differences between the capercaillie diet at Morangie Forest and in Abernethy Forest. Capercaillie in Morangie Forest and Abernethy Forest have a similar diet. Morangie capercaillie have a higher percentage of pine in their diet throughout the year compared to Abernethy capercaillie. Morangie capercaillie also have fewer *Vaccinium myrtillus* berries in their diet during July and August compared to capercaillie in Abernethy Forest. Other dietary items in Morangie and Abernethy capercaillie droppings were found in similar percentages.

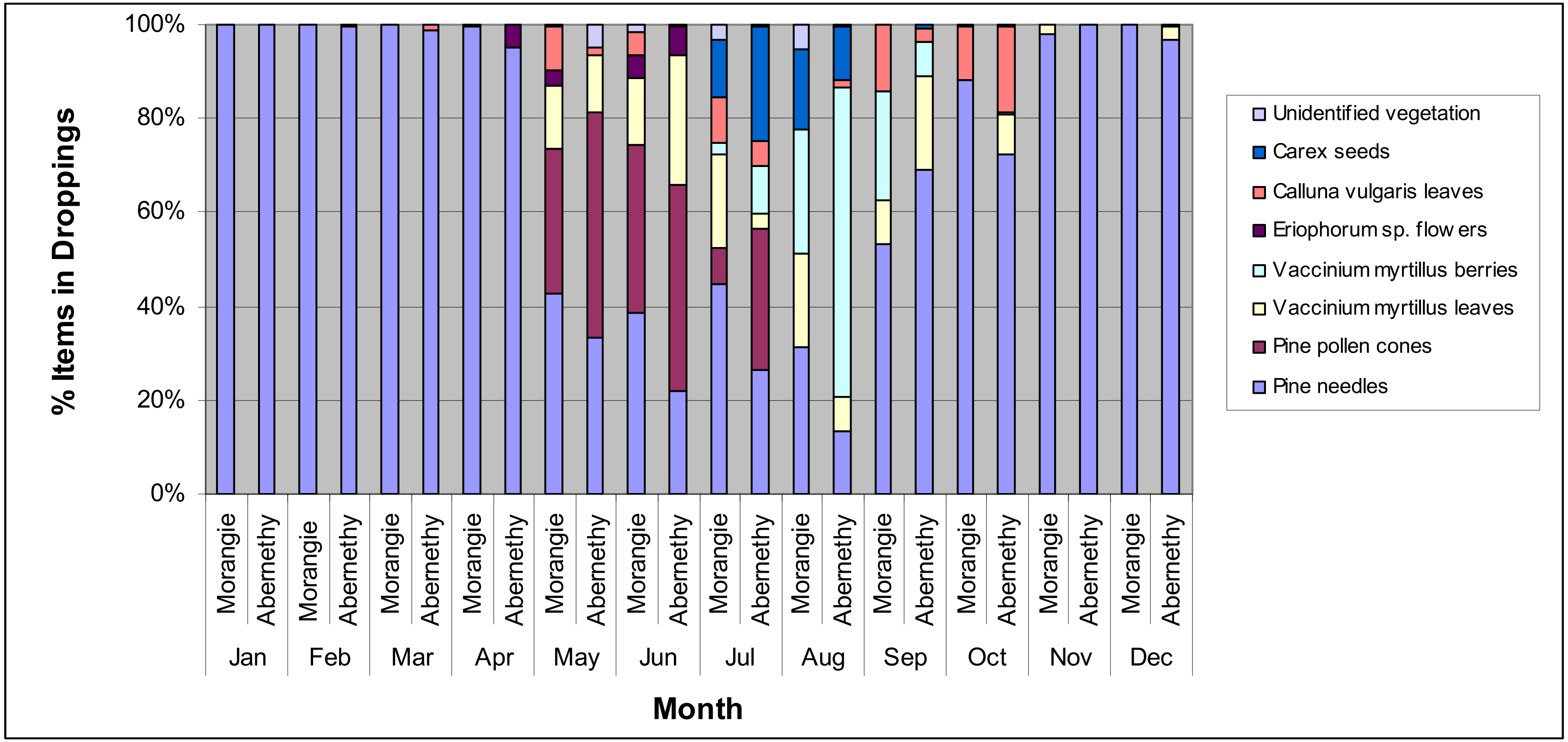


Figure 5.3 Difference between capercaillie diet at Morangie Forest and Abernethy Forest (Summers *et al*. 2004) using percentage of dietary items found in droppings each month

5.4.3 Comparison of Capercaillie Habitat

Table 5.2 highlights the differences between habitat used by capercaillie in Morangie Forest and Abernethy Forest. All habitat variables except distance to track and heather percentage cover are significantly different. Capercaillie in Morangie Forest are selecting significantly thinner higher trees, more closely spaced, with a higher percentage moss and grass cover and a lower percentage blaeberry cover than capercaillie in Abernethy Forest.

Table 5.2. Differences in habitat used by capercaillie in Morangie Forest and Abernethy Forest using a Mann-Whitney U Test

	Morangie		**Abernethy**		
Habitat Variable	**Median**	**Interquartile**	**Median**	**Interquartile**	**p-value**
Dbh	30	26 - 34.3	47.0	28.0 - 61.4	<0.001
Nearest neighbour	3.2	2.7 - 3.7	4.00	2.4 - 6.8	0.0132
Heather % Cover	18.8	6.3 - 50	30	20 - 75	0.0693
Blaeberry % Cover	0	0 - 18.8	40	20 - 55	<0.001
Grass % Cover	0	0 - 18.8	0	0 - 1.25	<0.001
Moss % Cover	34.4	12.5 - 68.8	10	3.8 - 10	<0.001
Height	15.5	13.8 - 17.5	13.4	4 - 14.7	<0.001
Distance to track	225	131.8 - 328.3	250	150 - 400	0.2951
Density	200	110-430	650	450-900	<0.001

5.5 Discussion

5.5.1 Diet of Capercaillie from Faecal Analysis

Results of capercaillie diet determination using droppings, generally agree with those found in previous diet studies on capercaillie (Zwickel 1966, Jones 1982, Picozzi *et al.* 1996). Results of both the broad and fine scale studies, shows that from November through to April, capercaillie in Morangie Forest have a diet that almost entirely consists of pine needles. From dietary analysis of 99 capercaillie crops from October through to December, Zwickel (1966) found 90% of material in crops was Scots pine. Jones (1982) found over 90% Scots pine in crops of capercaillie killed during winter months.

Capercaillie in Morangie Forest begin to exploit pine pollen cones during May and June. Scozzafava (2002) during a preliminary study at Morangie Forest also noted the presence of these pollen rich droppings during this time. Typically droppings took on a yellowish appearance and were easily recognisable as containing pollen. Clocker droppings (enlarged faecal droppings that results from infrequent defecation by an incubating hen) observed during the present study, were also found to entirely comprise of pine pollen (pers. obs.)

During July and August in Morangie Forest, a percentage of the capercaillies diet comprises of *Carex* sp seeds and *Vaccinium myrtillus* leaves. Picozzi et al. (1996) also found that capercaillie change to a diet of sedges and rushes that equals half the capercaillies diet during summer months.

During August, the percentage pine needles found in the capercaillies diet at Morangie Forest had fallen to an average of around 30% (Figure 5.3) although 60% of droppings still contained pine needles (Table 5.1a). Similar percentages were reported by Picozzi *et al*. (1996) for Sitka spruce. Also during August, an average of 27% (Figure 5.3) of the capercaillie diet at Morangie Forest comprised of *Vaccinium myrtillus* although over half the droppings analysed contained *Vaccinium myrtillus* berries (Table 5.1a). This is lower than most published values. Storch *et al*. (1991) studying diet of capercaillie in the Alps found that capercaillie droppings comprised 36% *Vaccinium myrtillus* berries in August. Rodriguez & Obeso (2000) studying diet of Cantabrian capercaillie found that during summer months droppings comprised 57% Vaccinium myrtillus. However, in accordance with the present study Picozzi *et al*. (1996) documented only small amounts of *Vaccinium myrtillus* being eaten by capercaillie during summer months in a Sitka spruce plantation. Jones (1982) also reported that capercaillie were present in Culbin Forest, Scotland even though *Vaccinium myrtillus* was rare, and that food supplied by commoner dwarf shrubs may have been important.

During September, the percentage pine in the capercaillies diet at Morangie Forest begins to rise again to over 50% (Figure 5.3) with 75% of droppings containing pine

(Table 5.1a). From September, the percentage pine in the capercaillie diet at Morangie Forest and the number of droppings containing pine increases reaching 100% by December (Figure 5.3, Table 5.1a).

5.5.2 Comparison of Capercaillie Diet

Capercaillie in Morangie Forest appear to have a similar diet in general to those in Abernethy Forest. The majority of capercaillie droppings in winter months at Morangie Forest comprised of pine needles (Figure 5.3). Summers *et al*. (2004) also found that capercaillie diet in Abernethy Forest was almost entirely based on Scots pine during November through to April (Figure 5.3). Therefore it appears that in both commercial plantations and semi-natural pinewoods pine needles comprise almost if not all of the diet of capercaillie during winter months. Capercaillie in Morangie Forest had higher levels of pine in their diets throughout the year than those at Abernethy Forest (Figure 5.3), suggesting that the reliance on pine year round of capercaillie at Morangie Forest is greater than that of capercaillie at Abernethy Forest.

Other capercaillie dietary items appear to be exploited in similar amounts in the diet of capercaillie at Morangie Forest and Abernethy Forest with the exception of *Vaccinium myrtillus* berries (Figure 5.3). During August, capercaillie at Abernethy Forest appear to be utilising higher amounts *Vaccinium myrtillus* berries in their diet than capercaillie in Morangie Forest (Figure 5.3). Reasons for this could be because Morangie Forest contained less *Vaccinium myrtillus* than in Abernethy Forest. Habitat data collected in study plots in Morangie Forest resulted in an average *Vaccinium myrtillus* cover of 15% whereas Summers *et al*. (2004) estimated average cover of *Vaccinium myrtillus* at 24%. Differences between blaeberry cover in Morangie Forest and Abernethy Forest were statistically significant (Mann-Whitney U Test, $p<0.001$) (Section 5.4.4).

There appears to be a sharper switch between a diet of pine and *Vaccinium myrtillus* during May in capercaillie from Abernethy Forest compared to capercaillie from Morangie Forest (Figure 5.3). This sharp switch is observed again during September when the diet of capercaillie at Abernethy Forest reverts back to predominantly pine based (Figure 5.3).

5.5.3 Comparison of Capercaillie Habitat

Results of a comparison of habitat use between capercaillie in Morangie Forest and Abernethy Forest found that capercaillie habitat use varied significantly between forests (Table 5.2). This is most likely a reflection of the habitat available within both forests. Capercaillie in Morangie Forest used areas of forest which had thinner higher trees, more closely spaced, with a higher percentage moss and grass cover and a lower percentage blaeberry cover than capercaillie in Abernethy Forest (Table 5.2). These habitat variables are all characteristic of plantation forests. One of the main differences between ancient native pinewoods and plantations is the age, and hence size, of the trees (Summers *et al*. 1999). In addition, the differing tree densities in semi-natural pinewoods and plantation forests result in different ground floras. The commonest plant of the field layer of semi-natural pinewoods is heather (Summers *et al*. 1999). Interestingly, percentage heather cover was one of the variables that was not significantly different in areas used by capercaillie within Abernethy Forest and Morangie Forest (Table 5.2).

Capercaillie are using areas in Morangie Forest with significantly less blaeberry than they are in Abernethy Forest (Table 5.2). Again this is a reflection of the amount of blaeberry available to capercaillie within Morangie Forest (15% cover) compared to Abernethy Forest (24% cover). However, results of the dietary analysis of droppings suggest that although there is less blaeberry available within Morangie Forest compared to Abernethy Forest, capercaillie in Morangie Forest are more actively selecting for it in their diet. This highlights the importance of encouraging blaeberry development within plantation forests.

The distance of capercaillie habitat from roads was not found to be statistically different between Abernethy Forest or Morangie Forest (Table 5.2). Capercaillie in both forests preferred areas of woodland 225-250m away from forest tracks or roads. Distance to roads was found to be an important predictor of capercaillie presence at both Abernethy Forest (Summers *et al*. 2004) and Morangie Forest (Chapter 4). Summers *et al*. (2007) hypothesised that human activity is a likely explanation for the avoidance of forest tracks concluding that it seems unlikely that there are other confounding effects that could account for track or road avoidance. However, the number of visitors to Morangie Forest is much lower than Abernethy Forest (pers. obs.) and it is possible that tracks and roads are creating barriers, effectively fragmenting the forest (Haila 1999) and increasing predation risk (Storch 1990) resulting in capercaillie avoidance of habitat close to tracks.

Results of the comparison of habitat use between capercaillie in Morangie Forest and Abernethy Forest suggest that commercial forests, although significantly different in structure from semi-natural pinewoods, can provide suitable habitat for capercaillie, albeit at lower densities.

5.5.4 Suggested Improvements to the Present Study

There are a number of issues concerning faecal dietary analysis including differing digestibility rates of dietary items and variation of particle size. Determining the diet is often essential to understanding an animal's habitat requirements. However making assumptions about a species habitat use from dietary analysis can be misleading due to dietary content of faeces representing less digested food fragments rather than a true representation of a species diet. Therefore it is important to know the digestibility of individual dietary items in order to correct for differential digestibility. An improvement to the present study could have been made by calculating digestibility of dietary items. This is also relevant in Chapter 3 where correction for differing digestibility could have allowed estimates of capercaillie population size to be made during summer months.

Using the same dietary determination method as Summers *et al.* (2004) was purposely done to allow comparison. However, this method involves selecting the nearest food fragment to intersections on a gridded petri dish and as a result is biased toward larger particle sizes. Therefore future studies could reduce this bias by using the grid only as a guide to counting over the whole petri dish.

