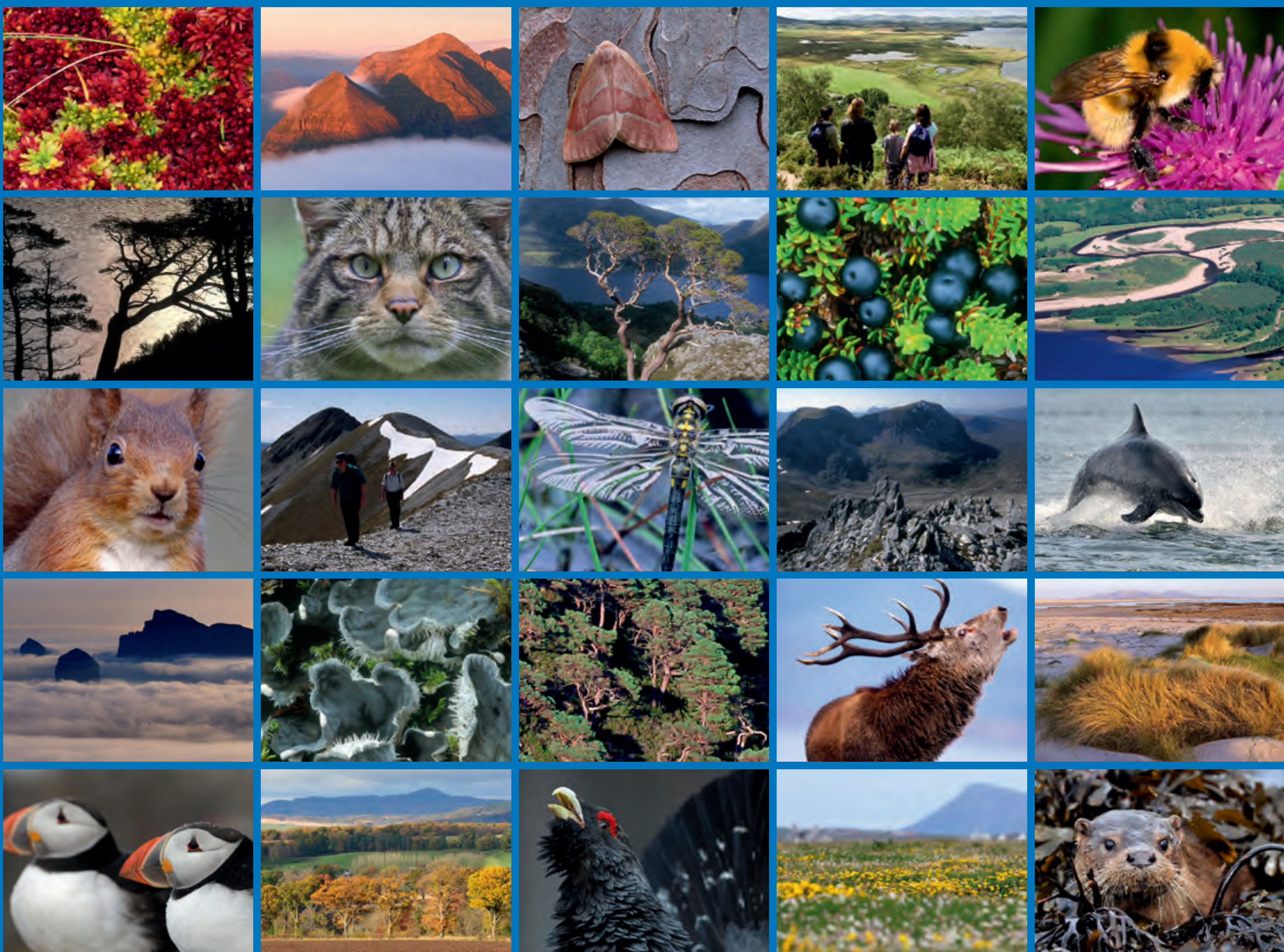
Scottish Natural Heritage
Commissioned Report No. 545

Spatial and structural habitat requirements of black grouse in Scottish forests



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COMMISSIONED REPORT

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Spatial and structural habitat requirements of black grouse in Scottish forests

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COMMISSIONED REPORT

Summary

Spatial and structural habitat requirements of black grouse in Scottish forests

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Background

Sympathetic management and placement of forests to provide/protect suitable habitat is a key focus of Scottish black grouse conservation. More information about how the species responds to forests' spatial and structural variation is required. We used lek data from 1992 and 2010 in the Tay region and from 2007 in Argyll, Galloway and Inverness regions to examine relationships between lek fate, size and habitat. We also used radio-telemetry data from 89 black grouse in the Tay region to examine individual use of forest habitat.

Main findings

- Lekking groups in Tay selected for moorland areas in both 1992 and 2010. Distributions between 1992 and 2010 shifted with changes in young forest components. Of all habitats, area of moorland or young conifer forest showed the smallest between-region variation (43-67% and 9-15% respectively).
- Moorland was the most selected habitat in most groups. Males also showed high selection for farmland and broadleaf woodland. Forestry (closed-canopy and unplanted patches) and new native pinewood habitats were generally avoided relative to moorland, except in adult females in autumn-winter (both) and spring-summer (new native pinewood). 78% birds using forestry moved < 600 m from the external edge. Such movements appeared greatest where larch and/or substantial unplanted areas (clearings/rides) were present. Females were associated with taller ground vegetation, higher densities of trees and more coniferous tree species (particularly larch).
- Use of older forest types (closed-canopy forestry, broadleaf woodland) relative to younger forest types (new native pinewood) generally increased with measures of winter severity. Survival, however, did not significantly differ between years. Older forests may provide above-snow foraging in severe winters and help buffer against poor survival.
- The following management recommendations are made: (1) conserve large and well connected areas of moorland adjacent to forests, (2) provide a diverse forest age and species composition at scale of lekking group and (3) constructively manage forest edges on moorland boundaries to facilitate access.

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1. INTRODUCTION

1.1 Background

Black grouse (*Tetrao tetrix)* declines in the UK have been well documented (Baines & Hudson, 1995; Hancock *et. al.,* 1999; Sim *et. al.,* 2008). They have been red-listed as a species of conservation concern due to their rapid rates of decline from an estimated 25,000 lekking males in the early 1990s to 5,000 males in 2005 (Eaton *et. al.,* 2009) and have had their own Species Action Plan since 1999. The species has at least three genetically distinct British populations: northern Scotland, England/southern Scotland and Wales (Höglund *et. al.,* 2011). Significant progress has been made in stemming the decline in abundance, but not range, in England (Warren & Baines, 2008) and Wales (Lindley *et. al.,* 2003). The Scottish black grouse population, which makes up approximately two-thirds of the UK population, experienced significant declines between the mid 1990s and mid 2000s, which were driven by significant declines in southern Scotland (Sim *et. al.,* 2008).

Black grouse occupy spatiotemporally transitional habitats, such as mosaics of grass or ericaceous shrub moorland and coniferous and/or broadleaf forest habitats or young growth forest (Baines *et. al.,* 2000; Cramp & Simmons, 1980). These provide resources at key stages of the annual cycle, such as a reliable source of winter food, a source of protein prior to nesting and lekking and suitable nesting and brood-rearing habitat (Baines, 1995). There is a spatial link between black grouse populations and forests in many parts of Scotland. For example, in Strathspey and Perthshire, black grouse leks had an average 24% forest cover within a 1 km radius and were on average 350 m from forest cover (unpubl. data). Data from wider Scotland have suggested more than 25% of leks were within forests and that more than 75% of leks were in forests or within 200 m of forest habitat (Grant & Dawson, 2005).

Black grouse may be less associated with forest habitat in Scotland than in Scandinavian populations (Parr & Watson, 1988), but more than in England (Starling-Westerberg, 2001). Recent declines in Perthshire have been associated with the maturation of commercial forest stands, particularly those of Sitka spruce *Picea sitchensis* and lodgepole pine *Pinus contorta* planted in the 1980s (Pearce-Higgins *et. al.,* 2007). These had originally acted as favoured habitats (Cayford, 1993), buffering against declines in non-forest habitats.

A multitude of conservation measures are now being advocated within commercial Scottish forests in an attempt to improve conditions for black grouse either within the forest or along its margins. Unlike similar initiatives in northern England on moorland and marginal farmland habitats which have successfully restored black grouse habitats and subsequent numbers (Baines *et. al.,* 2000), the principal mechanisms behind declines in Scottish forests are only poorly understood. Research to date suggests that numbers of breeding females decline with on-going forest maturation, but their breeding performance remains high (Baines *et. al.,* 2000). This suggests that the amount of suitable habitat for recruiting breeding yearling females probably diminishes with canopy closure. The spatial requirements for successfully breeding females are not clearly known, with provisional estimates suggesting 10 ha of suitable habitat for an adult female and brood, but up to 100 ha or more for a group of lekking males and associated females (Haysom, 2001).

Landscape changes are driven by many social, economic, cultural, scientific/technological and demographic factors (Nelson *et. al.,* 2006). On an international, national or regional scale, specific government policies can drive landscape change which in turn can influence populations of individual species. For example, the European Union's Common Agricultural Policy drove increases in agricultural production, and indicators such as national cereal yield were strong negative correlates of national farmland bird populations (Donald *et. al.,* 2001). UK Government policy in the late 20th century led to tax incentives to plant commercial forestry. This incentive ceased in 1988. Afforestation of peatlands in north-west Scotland led to direct displacement of threatened breeding populations of dunlin *Caladris alpina* (Lavers & Haines-Young, 1997). Current Scottish Government policy aims to increase forest cover in Scotland from the current 18% (Forestry Commission, 2011) to 25% by 2050, split as 'productive' forest (60%) and 'non-productive' forest (40%) (Forestry Commission Scotland, 2006). Initial aims are to increase new plantings to at least 10,000 ha per year (The Scottish Government, 2010) from the current approximately 5,100 ha. Combined with inevitable changes in the age-structure of current forests (Mason, 2007) both forested and non-forested areas in Scotland are likely to experience a high degree of habitat change within the next few decades.

Forest expansion policy poses a potential threat to black grouse habitats, but also an opportunity to adapt and manage forest development for the species' benefit. Adapting management of a habitat for a species requires knowledge of how, when and why a species uses that habitat. A more precise knowledge of the spatial and structural aspects of forest habitat use by black grouse is thus required to complement, guide and improve the cost effectiveness of current and future intervention work. In particular, this information is needed to inform forest design plans in black grouse areas. This project sought to contribute towards filling the essential knowledge gap through analyses of existing lek and forest habitat databases and a new programme of telemetry studies of males and females in and around commercial Scottish forests.

1.2 Project objectives

This report is the combined output of three projects. The first project, 'Spatial and structural habitat requirements of black grouse in Scottish forests partnership project', incorporated radio-telemetry from August 2009 to March 2012 as well as lek data from highland Perthshire. The second project, 'Effects of forest structure on black grouse populations', sought to put the Perthshire lek data in context of lek data from other regions of Scotland. The third project, 'Spatial and structural habitat requirements of black grouse in Scottish forests partnership project extension including effects of forest structure on black grouse populations', extended the radio-tracking period for six months (to make additional analyses possible) and synthesised the first two projects. The objectives of each project are outlined below, and the locations within this report of the data or discussions pertinent to each are given in square brackets.

1.2.1 Objectives of the first project

The objectives of 'Spatial and structural habitat requirements of black grouse in Scottish forests' were:

1) To generate general relationships between black grouse occupancy and forest structure through review and analysis of existing datasets, in particular those held on lek locations for the National Forest Estate in Scotland. Such an analysis would look at lek size (number of attending males) and persistency in relation to forest structure variables including size, age, species composition, proportion of unplanted ground and distance from external moorland habitats. This part of the research would be used to generate testable hypotheses regarding the relationship between black grouse lek positions and forest structure variables (chapters 2 and 5).

2) To identify field sites. The review would identify sites which have sufficient birds present to enable new field studies to be conducted or to alter our programme in years 2 or 3 of the project (study sites used are described in chapters 2 and 3).