Collecting habitat data from where dietary analysis droppings were located would have allowed investigation of the relationship between dietary content of droppings and the habitat in which they were found. Therefore a further improvement to the present study could be made by collecting detailed habitat data from locations of capercaillie droppings used in the dietary analysis. In addition, ascertaining the sex of dietary analysed droppings could allow indirect investigation of diet and habitat choice between capercaillie sexes. Sexing droppings according to size was shown to be inaccurate (pers. obs.). However, advances in genetic techniques now allow sex discrimination of droppings and would provide a more robust method for assigning sex to droppings.

Finally, the differences between the diet of capercaillie in Abernethy Forest and the diet of capercaillie in Morangie Forest could not be formally analysed due to incomplete raw data from Summers *et al.* (2004). Formal analysis would be conducted if raw data became available.

5.6 Conclusions

This is the first study in Scotland to investigate the annual diet of capercaillie in a commercial plantation. It is also the first study to directly compare habitat and diet of capercaillie within a commercial plantation with that in a semi-natural pinewood. Results suggest, in conjunction with previous studies in plantations, that capercaillie are eating more pine than those reported in semi-natural pinewoods. However, capercaillie appear to be selecting for *Vaccinium myrtillus* within Morangie Forest more than Abernethy Forest, strengthening evidence that blaeberry is a key food for capercaillie. Therefore forest managers should encourage *Vaccinium myrtillus* where possible.

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Chapter 6. Inferring Population Size, Connectivity and Dispersal of Capercaillie at Morangie Forest: Inference from Microsatellite DNA Polymorphisms

Abstract

Capercaillie feathers collected during fieldwork at Morangie Forest were genetically analysed to investigate population structure of capercaillie within Morangie Forest. Mark-recapture methods were used to calculate population size. Results from the present chapter show that the Morangie capercaillie population is genetically diverse with low levels of interrelatedness. There appears to be greater movement of individuals around Morangie Forest than previously thought, in addition to this, males and females behave differently in terms of movement and site fidelity. The capercaillie population size derived from mark-recapture data is estimated at 69 individuals. This is a similar estimate to the one derived in Chapter 3 using dropping counts. Results also show that the capercaillie population is not bounded within the forest and mixing with neighbouring populations is taking place. At present Morangie Forest, a Forestry Commission owned woodland and Novar Forest, part of a privately owned estate are managed as separate entities. Future management should strive to co-ordinate management between these forests and aim to establish further woodland as corridors between forests.

Chapter 6. Inferring Population Size, Connectivity and Dispersal of Capercaillie at Morangie Forest: Inference from Microsatellite DNA Polymorphisms

6.1 Introduction

In order to manage capercaillie populations effectively, it is important to understand the main ecological parameters defining the underlying structure of the population; primarily the size of the population, its level of isolation from neighbouring areas and the extent of movement of individuals within the population.

In the past, methods used to investigate capercaillie population structure employed the use of radio-tracking and banding, and counting using pointing dogs (Eliassen & Wegge 2007, Moss & Oswald 1985, Moss *et al.* 2000, Rolstad *et al.* 1988, Storch 1993). These methods were highly labour intensive, provided limited data sets, and caused a high level of disturbance to the birds, which is particularly problematic when dealing with endangered species (Storch & Segelbacher 2000). In addition, population estimates using lek, brood and dropping counts from the present study all yielded different estimates and therefore a more robust way of measuring the population would be useful for future management.

Advances in molecular biology now allow investigation of genetic population structure through analysis of DNA from feathers and faeces (Mäki-Petäys *et al*. 2007, Segelbacher *et al*. 2003, Storch & Segelbacher 2000). For a review of non-invasive genetic sampling and how this has been used in ecological studies, see Taberlet *et al*.1999.

Using microsatellite and mitochondrial DNA collected from feathers and faeces, and time since fragmentation and habitat loss as measures of fragmentation, Mäki-Petäys *et al*. (2007) examined the effects of forest fragmentation on the diversity and population structure of capercaillie in Finland. Results showed that the Finnish capercaillie population displays high levels of genetic diversity and weak genetic differentiation between sub-populations and that recent habitat fragmentation may not have been severe and sufficiently long-lasting to lead to changes in the genetic composition of the capercaillie. Examination of capercaillie metapopulations in the Alps using microsatellite DNA from feathers confirmed the previously hypothesised metapopulation structure and concluded that metapopulation connectivity is a key issue for capercaillie conservation (Segelbacher & Storch 2002). A further study investigating genetic differentiation of capercaillie populations across Europe, using microsatellite DNA from feathers, found evidence of reduced genetic diversity in isolated populations compared with the Alps and boreal forest. (Segelbacher *et al*. 2003).

Non-invasive genetic sampling can be used to evaluate issues important to species conservation and to determine management options for a species or for local populations. By examining the genetic structure of a species it is possible to clarify their conservation status including the effective population size, the geographic origin and the genetic vulnerability (genetic diversity, inbreeding and inbreeding depression) of the populations and/or species. The information obtained from genetic structure could also be used to dissect the recent historical changes underlying the present population structure, and to understand the species biology, for example of dispersal and breeding behaviour of the species (Mäki-Petäys *et al.*1997).

In 2001, the Scottish capercaillie population was estimated at 1000 individuals (Moss 2001). These were considered to be distributed into six separate metapopulations that were becoming increasingly isolated (Kenny Kortland pers. comm.). Whether such population structure was actually realised was examined by Piertney *et al.* (in press). The level of population isolation among the populations was inferred from the spatial distribution of microsatellite and mitochondrial DNA diversity. Microsatellite DNA analysis highlighted that the six putative populations were indeed genetically dissimilar, and therefore need to be treated as demographically independent units (Figure 6.1). In fact, results showed that the Deeside/Donside population (metapopulation 4) could be split into two according to the separate catchments and the Black Isle population (metapopulation 1) could be split into separate Morangie and Novar populations. Levels of genetic diversity in the Scottish capercaillie population were lower than populations of equivalent size and isolation within Europe (e.g. the

Black Forest), but higher than would be expected for a population that has been characterised by a series of demographically small reintroductions (Piertney *et al*, in press). Mitochondrial DNA analysis confirms the patterns resolved from microsatellite markers, except that there was evidence for dispersal between Moray and Cairngorm populations (metapopulation 2 & 3) (Piertney *et al*, in press). Discrepancy between the two types of markers is probably a consequence of sex-biased dispersal, with female mediated gene flow homogenising mitochondrial haplotype frequencies among populations, but lower levels of male mediated gene flow preventing a concomitant homogenisation of microsatellite allele frequencies (Piertney *et al*, in press).

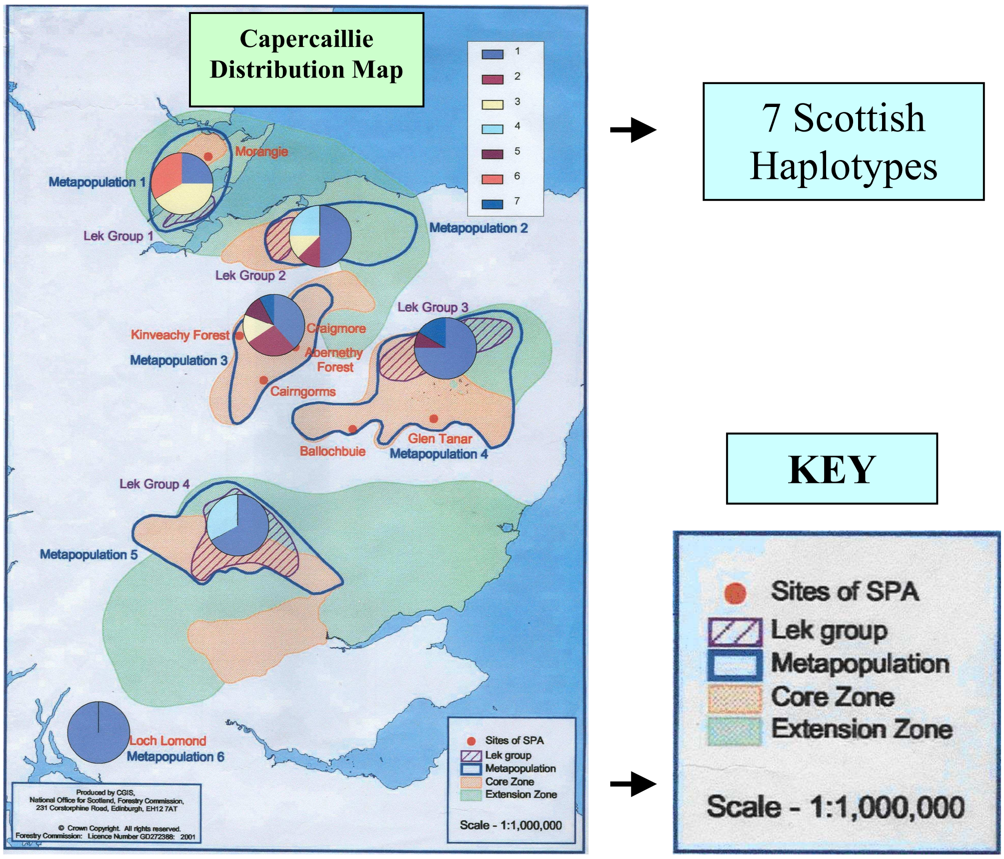

Figure 6. 1. Capercaillie Distribution Map for Scotland showing the geographical location and relative frequency of the 7 Scottish haplotypes ascertained from the broad-scale Scottish Survey

The broad-scale genetic survey showed that Morangie and Novar were genetically isolated populations with comparable levels of genetic diversity to the rest of the Scottish population (Piertney *et al*, in press). However, due to small feather sample sizes, limited information about within-population dynamics at Morangie Forest, including movement and mixing of capercaillie could be determined. More thorough genetic analysis of the Morangie population would facilitate direct estimation of population size and individual movement between Morangie and neighbouring populations.

Here I utilise a large data set of feathers collected in Morangie Forest from 2001-2003, to genotype the population at multiple microsatellite loci. The overall rationale is to identify individuals from multi-locus genotypes, and use the number of overall genotypes as a proxy for census of population size and composite genotypes as an individual marker. Statistical assignment approaches were also used to identify putative dispersers present within the population; these are individuals that have a composite genotype removed from those commonly observed within the population it was sampled. This allowed an opportunity to look in-depth within a metapopulation at a level that had not previously been studied. In addition to this, results were compared with the population level genetic survey results within Novar (part of metapopulation 1) and Moray (metapopulation 2), to explore whether a direct and indirect approach to inferring dispersal are equivalent and give the detail required to make management prescriptions for capercaillie metapopulations in Scotland.

Because the feathers collected were individually genotyped it allowed individual birds to be tracked over the study period. In essence, feathers found were "marked" as a certain individual by their genetic code, and then further feathers from that individual "recaptured" at later dates. Mark-recapture studies represent a powerful tool for conservation managers, and can be used in any situation where animals can be marked (or otherwise identified) and detected later by capture or sighting (Krebs 1998, Lettink & Armstrong 2003). The mark-recapture method is a powerful method for estimating abundance as long as the underlying assumptions are met (Thompson *et al*. 1998).

It was decided therefore, to use a mark-recapture approach (using feather DNA data) to estimate the capercaillie population. A preliminary study investigating the use of genetic mark-recapture as a viable alternative to traditional mark-recapture methods for birds has shown that it is an accurate method, with the advantage of being non-invasive (Bayard de Volo *et al*. 2005). In addition moulted feathers were found to be as reliable a source of DNA as blood (Bayard de Volo unpubl. data).

There are various methods for calculating population size using mark-recapture, depending on the type of population being investigated. In this study the Jolly-Seber method for open populations was used (Seber 1982). This method unlike Peterson (Peterson 1896) and Schnabel (Schnabel 1938) permits for birth, death, immigration and emigration. This method is particularly applicable as it accommodates data extending over many years (Larsen 1998).

6.2 Aims and Objectives

The main aim of this chapter is to genetically identify individuals in the capercaillie population using DNA extracted from feathers at Morangie Forest and use the results to estimate population size. A further aim is to establish the current genetic status of the capercaillie population in terms of genetic diversity and relatedness. In addition, a further objective is to investigate how capercaillie are moving within Morangie Forest and whether they are mixing with neighbouring populations.

To meet these aims four specific questions were addressed:

- What is the current genetic status of the capercaillie population in Morangie Forest?
- What is the population size of capercaillie at Morangie Forest and how does it compare to estimates using other methods?
- Are capercaillie moving and mixing genetically within Morangie Forest and is there a difference in movement between sexes?
- Are capercaillie in Morangie Forest moving and mixing genetically with neighbouring capercaillie populations?

6.3 Materials and Methods

6.3.1 Sampling

Between 2001 and 2003, 253 capercaillie feathers found while travelling between study faecal count plots within Morangie Forest were collected and put in plastic bags and frozen until analysis (4-32 months). Location of feather and date collected were recorded on the bag and in an Excel spreadsheet, where additional information was also noted. The majority of feathers were collected during the capercaillie breeding season and were therefore from adult and juvenile birds. The same route between plots was followed each month and feathers observed on this route were collected whenever seen. It is felt that the faecal count plots were distributed throughout the study area and therefore the route followed between plots was representative of the whole study area. Feathers collected were of varying quality.

6.3.2 Microsatellite Genotyping

From the 253 feathers collected, 141 yielded enough high quality DNA for routine genotyping. All 141 viable DNA extracts were genotyped at seven microsatellite DNA loci (TUT2-4, BG4-5, BG15 and BG18; Segelbacher *et al.* 2000, Piertney & Höglund 2001). PCR amplifications were performed in a total volume of 10µl using a MJ Research PTC-100 thermal cycler. Each reaction mix contained 3µl of DNA extraction (equates to approximately 10ng template DNA), 2.5mM $MgCl_2$, 75mM Tris-HCL (pH

9.0), 20mM $(NH_4)_2SO_4$, 0.01% (v/v) Tween-20, 0.2 mM of each nucleotide, 5 pmoles of each primer and 0.5 units of *Taq* polymerase. PCR profiles comprised 35 cycles of 45 second denaturation at 94°C, 45 second annealing at 53°C (for BG loci) or 60°C (for TUT loci), then 45 second extension at 72°C. Forward primers were labelled at the 5' end with a fluorescent tag (either 6-FAM, HEX or NED; Applera Ltd). PCR fragments were run on an automated ABI 3730 capillary DNA sequencer (according to the manufacturer's instructions) and alleles scored by comparison with a GS400 size standard, run concurrently within Genemarker software (Softgenetics Ltd).