3) To develop individual-based models on the use of forest habitats. Our studies would measure how individually radio-tagged birds use the forest habitat and would address questions such as the minimum patch size of habitat utilized in differing seasons, the grain of habitat patches used and the scale of movements made between patches within the grain. This component of the research would generate individual-based models to fine-tune the relationships generated in objective 1 for males and females (chapters 3, 4 and 5).

4) To design field experiments to test limiting habitat factors. Outputs from objectives 1 and 3 would be used to define habitat variables that may limit black grouse occupancy of the forest environment. These limiting factors would be used to design prescriptive replicated field experiments in which key habitat variables would be manipulated (chapter 5).

1.2.2 Objectives of the second project

The objectives of 'Effects of forest structure on black grouse populations' were:

1) To define what forestry composition variables influence the number of males attending a focal lek (Chapters 2 and 5).

2) To clarify whether the results of the above match predictions from the Perthshire data, and to what extent is there regional variation in forest effects? (Chapters 2 and 5).

1.2.3 Objectives of the third project

The objectives of 'Spatial and structural habitat requirements of black grouse in Scottish forests partnership project extension including effects of forest structure on black grouse populations' were:

1) To extend the radio-tracking phase in order to determine the extent of forest use in the key breeding months (radio-telemetry is described in chapters 2, 3 and 4).

2) To determine whether differential winter habitat use has any carry-over effects in terms of survival or breeding success (chapters 4 and 5).

3) To provide one comprehensive report of work and findings of the two preceding projects in their entirety and the extended fieldwork combined (all chapters).

2. LEK-SCALE PATTERNS OF HABITAT ASSOCIATION

2.1 Introduction

Species distribution models can be used to investigate the link between land-use and species' distributions for conservation planning (Guisan & Thuiller, 2005). Collecting reliable data about animal locations is logistically challenging (Bibby *et. al.,* 1992; Sutherland, 1996). In a lekking species such as black grouse the larger ornamented males display together on conspicuous, frequently traditional, display grounds which the smaller, cryptically-coloured females visit only briefly for copulation (Cramp & Simmons, 1980). Thus, typically, temporal and spatial relative population indices are based on counts of leks during the peak lekking period (Fedy & Aldridge, 2011; Sim *et. al.,* 2008). Lek data are also used as presence data or as proxies for local population density in species distribution models (Hjeljord & Fry, 1995; Pearce-Higgins *et. al.,* 2007).

As leks form visible, measurable cores of populations that are used to assess trends and distributions and to target management, it is important to address how their distribution relates to that of non-lekking activities (feeding, roosting, nesting, broad-rearing, *etc.*) in a landscape. The association of multiple leks or large leks with certain habitat characteristics is assumed to indicate an overall positive effect of those characteristics (Hjeljord & Fry, 1995; Pearce-Higgins *et. al.,* 2007). Alatalo *et al.* (1992) suggest black grouse lek size varies through local and annual variation in production of offspring in the previous summer. Nesting habitat models for the lekking Gunnison grouse (*Centrocercus minimus)* were able to strongly predict lek locations (Aldridge *et. al.,* 2012). It has been demonstrated that females are attracted disproportionately to larger leks (Alatalo *et. al.,* 1992) perhaps providing a positive feedback mechanism as more males are in turn more likely to be recruited into that lek. Applied research must focus on the habitat conditions that provide the resources through the year to enable a lekking group to exist.

2.1.1 Objectives

This chapter addresses objective 1 of the first project ('To generate general relationships between black grouse occupancy and forest structure', see Section 1.2.1) and objectives 1 ('To define what forestry composition variables influence the number of males attending a focal lek') and 2 ('To clarify whether the results of the above match predictions from the Perthshire data, and to what extent is their regional variation in forest effects?') of the second project (see Section 1.2.2). To this end we used black grouse radio-telemetry, lek surveys and habitat mapping to address the sub-objectives below:

1) To examine the extent to which leks represent spatial distribution of activity in the landscape, thus informing optimal management strategies near to existing leks and the spatial requirements of a lekking group.

2) To examine extent of habitat selection at a lekking group level in the Tay region, and how this may have changed with changing habitat composition between 1992 and 2010.

3) To examine which habitats were associated with leks that became extinct, were maintained or became established in the Tay region between 1992 and 2010.

4) To examine whether any particular habitats were associated with local population density across regions, using lek size as a proxy.

5) To assess variation in habitat composition around leks between different regions in Scotland.

2.2 Methods

2.2.1 Study sites

Lek data were taken from four regions of Scotland: Argyll, Galloway, Inverness and Tay. Tay was the most intensively studied population with radio-telemetry data and lek data collected from 1992 and 2010. Lek data from Argyll, Galloway and Inverness was only collected in 2007 and used for comparison with the Tay region. Broad locations of leks used in the four study regions are displayed in Figure 2.1. More detailed maps of the Tay study area in 1992 and 2010 are provided in Figure 2.2.

The black grouse population in south-west Scotland, containing the Argyll and Galloway regions, decreased by 49% between 1995-6 and 2005 (Sim *et. al.,* 2008). The black grouse population in north-west Scotland containing the Inverness region, and the north-east region containing the Tay region, did not change significantly over the same period (Sim *et. al.,* 2008).

2.2.2 Radio-telemetry data

Between August 2009 and October 2011 we caught poult and adult black grouse of both sexes using either point-dogs and a drag-net or using a high-power lamp and hand-net at night-time roosts (Aldridge *et. al.,* 2012; Baines & Richardson, 2007). We fitted them with Biotrack TW-3 or Holohil RI-2B or RI-2D tags at 10-17 g (battery life 15-30 months). These weighed the equivalent of less than 3% documented adult body-mass (Cramp & Simmons, 1980) as recommended by Kenward (2004). We recorded weekly diurnal radio-locations at arbitrary times, typically between 0800 h and 1800 h GMT. Using a directional antenna and radio-receiver we approached a bird to obtain a precise location, hence flushing the bird. The radio-location (point the bird flushed from) was recorded using a GPS (precision 3 m). Weekly flushes were not expected to affect fecundity or survival (Baines & Richardson, 2007). Females were flushed only once from nests (when the location was recorded) and never with young broods; males were never flushed from leks. We were able to detect the lek that males recruited into as they would attend these regularly. We were unable to establish fully the leks that females visited as visitations typically occur only once (visitations are made in order to copulate, and copulation will occur only once per season in a large majority of females: e.g. 88% of 109 females in Finland: Lebigre *et. al.,* 2007).

The annual cycle was divided into autumn-winter (1 October - 31 March) and spring-summer (1 April - 30 September) (see Whitaker *et. al.,* 2007). These divisions approximate the start of the peak mating period and the end of the brood break-up periods respectively. They also broadly match the spring/autumn female dispersal (Caizergues & Ellison, 2002; Warren & Baines, 2002).

2.2.3 Lek data

Lek data were taken from two separate sources. Some leks within the Tay study area were surveyed in 1992 and 2010 by the authors and these were combined with other leks surveyed by the Perthshire Black Grouse Study Group in the same years. Leks for Argyll, Galloway, and Inverness regions were counted by Forest Enterprise Scotland staff in 2007 as an inventory of leks on the National Forest Estate (Scotland's state-owned forest areas).

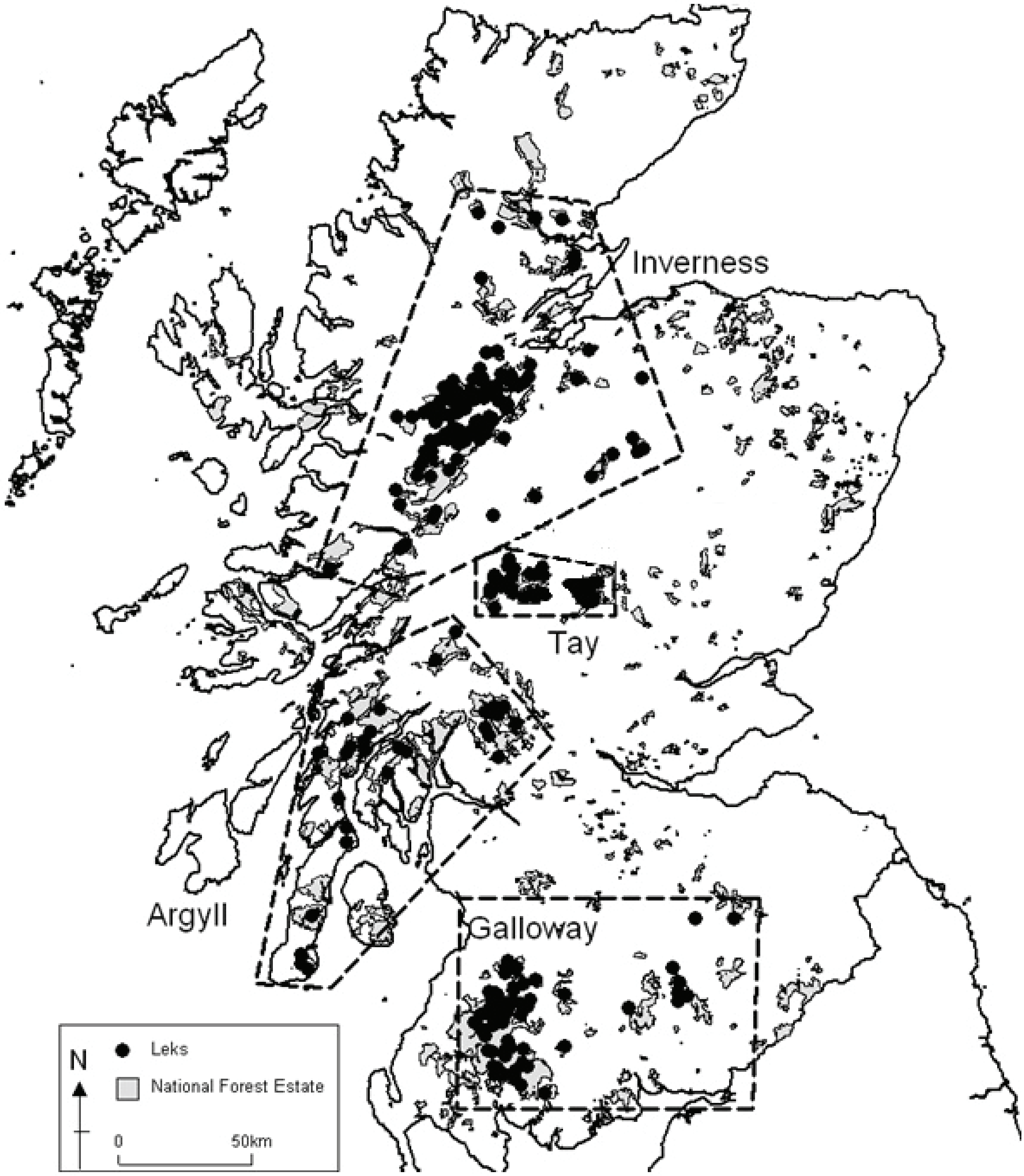


Figure 2.1. Locations and regional designations (enclosed dashed polygons) of leks for which data were used in this study. Locations of solo displaying males are also shown but these were excluded from analyses (see text). The radio-telemetry aspect of the study took place within the Tay region.