6.3.3 Data Analysis

Field data including feather number, location and date collected were combined with the results of the DNA analysis. This resulted in spreadsheet that allowed each feather sample to be identified to which individual bird it had come from and the sex of that bird.

6.3.3.1 Current Genetic Status

An important measure in population genetics is the degree to which genotypes conform to expectations based upon the Hardy-Weinberg equilibrium (Hardy 1908, Weinberg 1963). This measure is the relationship between the frequencies of alleles and the genotype of a population. Under random mating, an expected frequency of different genotypes is expected for a given allele frequency. Deviations from Hardy-Weinberg through an excess of heterozygotes indicates sex-biased dispersal, overdominant selection or the occurrence of outbreeding. Conversely, a deviation from Hardy-Weinberg through an excess of homozygotes indicates inbreeding, isolated populations or the presence of cryptic population sub-structure which may lead to the Wahlund Effect (Wahlund 1928). The Wahlund effect refers to reduction of heterozygosity in a population, caused by subpopulation structure. Namely, if two or more sub-populations have different allele frequencies then the overall heterozygosity is reduced, even if the sub-populations themselves are in Hardy-Weinberg equilibrium. The underlying causes of this population subdivision could be geographical barriers to gene flow followed by genetic drift in the sub-populations. It is important to ascertain the level of deviation from Hardy-Weinberg in the Morangie capercaillie population as this will have consequences for the management of the population. Genotype frequencies were tested against Hardy-Weinberg expectations using F-STAT software (Goudet, 2001). Levels of Genetic Diversity were also calculated using F-STAT.

Average relatedness for the capercaillie population was calculated using the program Kinship (Queller & Goodnight 1989, Goodnight & Queller 1999). Relatedness was estimated for males and females separately and the relatedness of individuals within Morangie was compared to that expected under random mating across the entire Scottish capercaillie population.

6.3.3.2 Population Size Estimate

In order to make inferences from the individual microsatellite genotype results, it is important to establish the probability of identity; that is the probability that two individuals will share the same composite genotype (7 loci). Probability of Identity was determined using Microsatellite Tool Kit (Park 2001), an add-in utility for Microsoft Excel.

The Jolly-Seber method of mark-recapture was used to calculate population size of capercaillie in Morangie Forest. The method makes certain assumptions that must be met by the data collected. In particular, the assumptions that capture probability is similar for individuals of a given type and that capture sessions are effectively instantaneous in comparison with the interval between sessions (Lettink & Armstrong 2003). This means that each survey must cover the entire study area and that effort should be consistent over this area. The duration of each survey should be <10% of the interval length between surveys (Lebreton *et al*. 1992).

In this instance, ‘captures’ or ‘capture sessions’ refer to when feathers (subsequently genotyped) were collected. Feathers were collected along a route that is thought to be representative of the study area. In addition all capercaillie moult during summer months and therefore the probability of collecting a feather from any given individual capercaillie within the study area is the same. Every capercaillie that had been genotyped from their feathers was assumed to have the same probability of surviving.

Surveys intervals were yearly with the majority of surveys taking place from July-September each year. The duration of the surveys was less than 7% of the interval length.

Using the formulae below, along with the numbers of individuals genotyped each year, the Morangie capercaillie population size was estimated.

Formulae:

$$\hat{\alpha}_t = \frac{m_t + 1}{n_t + 1} \qquad \hat{M}_t = \frac{(s_t + 1)Z_t}{R_t + 1} + m_t \qquad \hat{N}_t = \frac{\hat{M}_t}{\hat{\alpha}_t}$$

Where:

m_t = Number of individuals identified from genotyped feathers found in sample t

u_t = Number of individuals found that had not been previously identified from genotyped feathers in sample t

n_t = Total number of individuals identified from genotyped feathers found in sample $t = m_t + u_t$

s_t = Total number of individuals released after sample t (in this case individuals are not actually captured and released so $s_t = n_t$ as all individuals are assumed to still be alive immediately after shedding a genotyped feather)

R_t = Number of the s_t individuals identified from genotyped feathers at sample t and genotyped again in some later feather sample

Z_t = Number of individuals indentified from genotyped feathers before sample ***t***, not genotyped in sample ***t***, but genotyped in some sample after sample ***t***

Nt = is an estimate of the capercaillie population size at time ***t***

6.3.3.3 Movement and Spacing of Capercaillie

The sex of individuals was ascertained using the molecular sexing approach described in Fridolfsson & Ellegren (1999). For each individual a PCR was undertaken as described in section 6.3.2 except that the primers used replaced with the 2550F/2718R (Fridolfsson & Ellegren 1999) and the annealing temperature was reduced to 50°C. PCR products were run out on a 2% agarose gel, stained with Ethidium bromise and examined under UV light. Females are characterised by a two-banded pattern, whilst males have only a single band. Both positive and negative control PCRs (containing known male and female DNA, and replacing DNA with water, respectively) were run concurrently.

In order to look at the time and movement between samples and sexes, data was manipulated in Excel and then imported into ArcView 3.2. This allowed the distance between individual samples to be calculated.

Habitat data at the compartment level from the Forestry Commission database was compared between sexes to investigate spacing due to differing habitat requirements of the sexes.

6.3.3.4 Movement and Mixing

A Principal Co-ordinate Analysis (PCoordA) (Gower 1966) was conducted on the genetic distances among individuals (measured as Nei's *D*; Goudet 2001) in order to explore the mixing of capercaillie within Morangie and between sub-populations of Morangie, Novar and Moray. PCoordA translates individual genotype data into genetic distances that can be plotted in two-dimensional space, with Euclidean distance between points (individuals) proportional to their genetic similarity. Population genetic structure will theoretically be characterised by groups of points (representing a population of individuals) occupying different regions on a 2D scatterplot. PCoordA was conducted in GenAlEx (GENetic AnaLysis in EXcel) 6 (Peakall & Smouse 2006).

The most-likely number of genetically distinct units represented by the overall sample was estimated using the program Structure 2.1 (Prichard *et al*. 2000). Structure uses a Bayesian approach to infer the optimum number of genetic clusters *K*, without prior assumptions about geographic sampling or population membership. The analysis was undertaken with a prior parameter that the number of clusters was between 1 and 20. The program was run under both an admixture and no admixture model, with a burn-in period of 10,000 iterations with analysis based on the subsequent 100,000 iterations for each. The analyses was repeated ten times, to confirm the consistency of In-likelihood scores. The In-likelihood scores were used to calculate the posterior probability for each value of *K*, and the value with the highest posterior probability was chosen.

Assignment tests were also conducted to see whether any of the individuals sampled in the Morangie population have a genetic signature dissimilar to the rest of the population and hence may represent dispersers. Assignment tests were undertaken using the program GenAlEx (Peakall & Smouse 2006).

6.4 Results

6.4.1 Current Genetic Status

Overall allelic richness (number of alleles controlled for number of samples) was 5.2 averaged across the 7 loci (95% CI: 5.1, 8.9). Observed heterozygosity was 0.66 (95% CI: 0.48, 0.84). This level of diversity is such that the data can be used to identify individuals from feather samples and estimate genetic distance among individuals with a high level of accuracy.

Overall, there is a slight deviation from Hardy-Weinberg caused by a deficit of heterozygote genotypes. The test is significant at the 0.04 level, which is not significant after sequential Bonferroni correction for multiple probability tests. As such Hardy-Weinberg equilibrium can be assumed for this population.

Average relatedness for capercaillie males in Morangie Forest is 0.044 (95% CI: 0.013, 0.075) and for females is -0.039 (95% CI: -0.086, 0.008) Male relatedness is slightly higher (though not significantly so) than female relatedness. This reflects philopatric males and dispersing females.

6.4.2 Capercaillie Population Estimate

Given the inherent levels of genetic diversity (see 6.4.1) within the Morangie samples, the probability that two individuals will share the same composite genotype over 7 loci is extremely small. The software GenAlEx (Peakall & Smouse 2006) estimated the probability of identity among individuals at $4.53\text{x}10^{-6}$. This allows great confidence that two feathers with the same genotype came from the same bird. Even allowing for unrealistically high numbers of (first-order) related individuals within the population, the probability that two related individuals share the same composite genotype is low. Probability of identity in a population of individuals containing 50% first order relatives (simulated from genotypes of individuals given the population allele frequencies and then added to the overall population) is 0.0047.

From the 141 feathers successfully genotyped, 55 individuals were identified. From Table 6.1 it can be seen that similar numbers of individuals were identified each year from the genetic analysis of feathers. However, it can also be seen that the number of new individuals identified each year falls to eight in 2003. This is due to the majority of individuals in the population having already been genotyped rather than a lack of feather samples in 2003.

The minimum number of sampling periods to allow estimation of the population size with the Jolly-Seber method is three. The feather data collected from Morangie Forest spans three years and therefore the population size could only be estimated in 2002.

The formulae values in Table 6.2 were entered into the Jolly-Seber equation (see section 6.3.3.2 for equation) and the capercaillie population size for Morangie Forest in 2002 was estimated at 69 (95% CI: 40, 101) individuals.

Table 6.1. Table to show the number of individual birds genotyped from their feathers over a 3 year study period

	Year			
	2001	2002	2003	Total
No of individuals genotyped each year	24	36	26	86
No of new individuals genotyped each year	24	23	8	55
No of feathers from the same individual genotyped more than once in the same year	14	24	17	55
Total number of feathers genotyped each year	38	60	43	141

Table 6. 2. Table to show formulae values for the three year study period used in the Jolly-Seber equation to calculate population size (see 6.3.3.2 for equation)

Formulae Values	2001	2002	2003
Number of individuals identified from genotyped feathers found in sample t, m_t	na	13	18
Number of individuals found that had not been previously identified from genotyped feathers in sample t, u_t	24	23	8
Total number of individuals identified from genotyped feathers found in sample $t = m_t + u_t$, n_t	24	36	26
Total number of individuals released after sample t, s_t *	24	36	26
Number of the s_t individuals identified from genotyped feathers at sample t and genotyped again in some later feather sample, R_t	18	13	na
Number of individuals indentified from genotyped feathers before sample t, not genotyped in sample t, but genotyped in some sample after sample t, Z_t	na	5	na

* In this case individuals are not actually captured and released so $s_t = n_t$ as all individuals are assumed to still be alive immediately after shedding a genotyped feather

The Morangie Forest capercaillie population size estimate using microsatellite genotyping data is shown below, along with previous estimates of counts for capercaillie in Morangie Forest, listed in Chapter 3 (Table 6.3). Estimates of capercaillie numbers from monthly dropping counts, genetically analysed feathers collected monthly and brood counts conducted during July and August, sample adult and juvenile birds. Estimates from lek counts conducted in April only sample adult birds. The resulting capercaillie population estimates from the microsatellite genotyping data support the estimates found from the dropping counts. Estimates from dropping counts and genetic analysis are much larger than those from brood and lek counts.

Table 6. 3. Estimation of population size of capercaillie at Morangie Forest, using various methods.

Year	Estimate from dropping counts	Estimate from lek counts (assuming 1:1 sex ratio)	Estimate from brood counts (male, female & juveniles)	Estimate from genetic analysis
2002	63 (53, 79)	30	42	69 (95%CI:40,101)
2003	39 (33, 49)	30	39	na
2004	17 (14, 21)	42	32	na

6.4.3 Movement and Spacing of Capercaillie

From the results in Table 6.4, it can be seen that feathers from 15% of genotyped individuals were found in 2001, 2002 and 2003. 9% of feathers were found from genotyped individuals in 2001, and not again until 2003, and 9% were only found in 2001 and 2002. 15% of genotyped birds only had feathers found in 2003 and 33% only had feathers found in 2002.

Table 6. 4. Total number of individual genotyped birds whose feathers have been present or absent over the 3 year study period including breakdown of sexes

Year	2001	2002	2003		Total	% All	% Male	% Female
Presence of Individual	1	1	1		7	14.55	14.29	85.71
	1	0	1		5	9.09	100.00	0.00
	1	1	0		5	9.09	60.00	40.00
	0	1	1		6	10.91	16.67	83.33
	0	0	1		8	14.55	37.50	62.5
	1	0	0		7	12.73	42.86	57.14
	0	1	0		17	30.91	70.59	29.41
				Total	55	100.00		

It is interesting to note that 86% of individuals who had feathers found in 2001, 2002 and 2003 were female. In addition to this, 100% of individuals who had feathers found in 2001 and 2003, but not 2002 were male and 72% of individuals who had feathers found in 2002 only were male.

Table 6.5 shows the time elapsed between collection of feathers from individual birds. It can be seen that the average number of days between collection of feathers is greater in males (although not significantly so) than females.

Table 6. 5 Average number of days elapsed between collection of feathers from each individual over the 3 year sample period and average distance (km) between locations of feathers from the same individual during the 3 year study period.

	Average number of days between collection of feathers from individual birds	**Average distance (km) between collection locations of feathers from individual birds**	**Average distance (m) per unit time (days) between feathers collected from individual birds**
All	**174** (95% CI: 128, 220)	**1.37** (95% CI: 1.06, 1.68)	**233** (95% CI: 109, 357)
Male	**221** (95% CI: 113, 329)	**0.57** (95% CI: 0.27, 0.87)	**120** (95% CI: 0, 254)
Female	**150** (95% CI: 105, 195)	**1.78** (95% CI: 1.36, 2.20)	**272** (95% CI: 106, 438)

When investigating the distance between collection locations of feathers from individual birds, there is a significant difference between males and females. Feathers from female birds were found on average 1.21km further away from each other than male feathers (*t*-test, *p*-value = 0.000).