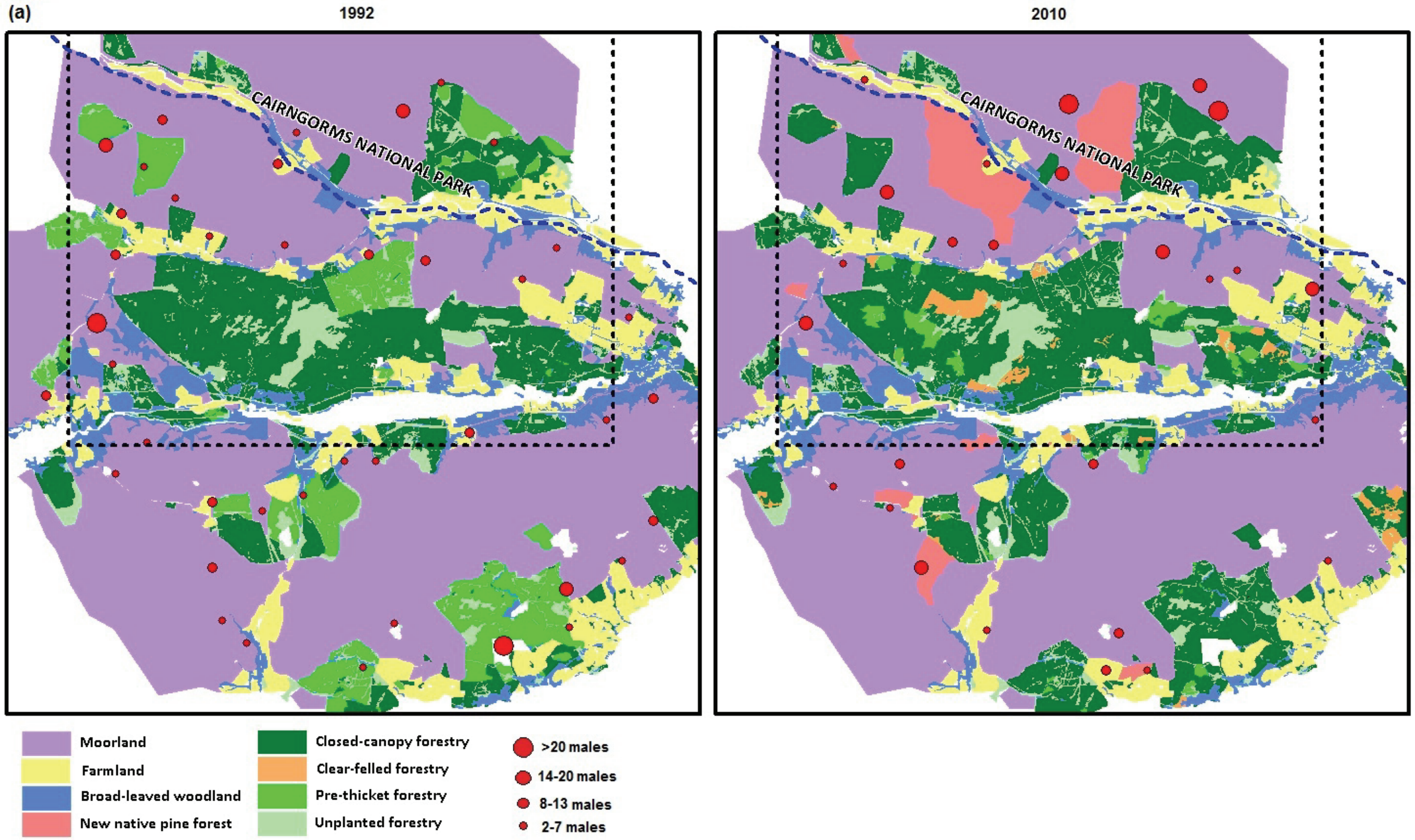


Figure 2.2a. Habitat coverage and lek locations in 1992 and 2010 for the Tay region at the Tummel area. Lek locations are stratified by number of displaying males as indicated by red circles. The solid lines represent the areas used in lek analyses and the dashed lines the areas for radio-telemetry analyses.

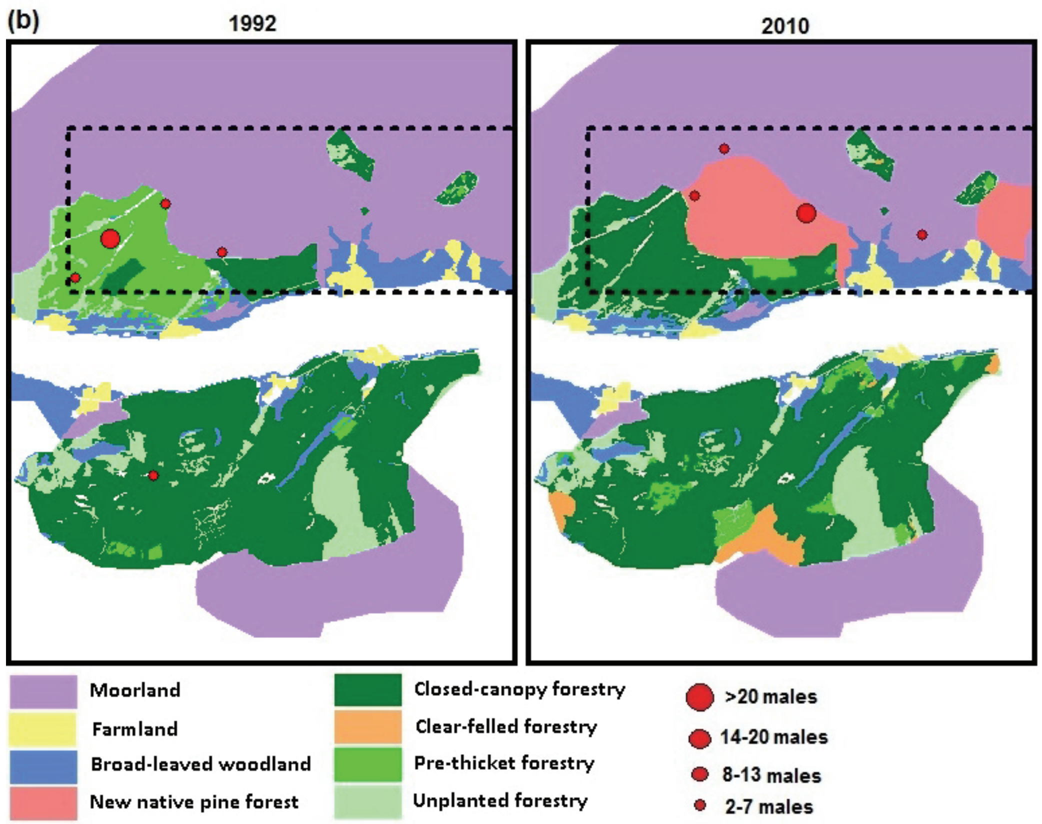


Figure 2.2b. Habitat coverage and lek locations in 1992 and 2010 for the Tay region at the Rannoch area. Lek locations are stratified by number of displaying males as indicated by red circles. The solid lines represent the areas used in lek analyses and the dashed lines the areas for radio-telemetry analyses.

Count methodology was similar across areas with one visit made in the second half of April and one in the first half of May (the period when the peak number of males will visit a given lek: Baines, 1996). Observers listened for display calls and visually scanned habitat with binoculars/telescopes according to a now national-standard protocol (Baines, 1996; Hancock *et. al.,* 1999; Sim *et. al.,* 2008). Visits were typically made within the first two hours after dawn and not in extremely wet or windy weather conditions. All displaying males were recorded and the count for a site was taken as the maximum number of males observed over the two visits. Maximum counts on grouse leks are resilient to some variation in the number of visits made (Fedy & Aldridge, 2011) so we included leks which only received a single count. The Tay region was subject to an intensive area-based survey, so we assumed that all leks in the area had been located. For the other regions however, counts targeted the National Forest Estate, so we could not assume the same.

The location of single displaying males is unlikely to be fixed, but may alter daily. Therefore compared to leks of two males or more their presence is less likely to be a function of surrounding habitat. Previous studies have either carried out separate analyses with and without single males (Pearce-Higgins *et. al.,* 2007, in which results were broadly similar for both) or excluded them altogether (Hjeljord & Fry, 1995); we took the latter approach. However, where a single male was within 1 km of a larger lek it was amalgamated into it as it would typically be considered to be a satellite bird. In such cases the location was assumed to be that of the largest lek. As all single males were excluded from further analyses, when we refer to leks we henceforth mean those of two males or more.

2.2.4 Habitat data around leks

We categorised the study areas into eight habitats (Table 2.1), plus ‘other’ (areas unsuitable for black grouse, e.g. buildings, roads and water bodies). These habitats are defined principally in terms of homogeneous land-use but there were clear vegetation structure and composition differences between them. Forestry stands were split into pre-thicket and closed-canopy based on previous black grouse studies which have shown that populations thrive in pre-thicket stands but decline rapidly at canopy-closure. 'Canopy closure’ coincides with a large reduction in cover of ground vegetation (Cayford, 1993; Owen, 2011). In plantations with little open space, both densities of males and females in August, and nesting females have been shown to reach zero at approximately 14 years (Baines *et. al.,* 2000) so we defined closed-canopy compartments as aged 14 years or more since planting. In reality, closure is likely to occur gradually and at different times within and between compartments and species (Owen, 2011), but it is necessary when dealing with large areas of forestry to set pre-determined fixed criteria to define forest growth stages (e.g. Hjeljord & Fry, 1995; Pearce-Higgins *et. al.,* 2007).

We delineated homogeneous habitat patches by a combination of drawing polygons from satellite images (Liu *et. al.,* 2010), field reconnaissance (Scott *et. al.,* 1998; Sutherland & Green, 2004) and forestry stock-maps. Map data were amalgamated and managed in MapInfo v. 11.0 (MapInfo Corporation, 2011) with MapBasic v. 10.0 (MapInfo Corporation, 2009), Google Earth v. 5.1 (Google Inc., 2009) and Quantum GIS v. 1.4.0 (Quantum GIS Development Team, 2010).

The percentage of each habitat type was measured within a 1 km radius of each lek site. Because lek positions are dictated by animals' choices or behaviour, which is what we were assessing, spatial autocorrelation would not be a problem except where overlap of radii occurred. Within region-years, we avoided overlap by equally splitting areas of overlapping radii. Mean overlap of radii was 5.3%, so areas around leks were only reduced on average by 2.7%. Because the Tay region had been subject to area-based surveys, study site habitat data were taken from an area created from a minimum convex polygon of all leks and their 1 km radii so we could compare habitat adjacent to leks to that in the landscape as a whole. For the other three regions we only mapped habitat within 1 km radii of all leks.

Table 2.1 - Descriptions of habitats defined in the study and their dominant tree-layer and field layer components.

Habitat	Location, structure and management	Tree layer	Field layer
Moorland	Open land previously or currently managed for red grouse *Lagopus lagopus scoticus* shooting and/or red deer *Cervus elaphus* stalking; some extensive sheep *Ovies aries* or cattle *Bos primigenius* grazing; little deer exclusion	Generally few and very sparse. Some taller eared-willow *Salix aurita* scrub layer	Variable, but with ericaceous dwarf shrub (particularly heather *Calluna vulagris*), purple moor-grass *Molinia caerulea* or peat moss *Sphagnum spp.* generally dominant
Farmland	More intensively grazed pasture typically at lower altitudes; generally improved; some cereal fields	None except for occasional single trees along boundaries	Grass (Poaceae) dominated
Broadleaf woodland	Typically along riparian habitats or moorland margins; little management except some grazing by sheep in wood pasture areas	Birch *Betula spp.* dominant with some rowan *Sorbus aucuparia*, aspen *Populus tremula* and willows *Salix spp.*	Grass dominated
New native pinewood	On previous moorland, approximately 14 years old or less; sparsely planted trees in clumps with approximately 20% open ground in between; fenced against red-deer and sheep intrusion; planted under government subsidy	Sparsely planted scots pine *Pinus sylvestris* dominant; some birch, rowan *Sorbus aucuparia* and oak *Quercus spp.* intermingled, combined with many naturally regenerating individuals	Variable, but with ericaceous dwarf shrub (particularly heather), purple moor-grass or peat moss generally dominant
Unplanted forestry	Areas enclosed within commercial forestry not planted, including tracks/rides; also areas where severe crop failure has left open areas; deer generally excluded or lethally controlled	Generally few and very sparse, some natural regeneration of birch, rowan and conifer species, especially close to crop edges	Variable, but with heather, purple moor-grass or peat moss generally dominant
Closed-canopy forestry	Commercial forestry stands where crop canopy has closed over (14 years or older)	Densely planted and dominated by monoculture Sitka spruce, Scots pine, lodgepole pine and larch *Larix spp.*	Generally little field layer, except for in glades formed by variable growth or wind-blow
Clearfell forestry	Commercial forestry stands that have been harvested but not restocked	Generally none, except some naturally regenerated lone or small groups of Scots pine or birch	Dominated by a brash layer, with ericaceous shrubs or grass regenerating between
Pre-thicket forestry	Commercial forestry stands where crop canopy has yet to close over (under 14 years old)	Densely planted and dominated by monoculture Sitka spruce, lodgepole pine and larch	Generally ericaceous or grass regenerating between trees