Most notably, a female was genotyped 10 times over 3 years and moved a maximum of 5.64km over the study period (Figure 6.2).

Using average distance per unit time as a measure of capercaillie movement shows that females move, on average, over twice that of males in the same time. However, when analysed this result was not significant.

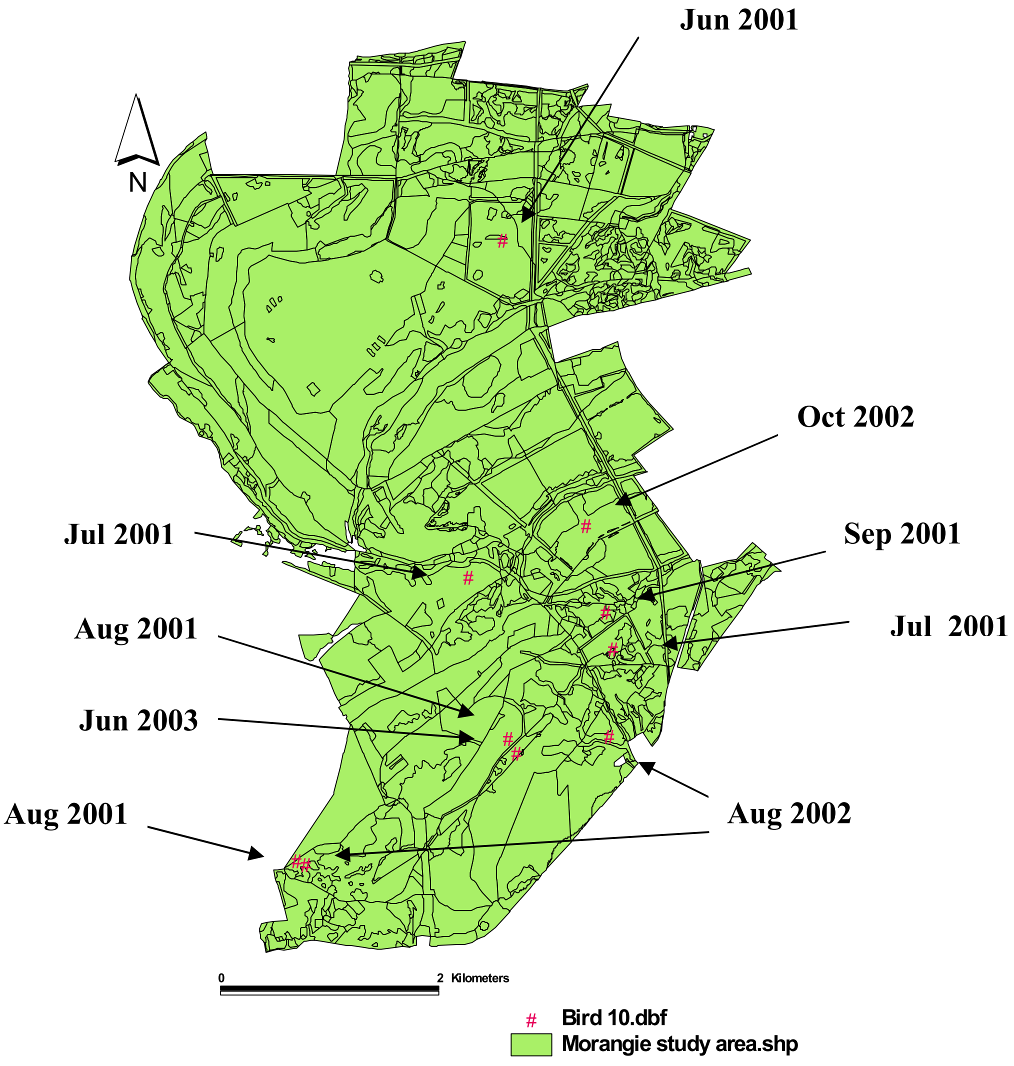

Figure 6. 2. Location and year feathers found in Morangie Forest from female over 3 year study period.

As well as moving the greatest distance throughout the study period, this female appears to be utilising much of the forest. In contrast, a male found 6 times over the three year study period, moved a maximum of 0.36 km in that time, and his feathers were found in exactly the same location between 2002 and 2003, and almost identical positions in 2001 and 2002 (Figure 6.3).

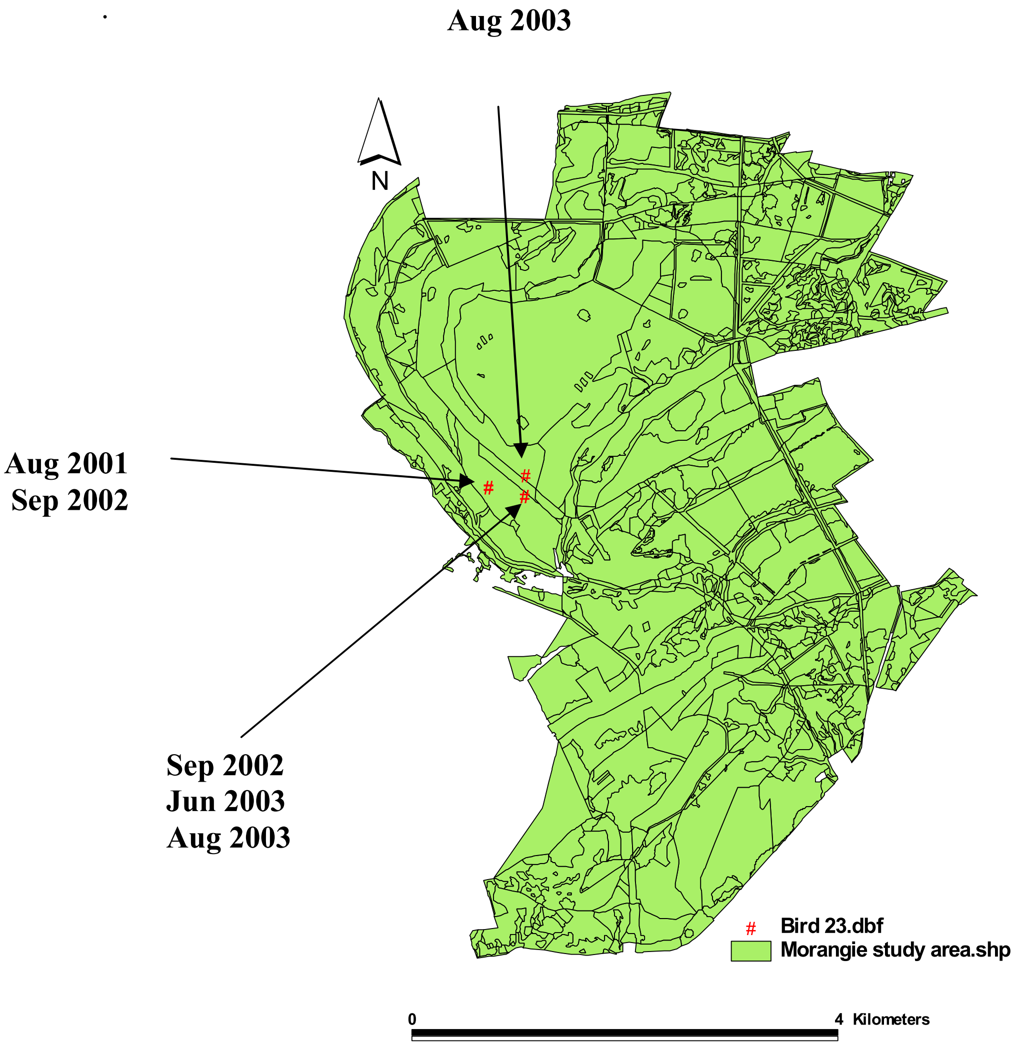

Figure 6. 3. Location and year feathers found in Morangie Forest of male found over 3 year study period.

Feather locations, according to sex, were plotted on a map of Morangie Forest to investigate any difference in spacing between male and female capercaillie (Figure 6.4). It appears that capercaillie are not segregated by sex to different areas of the forest during summer months, with the exception of Tain Hill, where all feathers found were female. In 2002, within a 2km^2 area six females were found suggesting that female home ranges must overlap in summer months.

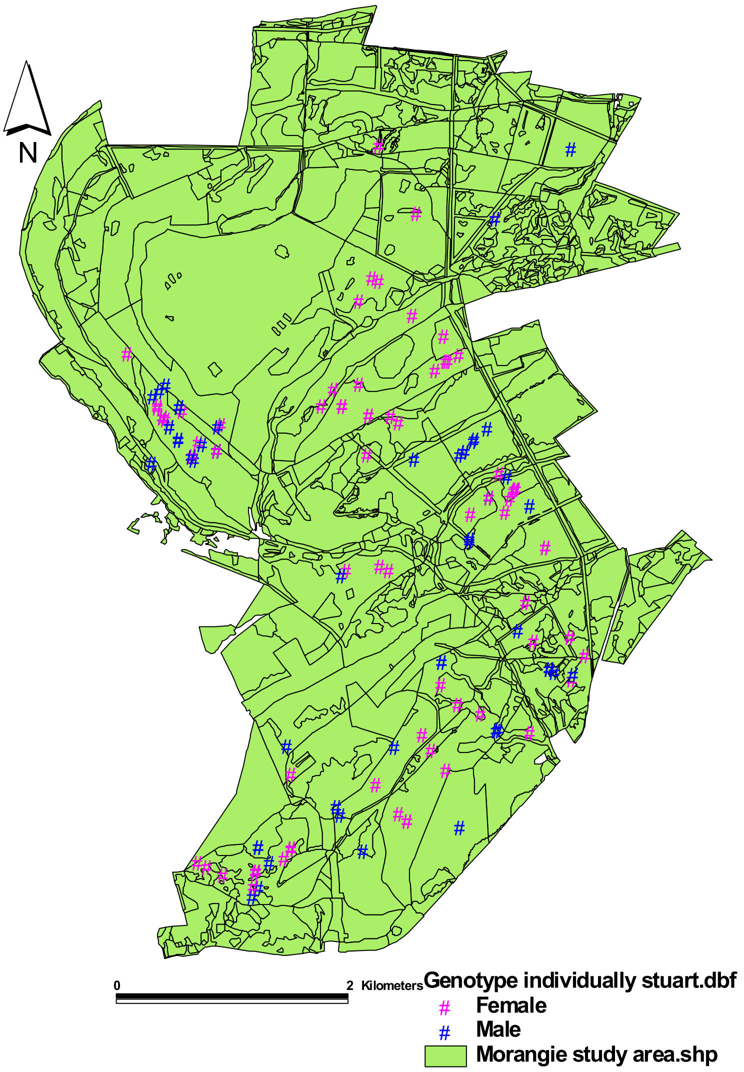

Figure 6. 4. Spacing of birds according to sex in Morangie Forest.

Analysis of habitat data at a compartment level, for each of the feathers genotypes, did not show any significant differences in habitat used by male and females during this time.

6.4.4 Movement and Mixing

Genetic distances were calculated among individuals in Morangie Forest, and then translated into Eigenvalues and plotted on a PCoordA graph (Figure 6.5).

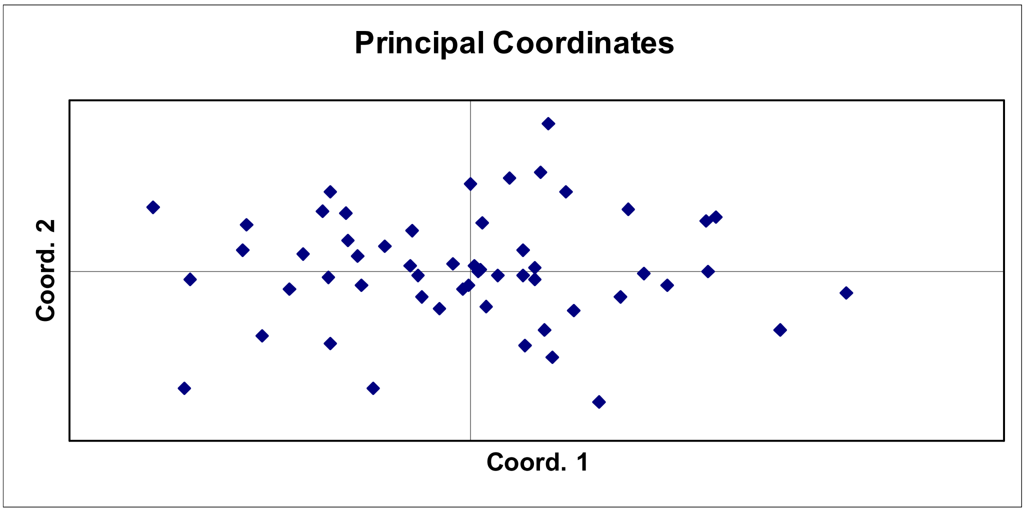

Figure 6. 5. PCoordA plot for capercaillie genotyped in Morangie Forest.

There was no apparent partitioning of points in different places over the PCoordA plot and therefore there is no suggestion of significant sub-structuring in the population within Morangie forest. This assertion was confirmed using the maximum likelihood assessment of the number of distinct sub-groups within Morangie. For all Morangie samples, analysis indicated a single genetic population.

PCoordA was then run to look at the closeness of the Morangie population to that of neighbouring Novar and Moray populations. Genotypes for Novar & Moray were obtained from Piertney *et al.* (in press) (Figure 6.6).