We defined three groups of leks: those present in 1992 that had become extinct by 2010, those that were present in both years, and those that were not present in 1992 but had established by 2010. We calculated log-ratio of change in each habitat within a 1 km radius of a site in 2010 and that site in 1992. Occasionally the precise location of a lek site in 1992 had drifted, and in such cases we used the radius around the 1992 location.

2.2.5 Statistical analyses

We carried out analyses in R 2.11.0 (R Core Development Team, 2010). We calculated the distance of all radio-locations and nest sites to lek sites during the three year radio-telemetry study period 2009-2012. We calculated distances to males' attended lek. As we did not know the leks that females visited we calculated distances only to the nearest lek (Warren *et. al.,* 2011). Following post-natal dispersal, females will remain in the area of a single lekking group in successive years (Soulsbury *et. al.,* 2011). Since we calculated distance to nearest lek for females, and in our area juveniles would typically disperse from near a paternal lek to near a mating lek, our method should not be affected by female dispersal distances. As distance from lek was calculated differently for males and females we carried out separate analyses on them. Within each sex we tested for a season effect in distance to lek. Using the 'lme4' package (Bates *et. al.,* 2012) we fitted generalised linear mixed models (GLMMs), with normal error distribution and identity link function, to the data with distance from lek (log-transformed) as the response variable, and season (two levels: autumn-winter / spring-summer) as the fixed effect. Because flushes of the same bird or males from a lek could not be considered independent we included factorial random effects lek ID and bird ID-within-lek ID for males and bird ID for females. From the data, we estimated the cumulative proportion of radio-locations within lek radii from 0.5 km to 4.0 km, in 0.5 km increments, and plotted these to examine spatial distributions in relation to lek sites.

We used compositional analysis to examine: (a) whether there was apparent selection for lek sites based on habitat composition around leks compared to habitat in the study site in the wider Tay region; (b) whether certain habitats in the Tay region were more associated with leks that went extinct between 1992 and 2010 or had become established between 1992 and 2010; and (c) whether certain habitats were associated with a smaller or larger lek size in the four regions in the years leks were monitored (Tay in 1992 and 2010, all other regions in 2007). For (a) and (c) we carried out analyses for each year separately, since the management of habitats available or within lek radii differed between years (Table 2.2). We carried out compositional analyses using the contributed packages ‘Adehabitat’ (Calenge, 2006), ‘Vegan’ and ‘lmPerm’.

Direct comparison of mean composition within lek radii and composition within the study site for each habitat cannot be used for assessing habitat selection for two reasons. Firstly, the mean composition values can be heavily skewed by a relatively small number of individuals that use a habitat a lot or a little. Secondly, the unit sum constraint means that the percentage cover of each habitat in a home-range or study area is not independent (Aebischer *et. al.,* 1993 b). Compositional analyses of habitat selection can address these issues by using non-parametric statistical comparisons and rendering the habitat data linearly independent via log-ratio transformations. We still presented mean and standard error percentages for reference.

Compositional analysis allows for multivariate analyses to be carried out to investigate the effects of multiple factorial and/or continuous covariates as necessary (Aebischer *et. al.,* 1993 a, b; Novoa *et. al.,* 2002). In the initial multivariate analysis-of-variance (MANOVA) stage of compositional analysis we used non-parametric MANOVA because we could not assume multivariate normality (Aebischer *et. al.,* 1993 b). Our test statistic was Wilk’s Λ (Aebischer *et. al.,* 1993 a) when comparing paired availability and use (for habitat selection analyses) or Anderson's (2001) *F* when comparing composition components against factorial or linear covariates. In each case *P*-values were obtained using randomisation.

Table 2.2 - Replacement table for habitats in the Tay study area showing the percentage area replaced by one habitat with another between 1992 and 2010. Changes in habitats are shown in bold. Habitat codes are: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, UN = unplanted forestry, CC = closed-canopy forestry, CF = clearfell forestry, PT = pre-thicket forestry. For clarity zeroes have been replaced by '-'.

		1992								
		MO	**FA**	**BW**	**NP**	**UN**	**CC**	**CF**	**PT**	***2010 total***
2010	MO	54.0	-	-	-	-	-	-	-	*54.0*
	FA	-	7.1	-	-	-	-	-	-	*7.1*
	BW	-	-	6.6	-	-	-	-	-	*6.6*
	NP	**4.6**	-	-	-	-	-	-	-	*4.6*
	UN	-	-	-	-	5.1	-	-	-	*5.1*
	CC	-	-	-	-	-	14.1	-	**6.5**	*20.6*
	CF	-	-	-	-	-	**1.1**	-	-	*1.1*
	PT	-	-	-	-	-	**1.1**	-	-	*1.1*
	1992 total	*58.6*	*7.1*	*6.6*	-	*5.1*	*16.3*	-	*6.5*	

In compositional analyses, the inferentially dependent variable can be placed as the independent variable so that MANOVA can be carried out with multiple habitats within a composition (Aebischer *et. al.,* 1993 a). Thus our independent variables were (a) a binary variable 'area considered' (two levels: study site / within 1 km of lek; their comparison constitutes analysis of selection), (b) a binary variable 'fate' between 1992 and 2010 (two levels: extinct / established), and (c) a continuous variable 'lek size' (square root transformed). Our dependent variables for (a) and (c) were log-ratios of all but one habitats over the remaining habitat type (the choice of which is arbitrary: Aebischer *et. al.,* 1993 b). For (b) our dependent variable was the log-ratios of change in all-but-one habitats over the remaining habitat. Where an independent variable showed a significant effect within MANOVA, a ranking matrix was constructed for that variable which indicated which habitats were associated more with either (a) lek areas versus the study site, (b) extinct versus established lek sites, or (c) a higher or lower value of lek size. The mean log-ratios of each possible pair of habitats were calculated and the results cast into a ranking matrix (Aebischer *et. al.,* 1993 a). Randomisation tests were used to carry out pairwise tests between habitats at $P = 0.05$. Multiple pairwise tests are standard within compositional analyses (Aebischer et al. 1993 a). We did not adjust our α-level because there is no standard limit over which such adjustments should be made (Gotelli & Ellison, 2004).