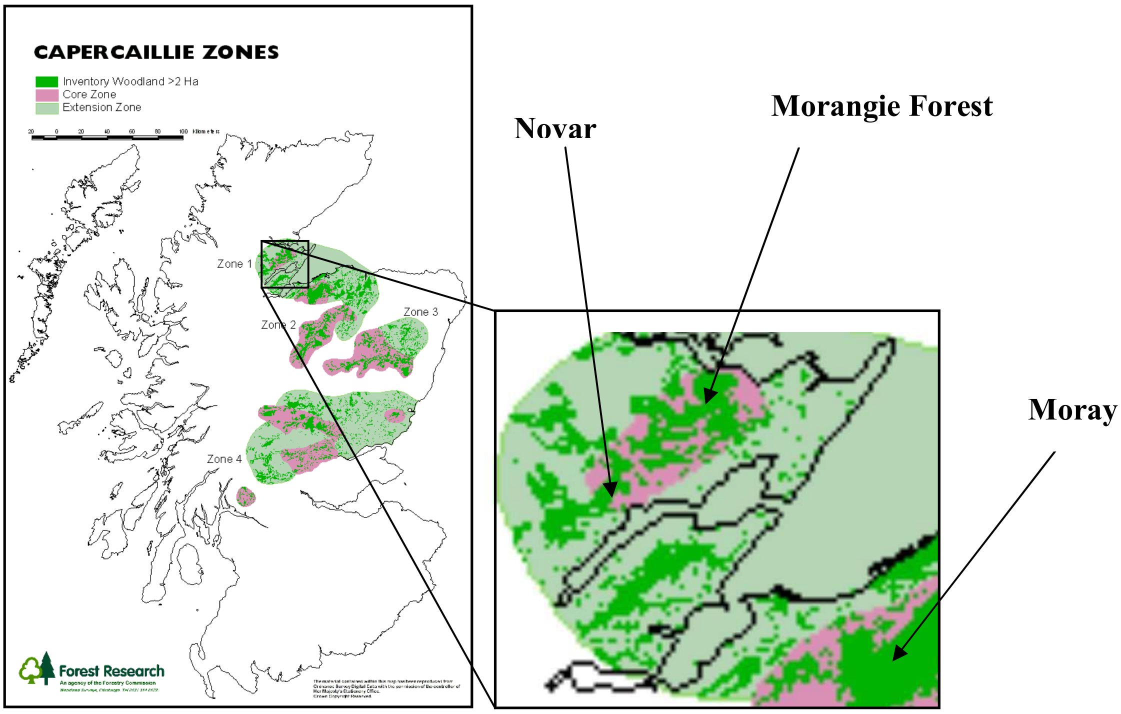

Figure 6. 6. Map to show location of Novar Forest and Moray forests in relation to Morangie Forest.

Morangie and Moray samples were grouped together, and then a maximum likelihood test of the number of distinct genetic groups within the sample was performed. The most likely value of two was returned, highlighting that the two locations do not form a single genetic population. This is further illustrated by the separation of samples from Morangie and Moray in the PCoordA plot below (Figure 6.7).

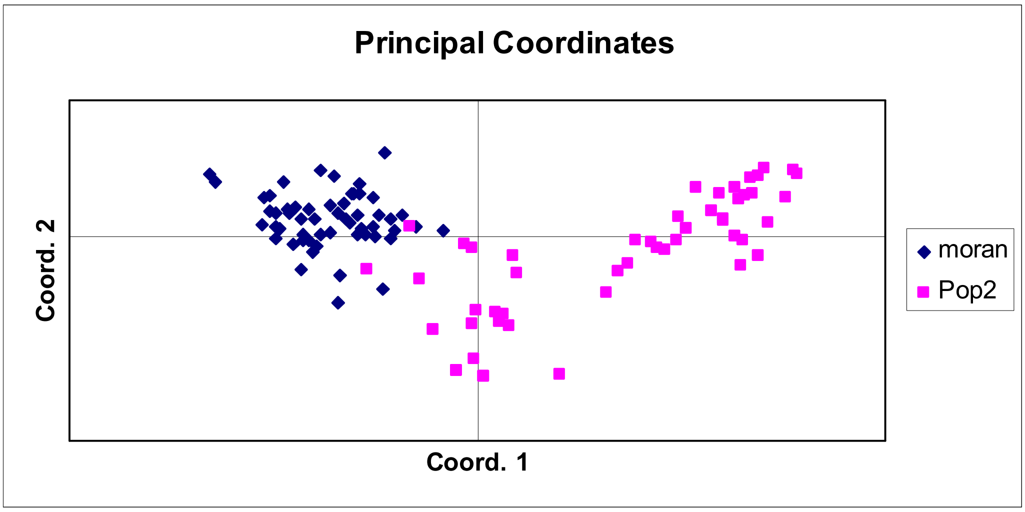

Figure 6. 7. PCoordA plot for capercaillie from Morangie Forest (blue) and Moray forests (pink)

Figure 6.7 support the Maximum Likelihood test result, clearly showing two separately distinct populations with non-overlapping distributions.

Morangie and Novar samples were then grouped and the Maximum Likelihood value calculated, this also returned a maximum likelihood value of two, though the log likelihood test separating the likelihoods of two or one population is insignificant. The PCoordA plot (Figure 6.8) clearly groups the individuals from Morangie and Novar together, although the two groups are not totally intermingled, there is a lot of overlap between them.

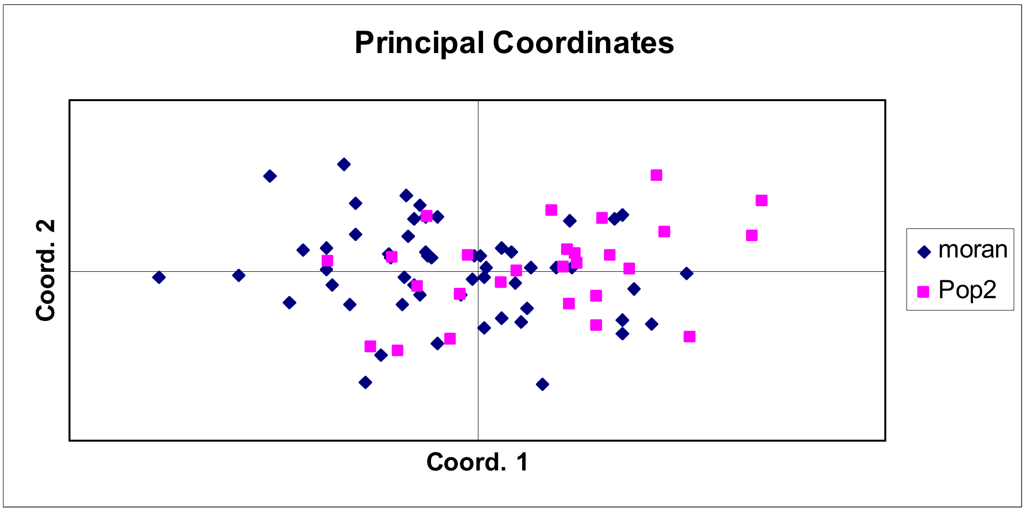

Figure 6.8. PCoordA plot for capercaillie from Morangie Forest (blue) and Novar Forest (pink).

Assignment tests were carried out to see if any individuals genotyped within the Morangie population were genetically more similar to individuals from a different population. In the analysis between Morangie and Moray, one male was found to be genetically more similar to individuals from Moray. He was found at Morangie in August 2002 and was not sampled again. In the analyses between Morangie and Novar, 13 birds from Morangie were genetically more similar to individuals from Novar (Table 6.6).

Table 6.6. Morangie birds found to have Novar genetic signature.

Bird I.D	Sex	No of times sampled	No of years present	Average distance moved (km)
1	Female	5	2	2.29
2	Male	3	3	0.18
8	Female	2	2	1.52
17	Female	3	2	0.21
27	Female	4	3	4.18
28	Female	1	1	one sample
30	Male	2	1	0.13
31	Female	2	1	1.52
32	Female	8	3	2.01
33	Male	2	1	same day
40	Female	3	2	0.05
42	Female	3	1	0.80
48	Female	1	1	one sample
Average		3	1.77	1.29 (95% CI: 0.35,2.23)

6.5 Discussion

6.5.1 Current Genetic Status

Current genetic diversity of capercaillie at Morangie Forest is comparable with that of other Scottish populations, and also with that observed in fragmented populations of equivalent size in Continental Europe (Piertney *et al*, in press).

Deviation from Hardy-Weinberg, with a deficiency of heterozygotes was observed, and is characteristic of some of the populations in the broad scale Scottish survey (Piertney *et al*, in press), and reflects small, semi-isolated population with some inbreeding in the allelic coancestry.

Observed heterozygosity of the Morangie capercaillie population was 0.66, which was the second highest from the 6 main capercaillie populations but comparable with the other populations.

Allelic richness was 5.2 for the Morangie capercaillie population, which was higher than any of the other Scottish populations. More pertinently, this value is higher than previous estimates made at Morangie Forest (Piertney *et al*, in press). This is partly due to the larger sample size in the present study, however subpopulation 2 and 3 had comparable numbers of samples. Therefore it appears that in comparison to the other Scottish populations, the Morangie capercaillie population is relatively secure in terms of genetic diversity.

On average, individuals in Morangie Forest have a signature of an unrelated population. Male relatedness is significantly higher than females, suggesting that there is limited dispersal at natal sites and lek fidelity by males and that females are the dispersing sex (Höglund 2003). Results from 6.4.3, investigating movement and spacing of capercaillie, also supports male fidelity and female movement. Results within Europe also found higher relatedness in males than females (Segelbacher 2002). These results further highlight that both sexes within the capercaillie population at Morangie are sufficiently mixing with unrelated individuals, maintaining a genetically outbred population.

The present results might also explain why observed female movement within Morangie is greater than males. Greenwood (1980) stated that males benefit from philopatry because of familiarity with the resources and females benefit from dispersal, which allows them to choose among males and their defended resources. By dispersing, females also avoid inbreeding. There has been conflicting evidence to support female dispersal in capercaillie, Storch (1997) and Segelbacher & Storch (2002) supported female dispersal, whereas Mäki-Petäys *et al*. (2007) found no evidence for sex-biased dispersal. The results of this study would suggest that females are the dispersing sex. This is what is characteristic for avian species (Greenwood 1980).

6.5.2 Capercaillie Population Estimate

The estimate of 69 individuals in the Morangie capercaillie population, derived from the Mark-Recapture data, agrees with the estimate of 63 from the dropping count data for 2002. This figure would make the capercaillie population in Morangie just above the minimum viable population size of 60 identified by Marshall & Edward-Jones (1998). However the figure is much larger than that found by brood and lek counts, which are the standard methods used to establish population estimates for capercaillie at present. Lek count data is only a count of adult birds and does not include juveniles recruited into the population within same year and could account for the lower population estimate from lek counts. In addition, areas searched during brood and lek counts are areas where birds have been seen regularly, and although these areas are systematically searched, they don't account for the whole forest. Dropping data collected during this study suggests that capercaillie are using areas outwith the areas covered in brood and lek counts. The conservation forester working at Morangie forest in 2002 estimated the population to be over 50 individuals (C. Leslie pers. comm.). Scozzafava (2002) also estimated a population of around 61 capercaillie during a preliminary study conducted during summer 2001 in Morangie Forest. Therefore, it seems reasonable to conclude that lek and brood counts are perhaps underestimating the population of capercaillie in Morangie Forest. However, lek and brood counts are cost effective measures that show trends in population size. Continued collection of feathers and dropping counts over the entire forest would be costly in terms of time and money. Choice of method therefore depends upon whether absolute population counts are required, or whether an index of population size sensitive to trends in the absolute population size would suffice.

6.5.3 Movement and Spacing of Capercaillie

The analysis of movement of capercaillie in Morangie shows that females are moving significantly longer distances than males. Previous studies have shown the opposite, with males having the same sized home range as females (Storch 1995) or moving up to twice as far as females (Gjerde & Wegge 1989, Rolstad & Wegge 1987, Storch 1993). It is possible that males have been under-sampled and they are moving to areas outwith the study area or that during moulting, due to their conspicuous nature they are choosing better hiding places than females, resulting in fewer male feathers being located. In addition to this, after leaving the lek area males will move straight to traditional areas to moult. Females on the other hand will move to nesting grounds, brood habitat and then to traditional areas to moult which could explain the differences in areas used. Because the feather data represents mostly summer based movements of capercaillie, the amount of movement is likely to be an underestimation of the capercaillies annual home range. Storch (1993) found the annual home range width of female capercaillie to be between 1.6-5.4km, and for males between 2.2-8.3km. The present results support Storch's findings for females, but underestimate the results Storch found for males. When compared to documented summer home ranges of females 1.62 km^2 ± 1.06 and males 2.48km^2 ± 1.42 (Storch 1993), the present results generally agree with those for females but are still significantly lower than those documented for males. It is possible that male home ranges are constrained by habitat patch size. Home ranges calculated by Storch (1993) were based in 50km^2 of forest, in addition home ranges determined by Rolstad *et al.* (1988) were located in 45km^2 of forest. Morangie forest is around 35km^2 and therefore capercaillie home range may be constrained by the bounds of the forest. However this appears unlikely as female movement in Morangie forest is equal to that reported by Storch (1993) and Rolstad *et al.* (1988).

An investigation into the spacing and habitat use of capercaillie during summer, found that both sexes of capercaillie return to the same summer ranges in consecutive years (Rolstad *et al*. 1988). Mean annual changes in the central position of these summer ranges were 367 and 433m for adult males and females respectively. This was evident in some of the individuals in the present data. Rolstad *et al*. (1988) also found that males made a distinct movement from their spring to summer ranges between 20th May and 20th June and within their summer ranges they showed a clumped distribution, although they did not associate with each other. Again the results of the present study would suggest that males are within their summer ranges when feathers were collected.

Habitat differences between male and female summer ranges have been reported by Rolstad & Wegge (1988) and Storch (1993). Rolstad & Wegge (1998) reported that females preferred younger plantations as well as denser habitat than males throughout the summer. Conversely Storch (1993) reported that females preferred old forest and used clearcuts more than expected. Personal observations within Morangie Forest would support female capercaillie using younger, denser habitat. Many areas where females were regularly sighted during summer months, and where nests were found, were in younger less thinned areas of woodland within Morangie Forest. This was also supported by the results of the habitat analysis of capercaillie sightings (chapter 5). However, when analysed at the compartment level, no significant differences were found between male and female feather locations and summer habitat use.

6.5.4 Movement and Mixing

Results of Principle Coordinate Analysis (PCoordA) show that Capercaillie from Morangie Forest are from a single genetic population, this agrees with the previous results found from the broad-scale genetic study (Piertney *et al*, in press). However, results from between population analysis show that capercaillie from Morangie and Novar are genetically more similar than previously considered. The PCoordA plot (Figure 6.8) shows significant overlap in genetic distances between birds from Morangie and Novar, and although the Maximum Likelihood value of the number of distinct genetic clusters does not allow them to be considered as one population (i.e. K=2; see section 6.3.3.4), the level of genetic distinctiveness between the two is less than previously thought from the broad-scale Scottish survey (Piertney *et al*, in press). Morangie and Moray were confirmed to be separate populations.

This result has significant implications for the management of capercaillie in Morangie Forest. Piertney *et al.* (in press) stated that there was significant genetic divergence between Morangie and Novar sub-populations and Donside and Deeside sub-populations and as a result capercaillie in Scotland should be considered as comprising at least eight populations, instead of six, and habitat continuity should not be used to assume gene flow or population continuity. In direct contrast, the results of the present study, show that there is significant mixing occurring between Morangie and Novar Forest and that they should managed as a single metapopulation. Results of the assignment test also support the management of Morangie and Novar as one metapopulation; 13 (24%) of the Morangie birds genotyped had a Novar genetic signature.

The results of the assignment tests also provide evidence to support female dispersal of capercaillie at Morangie, discussed in the last section. 77% (10/13) of the Morangie capercaillie with a Novar genetic signature were female suggesting that females are the dispersing sex at Novar.

Discrepancy between the Piertney survey (Piertney *et al*, in press), which was based on relatively few individuals, and the current study, which was based on a much larger sample size, highlight potential problems of attempting to define demographically distinct populations from a limited number of individuals. An underlying assumption of population genetic surveys is that the allele frequencies resolved within a sample reflect those in the larger population. Clearly, in dynamic populations where non-invasive sampling via feather collection underpins genetic characterisation, such inference cannot be assumed.

6.6 Conclusion

In conclusion, results from the present chapter have given new insights into the genetic population structure within a Scottish metapopulation. The Morangie capercaillie population is genetically diverse with low levels of interrelatedness. There appears to be greater movement of individuals around Morangie Forest than previously thought, in addition to this, males and females behave differently in terms of movement and site fidelity. The current Capercaillie Management Plan (Leslie 1998) for Morangie Forest identified core areas and zones to specifically manage for capercaillie. Results of this study would suggest that management for capercaillie should encompass the entire forest.

Results confirm previous population estimates of around 60-70 birds from dropping counts and personal observations (C.Leslie pers. comm.).

Results also show that the population is not bounded within the forest and mixing with neighbouring populations is taking place. At present Morangie Forest, a Forestry Commission owned woodland and Novar Forest, part of a privately owned estate are managed as separate entities. Future management should strive to co-ordinate management between forests and aim to establish further woodland as corridors between forests. It is vital to get collaboration and co-operation between private and public bodies in order to conserve capercaillie at the metapopulation level; this is where co-ordinated approaches to conservation like those stimulated by the EU LIFE project are beneficial. Further feather sampling in Novar Forest would allow more detailed insight into the movement of birds between forests and any source-sink dynamics occurring.

The present chapter also highlights the need for sample sizes large enough to capture all the genetic diversity present within a population. The original broad-scale study (Piertney *et al*, in press) used a sample size of 28 individuals from Morangie Forest, the present study had 141 successfully genotyped feathers, of which comprised 55 individuals. It would appear that an adequate sample of individuals was obtained in the study to provide reliable information on the genetic structure of the population at Morangie Forest.

To completely explore the dynamics of capercaillie within Morangie Forest it would be useful to collect feathers from leks as this would allow further insight into lek relatedness and dispersal. Also developing a more stratified sampling regime for gathering feathers, would allow more certainty that all individuals present in the population are being sampled. In addition, with the analysis of faeces for DNA becoming a more established method for genotyping individuals, it could be possible to incorporate DNA analysis of faeces into further studies; this would allow investigation of movements of capercaillie throughout the entire year, rather than through the moulting period.

A key question resulting from this chapter is whether feather sampling could/should ever replace physically counting capercaillie as the basis for a national survey? The advantages of feather sampling are that it is thought to be less invasive than physically counting capercaillie and it can accurately determine individuals in a population. In addition, if it were to become the basis for the national survey, it would allow further insight into how capercaillie are moving and mixing within and between populations. A minimum population value would be attainable after a year of feather sampling with estimates of population size attainable after three years. A disadvantage of feather sampling is the cost of applying the method to the whole of the capercaillie population. More that one site visit would be required to collect feathers, whereas only one visit is required for direct counts, and additional genetic analyses costs would also have to be considered. In addition, it could be argued that visiting capercaillie sites on a number of occasions during summer months to collect feathers could actually cause more disturbance than the present national survey, which is conducted during winter months. In conclusion, feather sampling could represent an alternative to traditional direct counts, however, until the effects of human disturbance on capercaillie are fully realised it would be unadvisable to use a method that may result in more disturbance to the capercaillie than the one used at present.

6.7 Bibliography

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Chapter 7. Final Conclusions

7.1 Introduction

This chapter summarises the general conclusions from this study, suggests recommendations for managers of working forests and proposes further research to understand capercaillie ecology in working forests. Each of the original aims will be identified and the success of the present study in achieving them will be discussed.

7.2 Main Conclusions

The overall aim of this study was to investigate capercaillie ecology in a managed productive forest and produce management prescriptions with the aim of facilitating direct transfer of scientific knowledge into management action. Within the overall aim there were four specific objectives. The first of which was to:

- Gain insight into the capercaillie population size and distribution in Morangie Forest by testing the use of dropping counts as a monitoring tool.

Results of the study showed that dropping counts did indeed allow a non-invasive method of ascertaining information about the capercaillie population at Morangie

Forest. Dropping counts gave population estimates that were in agreement with estimates from other measures. In addition the counts were sensitive to changes in the population dynamics of capercaillie in Morangie Forest, clearly showing movement of birds around the forest during the year, and a reduction in numbers over the three year study period.

However, the use of dropping counts was not without its problems; it was a time consuming way of gaining information about capercaillie populations and was subject to error caused by varying digestibility and decomposition factors throughout the year. On its own, purely as a method of gaining information about capercaillie populations, it would be too expensive and time consuming to implement as a monitoring tool year around. However, winter counts represent a compromise that would still allow information about changes in the location and population size of capercaillie, with little bias from digestibility and decomposition factors. Also combining other measures of capercaillie use with dropping counts could make using counts as a monitoring tool more viable. Habitat and dietary information can be derived from capercaillie droppings and in the light of new genetic techniques available that determine individuals and sex from droppings and feathers, (discussed later) counts can perhaps be used in conjunction with these measures to allow further insights into capercaillie populations for little extra effort.

A second specific objective of the study was to:

- Investigate the distribution of dropping counts as an indicator of capercaillie presence in Morangie Forest in relation to multi-scale habitat factors.

Results from this chapter stressed the importance of including measurements on varying scales of capercaillie habitat use if capercaillie presence was to be explained. Capercaillie within Morangie Forest appear to be selecting habitat primarily at a radius of 50m and beyond. Results also showed that using data derived from the FC compartmental database or from geo-authorectified aerial photographs produced better predictions of capercaillie habitat use than using variables collected from the field. These findings emphasise the importance of adopting a large-scale management approach for capercaillie. Habitat models that successfully predicted capercaillie presence and absence in Morangie Forest have been made and have the potential to be used as a basis for predicting capercaillie habitat use in other commercial forests.

Capercaillie do not appear to be making habitat choices based on the percentage of blaeberry present within Morangie Forest. However, results of the dietary analysis (Chapter 5) showed that capercaillie at Morangie Forest were selecting for more blaeberry in their diet relative to its availability than capercaillie in a semi-natural pinewood.

The present study explained winter habitat use of capercaillie to a greater degree than capercaillie use in other seasons. Therefore specific summer habitats, such as those used by hens with broods or for moulting were under-represented. Due to the inaccuracies associated with sexing droppings according to size, a full investigation of habitat use between the sexes could not be conducted. Advances in molecular sexing techniques from faeces, since the start of this study, may allow this to be further investigated. Using capercaillie sightings and feathers along with habitat data from the FC compartmental database allowed some investigation of habitat use between the sexes and showed that there are differences in habitat selection between the sexes.

The third specific objective was to:

- Investigate habitat and diet of capercaillie in Morangie Forest in comparison with capercaillie habitat and diet in a semi-natural pinewood.

The diet of capercaillie in Morangie Forest was successfully ascertained and compared to the diet of capercaillie in Abernethy Forest (Summers *et al*. 2004). Annual diet of capercaillie in Morangie and Abernethy Forest was similar, although capercaillie in Morangie Forest appeared to be selecting for blaeberry more than capercaillie in Abernethy Forest. In addition, capercaillie diet at Morangie Forest contained higher amounts of pine throughout the year in comparison with capercaillie at Abernethy Forest. Identification of all food fragments from droppings requires specific expertise and some discrimination of species could not be fully achieved in the present study. In particular, the relative proportion of Scots and Lodgepole pine in the diet of capercaillie in Morangie Forest could not be established.

Comparison of habitats used by capercaillie in Morangie Forest and those used in Abernethy Forest highlighted the differences in the structure between the two forests. Capercaillie in Morangie Forest used areas of forest which had thinner higher trees, more closely spaced, with a higher percentage moss and grass cover and a lower percentage blaeberry cover than capercaillie in Abernethy Forest. In addition, capercaillie in both forests preferred areas of woodland 225-250m away from forest tracks or roads.

Detailed dietary analysis was conducted on a number of droppings randomly collected each month from Morangie Forest. Although these dropping gave an insight into capercaillie diet in Morangie, it would have been more worthwhile collecting droppings from specific areas within Morangie Forest, where detailed habitat analysis had been conducted. This would have allowed capercaillie diet to be explored in relation to availability in the surrounding habitat. This was not possible within the present study due to the lack of fresh droppings in study plots during summer months. In addition, it would have been interesting to explore whether exotic conifers used for roosting were also used for feeding. This could have been possible by analysing roost droppings that were collected under spruce and larch trees.

Analysis of diet according to sex would have been advantageous and would have further highlighted suspected differences in habitat use between the sexes. The advances in molecular sexing techniques from faeces, since the start of this study, may be one way of achieving this.

However, the importance of the present results should not be underestimated. Before the present study, fine-scale dietary analysis of capercaillie droppings in a pine plantation had not been explored. These findings therefore have important implications for management of working forests.

The final specific objective of the present study was to:

- Investigate the genetic structure of the capercaillie population at Morangie Forest.

Development of genetic techniques for obtaining DNA from feathers, which became available after the start of the present study, allowed investigation into the genetic population structure of capercaillie in Morangie Forest. This was the first study of genetic population dynamics within a capercaillie metapopulation in Scotland. Results showed that the capercaillie population at Morangie Forest is genetically diverse with low levels of interrelatedness. Previous broad-scale genetic analysis of capercaillie across Scotland found no evidence of mixing between capercaillie in Morangie Forest and Novar, and as a result, concluded that there was no need manage the two forests as one metapopulation. However, present results based on a larger sample size, showed that there was substantial mixing occurring between capercaillie in Morangie Forest and those in neighbouring Novar Forest. As a result it is imperative that moves are made to link this metapopulation. The findings of this study highlight the problems of attempting to define demographically distinct populations from snap shot surveys.

This study was unable to fully explore movement of capercaillie throughout the year as the feathers that the study was based on were mostly found when capercaillie were moulting during summer months. Again, with the advances in genetic analysis of faeces, capercaillie population numbers and movement could be explored year round.

7.3 Management Recommendations

The results of this study suggest that multi-scale management for capercaillie in working forests would be most beneficial.

From the results of the present study a number of specific management recommendations can be made at the within stand, stand and landscape scale:

Within Stand

- The preference of capercaillie in Morangie Forest to areas with higher percentages of Scots pine and preference for presence of old Scots pine supports

Scots pine as the preferred tree species of capercaillie in Scotland. To benefit capercaillie, forest managers should aim to use high percentages of Scots pine in future plantings. However, it is worth noting that capercaillie hens were observed nesting in compartments of lodgepole pine within Morangie Forest, and cock capercaillie were observed roosting under spruce and larch trees (pers. obs.). Therefore small areas of other tree species within larger compartments of Scots pine should be beneficial for capercaillie. Structural elements such as areas of windthrow and overturned trees provided valuable ground cover for capercaillie within Morangie Forest and should be retained (pers. obs).

- Results of the present study show that capercaillie are selecting for blaeberry within their diet, although percentage ground cover of blaeberry was not found to significantly influence capercaillie habitat choice within Morangie Forest. Forest managers, within the constraints of timber production, should aim to obtain a blaeberry cover of 15-20%. The current level of blaeberry cover in Morangie Forest is 15%, demonstrating that a working forest, where timber production is the primary objective, can still be suitable in terms of blaeberry cover. However, results of the dietary analysis suggest that blaeberry development should still be encouraged within Morangie Forest.

Stand

- There is strong evidence from this study to suggest that capercaillie avoid areas where there is fragmentation of habitat and prefer more continuous areas of forestry. Therefore large areas of clearfelling should be discouraged and a movement to continuous cover systems welcomed. Morangie Forest is already in the process of being converted to continuous cover.

- Thinning racks should be used to open up areas of more dense plantation. Evidence from this study has shown that capercaillie prefer areas with higher densities of thinning racks. This appears to be for a number of reasons including: access to other areas of forestry, escape routes from predators, suitable roosting sites and utilisation of the ground vegetation present on rides and racks. This could therefore open up previously unused areas of forestry to capercaillie. Care must be taken not to create gaps with a width of 10 metres or more, as evidence from other studies has shown that predation risk is increased in rides over 10m wide.

- Results of the study also suggest that capercaillie avoid forest habitat 200m from the edge of roads. It is not clear whether this is an effect of disturbance or edge effect. Regardless of which, the number of roads should be minimised in areas used by capercaillie, or placed if possible around the edge of forests where capercaillie would be unlikely to use habitat anyway. Where roads dissect capercaillie habitat, planting strips of spruce along roads may reduce the amount of habitat avoided by capercaillie.

- Results of the study suggest that priority management for capercaillie should be given to areas of forestry located on southern sunny slopes at higher elevations within the forest, if other habitat components are suitable.

Landscape

Making management recommendations at a forest scale and below will be of limited impact if management of capercaillie at a landscape scale is not considered. Therefore the main management recommendations at a landscape level, from the results of this study are to:

- Join up of existing forest fragments by use of woodland corridors or stepping stones in order to facilitate mixing between metapopulations of capercaillie in Scotland.

- Look for mechanisms to ensure consistent and sympathetic management across the range of the metapopulation.

The importance of managing separate capercaillie populations as metapopulations has been highlighted in this study and therefore a priority for capercaillie management has to be a concerted effort to join existing forest areas in Scotland, in order to maintain the genetic diversity of the existing capercaillie population and create areas for expansion of the population. This would require national funding and a management group to oversee implementation of these corridors and also to facilitate the substantial liaising that would be required between forest owners. However, taking these somewhat dramatic measures may be the only way to stop the second extinction of capercaillie from Scotland.

7.4 Further Research Priorities

Given the recent advances in genetic analysis of faeces and feathers in addition to the results of the present study, further research priorities in Morangie Forest should focus on exploration of habitat use between sexes and during summer months, utilising these non-invasive genetic techniques. This would further build upon habitat information already determined and allow more specific management recommendations to be made for capercaillie in Morangie Forest. A more comprehensive genetic investigation of the capercaillie population in neighbouring Novar Forest would be useful to further quantify the extent of mixing occurring in Novar Forest and allow more detailed proposals for metapopulation management of Morangie and Novar Forest.

Research priorities for capercaillie beyond Morangie Forest should focus on landscape studies encompassing the whole of Scotland.

7.5 Final Conclusion

With the current plight of capercaillie in Scotland, which puts the species at risk of a second extinction in Britain (Moss 2001) it is imperative that urgent actions towards the conservation of capercaillie in Scotland are implemented. With the emphasis being placed on working forests as the future for capercaillie in Scotland, it is important that guidelines for forest managers are based on research within these forests and not extrapolated from studies in semi-natural woodlands. The present study has successfully contributed towards such guidelines, and has enabled previous unknown insights into the ecology of a capercaillie population within a working forest to be determined.

7.6 Bibliography

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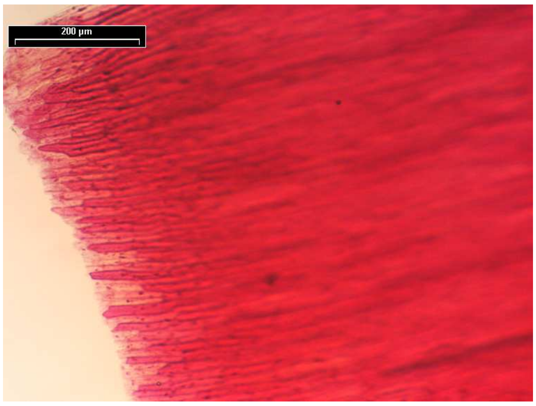
Chapter 8. Appendices

8.1 Habitat Variables Entered in Logistic Models

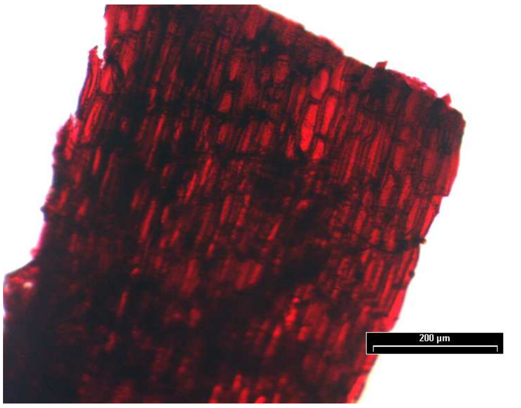
VARIABLE	FIELD	COMPARTMENT	DEM	AERIAL PHOTOS	10M	50M	100+M	ALL VARIABLES
MAIN TREE SPECIES IN PLOT	1	0	0	0	1	0	0	1
NO OF TREES	1	0	0	0	1	0	0	1
NO OF SPECIES	1	0	0	0	1	0	0	1
TOP HEIGHT(M)	1	0	0	0	1	0	0	1
TREE MAX DBH	1	0	0	0	1	0	0	1
TREE AVERAGE DBH	1	0	0	0	1	0	0	1
TREES/HA	1	0	0	0	1	0	0	1
BA/HA	1	0	0	0	1	0	0	1
NO OF GROUND VEGETATION SPECIES	1	0	0	0	1	0	0	1
HEATHER %	1	0	0	0	1	0	0	1
HEATHER TOPHEIGHT	1	0	0	0	1	0	0	1
BLAEBERRY %	1	0	0	0	1	0	0	1
BLAEBERRY TOPHEIGHT	1	0	0	0	1	0	0	1
GRASS %	1	0	0	0	1	0	0	1
GRASS TOPHEIGHT	1	0	0	0	1	0	0	1
MOSS %	1	0	0	0	1	0	0	1
MOSS TOPHEIGHT	1	0	0	0	1	0	0	1
TOTAL TOPHEIGHT	1	0	0	0	1	0	0	1
NO OF GROUND VEGETATION SPECIES	1	0	0	0	0	1	0	1
TOTAL TOPHEIGHT	1	0	0	0	0	1	0	1
HEATHER %	1	0	0	0	0	1	0	1
HEATHER TOPHEIGHT	1	0	0	0	0	1	0	1
BLAEBERRY %	1	0	0	0	0	1	0	1
BLAEBERRY TOPHEIGHT	1	0	0	0	0	1	0	1
GRASS %	1	0	0	0	0	1	0	1
GRASS TOPHEIGHT	1	0	0	0	0	1	0	1
MOSS %	1	0	0	0	0	1	0	1
MOSS TOPHEIGHT	1	0	0	0	0	1	0	1
ELEVATION - ANNE KATHERINE	0	1	0	0	0	0	0	1
ALTITUDE FC DATABASE	0	1	0	0	0	0	0	1
YIELD CLASS FROM FC DATABASE	0	1	0	0	1	0	0	1
TREE SPECIES FROM FC DATABASE	0	1	0	0	1	0	0	1
TREE SPACING FROM FC DATABASE	0	1	0	0	1	0	0	1
SPRUCE % AREA	0	1	0	0	0	1	0	1
SP (OTHER) % AREA	0	1	0	0	0	1	0	1
ROTATION	0	1	0	0	0	1	0	1
OPEN GROUND % AREA	0	1	0	0	0	1	0	1
NO OF SPECIES	0	1	0	0	0	1	0	1
NO OF POLYGONS	0	1	0	0	0	1	0	1
NO OF BOUNDARY LINES	0	1	0	0	0	1	0	1
MAIN TREE SPECIES	0	1	0	0	0	1	0	1
LP % AREA	0	1	0	0	0	1	0	1
LARCH % AREA	0	1	0	0	0	1	0	1
BROADLEAVES % AREA	0	1	0	0	0	1	0	1
AVERAGE YIELD CLASS 50M	0	1	0	0	0	1	0	1
ALL OTHER SPECIES % AREA	0	1	0	0	0	1	0	1
AGE IN 50M, WEIGHTED BY % COVER	0	1	0	0	0	1	0	1
TREE SPECIES 50M SP (OLD) % AREA	0	1	0	0	0	1	0	1
SIZE OF COMPARTMENT	0	1	0	0	0	0	1	1
NO OF POLYGOMS 100M	0	1	0	0	0	0	1	1
LENGTH OF BOUNDARY LINES (M) 100M	0	1	0	0	0	0	1	1
AGE IN PLOT COMPARTMENT	0	1	0	0	0	0	1	1
ACCUMULATED TEMPERATURE	0	0	1	0	0	0	0	1
MOISTURE DEFICIT	0	0	1	0	0	0	0	1
ELEVATION	0	0	1	0	0	0	0	1
SLOPE	0	0	1	0	0	0	0	1
ASPECT	0	0	1	0	0	0	0	1
HILLSHADE	0	0	0	1	1	0	0	1
PRESENCE OF OLD PINE	0	0	0	1	0	1	0	1
PRESENCE OF OLD PINE	0	0	0	1	0	1	0	1
NO OF ROADS	0	0	0	1	0	1	0	1
NO OF RIDES	0	0	0	1	0	0	1	1
DISTANCE TO ROAD MEASURING TOOL	0	0	0	1	0	0	1	1
DISTANCE TO ROADS ANNE KATHERINE	0	0	0	1	0	0	1	1
DISTANCE TO OLD PINE	0	0	0	1	0	0	1	1
% RIDE COVER	0	0	0	1	0	0	1	1
RIDE LENGTH	0	0	0	1	0	0	1	1
% OPEN SPACE	0	0	0	1	0	0	1	1
% FOREST	0	0	0	1	0	0	1	1
% FOREST COMPLETE	0	0	0	1	0	0	1	1
% FOREST SCATTERED	0	0	0	1	0	0	1	1
% FOREST OPEN	0	0	0	1	0	0	1	1
DIVERSITY IN LAND USE	0	0	0	1	0	0	1	1
WOODLAND TYPES	0	0	0	1	0	0	1	1

8.2 Digital Images of Diet Reference Collection

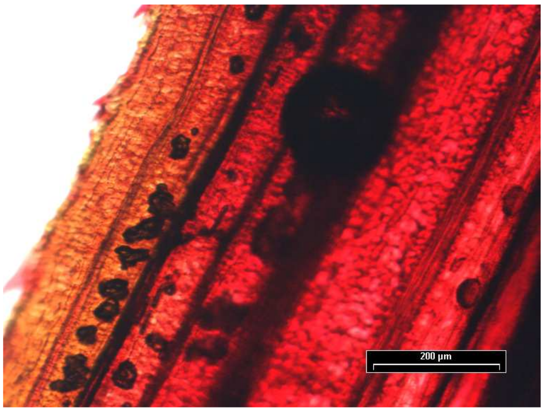


***Calluna* Flower x 10**

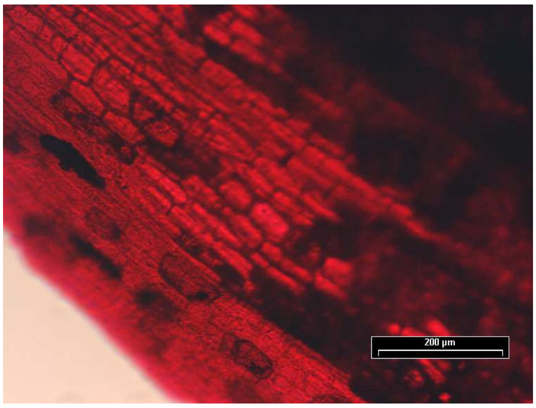
***Calluna* Flower x 10**



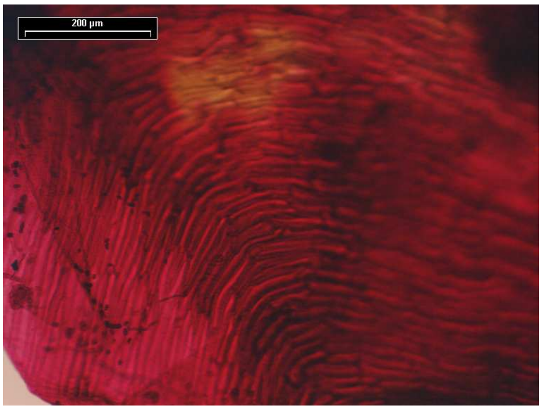
***Calluna* Stem x 10**



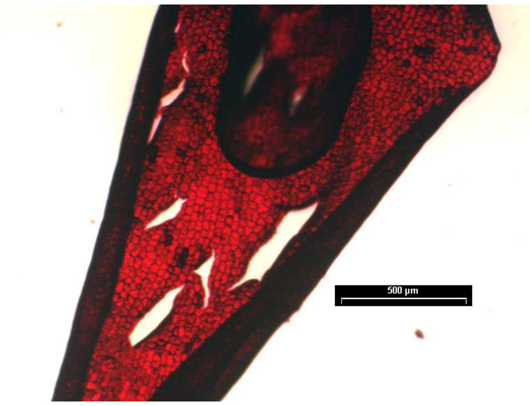
***Carex* Leaf x 10**



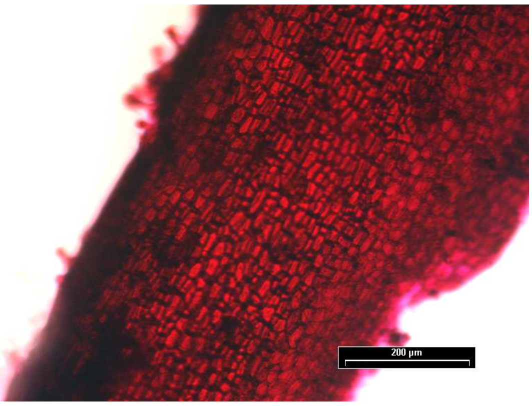
***Carex* Seed x 10**



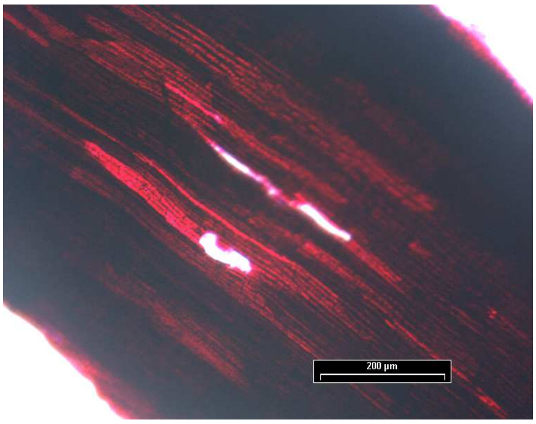
***Empetrum* Fruit x 10**



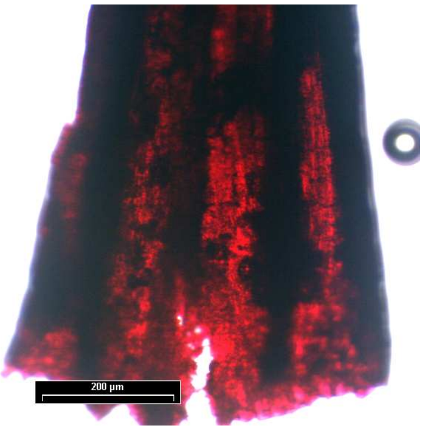
***Empetrum* Leaf x 4**



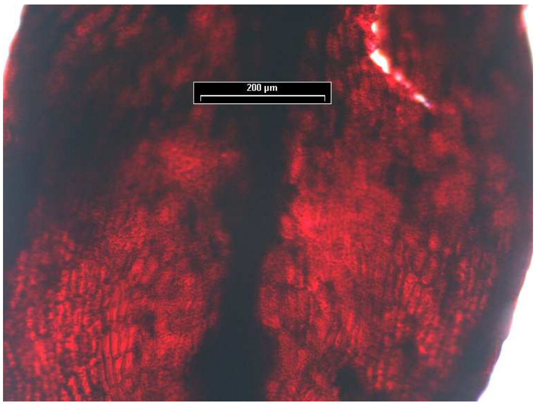
***Empetrum* Stem x 10**



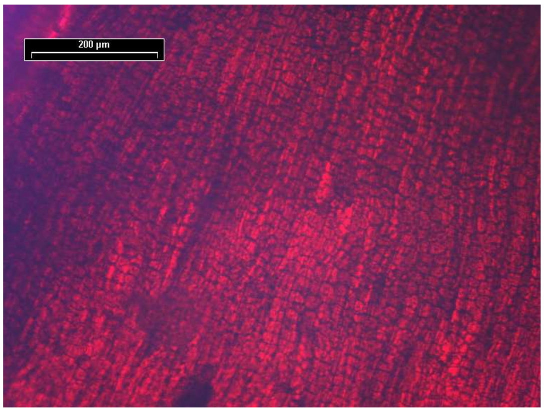
***Eriophorum* Seed x 10**



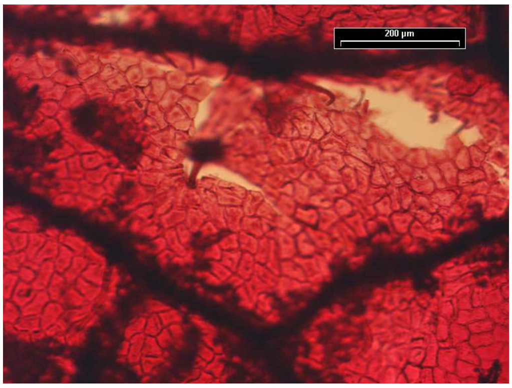
***Juncus* Leaf x 10**



***Juncus* Seed x 10**

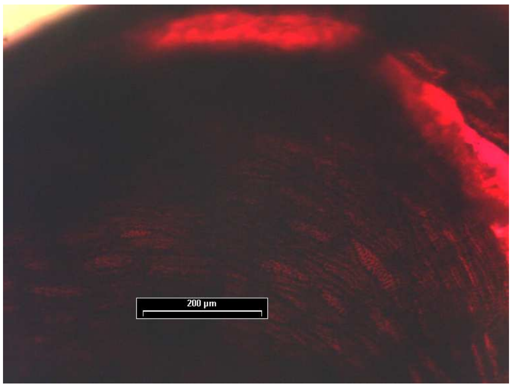


Rowan Seed x 10



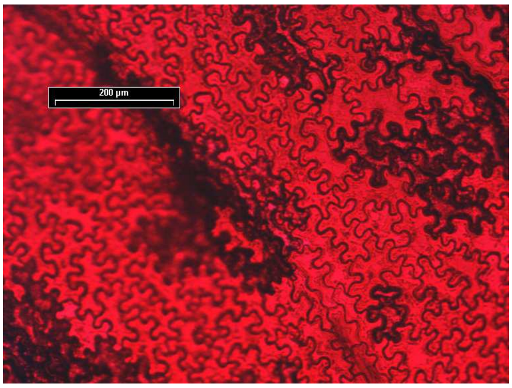
Birch Leaf x 10

Birch Stem x 10

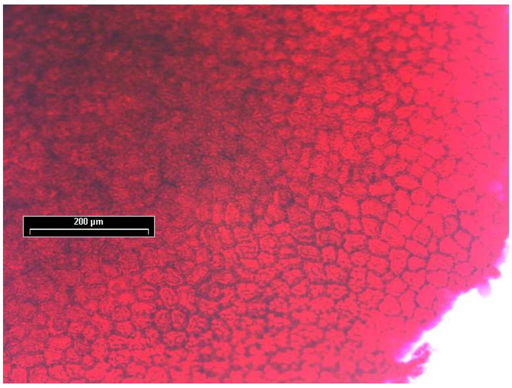


Blaeberry Seed x 10

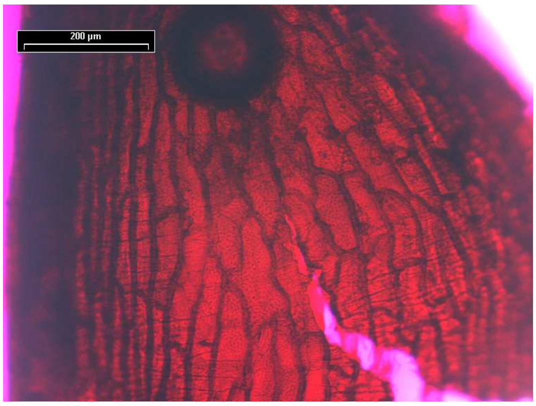
Blaeberry Stem x 10



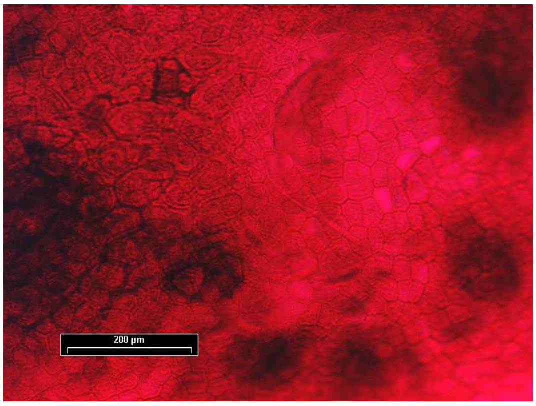
Bracken Leaf x 10



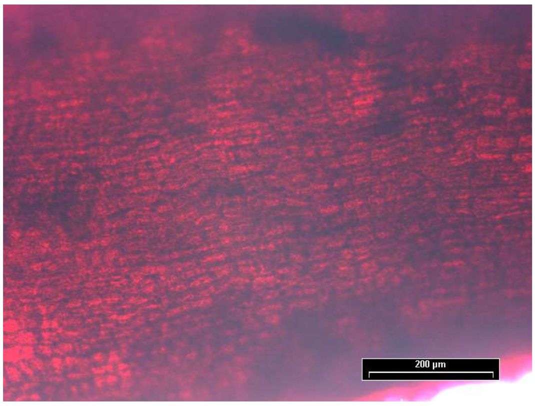
Cowberry Leaf x 10



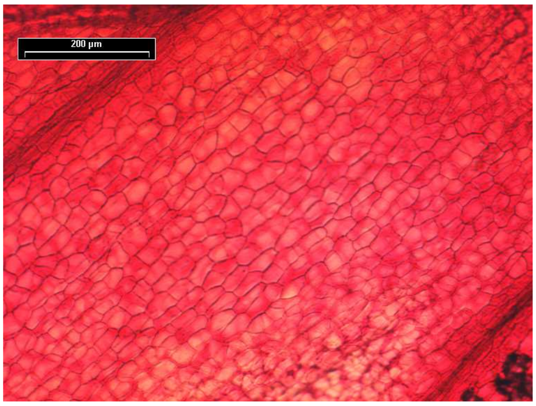
Cowberry Seed x 10



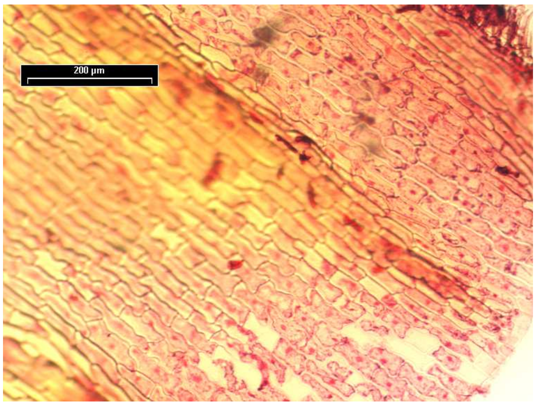
Cowberry Skin x 10



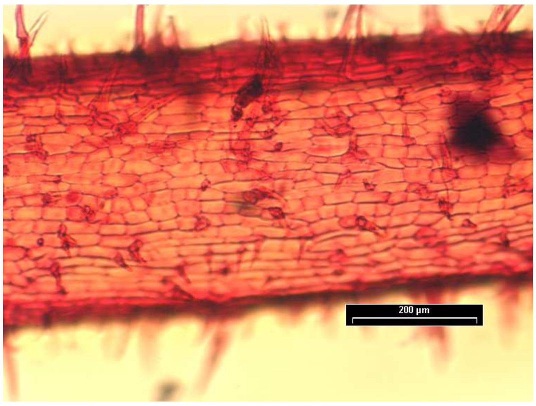
Cowberry Stem x 10



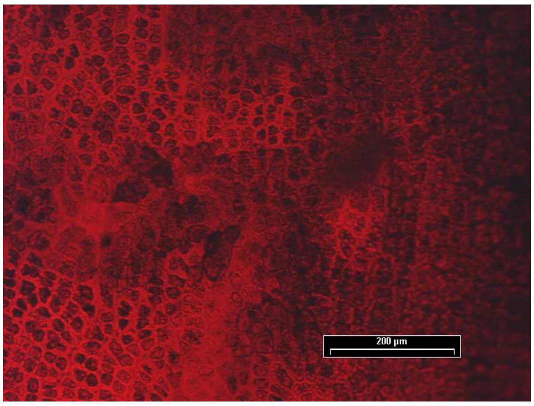
Erica Flower x 10



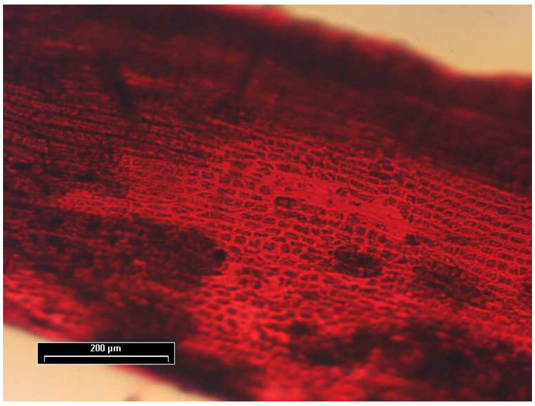
Erica Leaf x 10



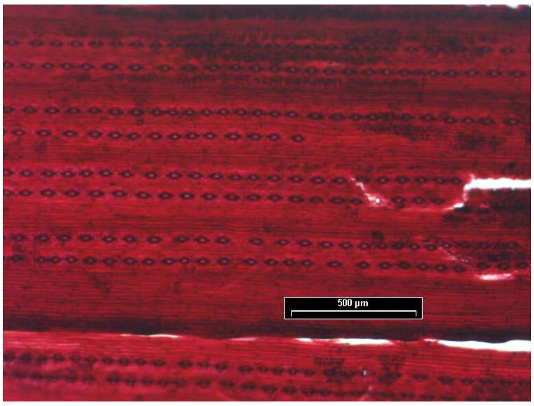
Erica Stem x 10



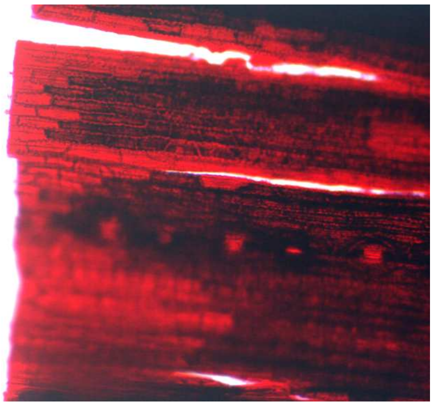
Rowan Berry Skin x 10



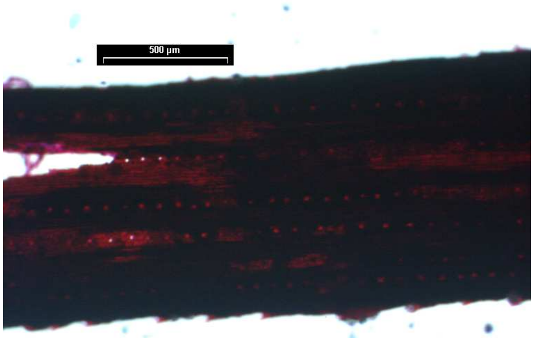
Rowan Stem x 10



Scots Pine Needle x 4



Sitka Spruce Needles x 10



Lodgepole Pine Needle x 4

Larch Needle x 10