To visualise selection, lek size or lek fate patterns, we took the difference in the log-ratio ('used' minus 'available' in selection analyses, 'established' minus 'extinct' in fate analyses) or the slope of the log ratios (against square root of lek size) for a matrix of habitats considered . This is the equivalent of creating a ranking matrix (Aebischer *et. al.,* 1993a). Then for each habitat in turn we took the mean and standard error value against all other habitats considered and plotted them on bar charts. These charts can be viewed as plots of relative selection of each habitat and confidence in its ranking. To assess regional variation in habitats around leks (2010 for Tay, 2007 for the other three regions) we calculated their coefficient of variation (standard error divided by the mean).

2.3 Results

2.3.1 Distances of radio-locations to leks

Distances of radio-locations from lek sites varied significantly with season for males (X^2_1 = 22.11, P < 0.001) but not for females (X^2_1 = 1.08, P = 0.300), so only males were considered separately by season. The asymptotes of the cumulative percentage of mean distances (Figure 2.3) show that for nests (n = 17), females and spring-summer males activity was concentrated within 1.5 km (each >70%), and for autumn-winter males within a wider area.

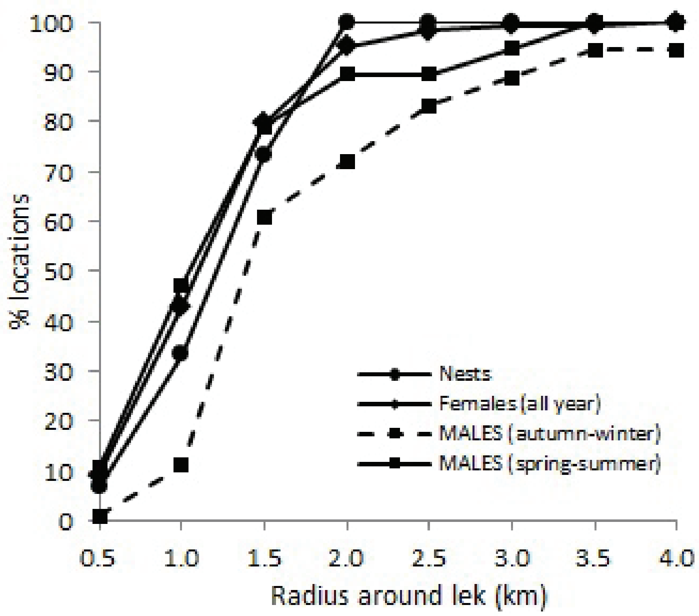


Figure 2.3. Cumulative percentage locations for each group within a given radius (km) around a lek for nests (n = 17), female locations (n = 666), spring-summer male locations (n = 467) and autumn-winter male locations (n = 554).

2.3.2 Habitat change and lek distributions in the Tay region

Habitats within the Tay region changed between 1992 and 2010 (Table 2.2). There were four types of habitat patch change in the study site. Moorland was converted to new native pinewood in 4.6% of the area, although 54.0% of the total area remained as moorland cover. Identical amounts of closed-canopy forestry in 1992 had become either clear-fell or pre-thicket forestry by 2010 (each 1.1% of the study area), and 6.5% of the study area had matured from pre-thicket to closed-canopy forestry. Overall the total cover of closed-canopy forestry increased from 16.3% to 20.6%.

We found significant selection at the scale of the lekking group in both years (Table 2.3). Moorland was significantly selected relative to farmland, pre-thicket forestry and closed-canopy forestry, but not relative to unplanted forestry and broadleaf woodland in 1992. It was also positively selected relative to all other habitats in 2010 (note that different habitats were available in analyses). In 1992, unplanted forestry was significantly selected relative to pre-thicket and closed-canopy forestry. The dominant ranking of moorland along the selection-avoidance gradient is evident in both 1992 and 2010 (Figures 2.4a and b), and there is a relatively high confidence in this rank (relatively narrow standard error bars). There is more ambiguity around the ranks of other habitats.

Table 2.3 - Compositional analyses results for Tay region data: habitat selection within 1 km of leks relative to the study site in 1992 and 2010, relationship between management habitat composition and lek fate between 1992 and 2010 and relationship between habitat composition and lek size in 1992 and 2010. Pairwise differences are only shown for significant analyses. Habitat codes are as follows: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, UN = unplanted forestry, CC = closed-canopy forestry, CF = clearfell forestry, PT = pre-thicket forestry. For brevity, a vertical line ('|') indicates where more than one habitat was significantly different (">>") to another habitat in pairwise tests.

Test	Year(s)	Statistics	Habitats considered	Pairwise (P < 0.05)
				most>least
Selection	1992	$\Lambda = 0.59$ $P = 0.002$	MO,FA,BW,CC,UN,PT	MO>>FA|PT|CC; UN>>PT|CC
	2010	$\Lambda = 0.15$ $P = 0.002$	MO,FA,BW,NP,CC,UN	MO>>FA|NP|BW|CC|UN
				established>extinct
Lek fate	1992-2010	$F_{1.44} = 3.23$ $P = 0.023$	MO,NP,CC,CF,PT	NP>>CF|CC
				larger>smaller
Lek size	1992	$F_{1,43} = 0.44$ $P = 0.699$	MO,FA,BW,CC,UN,PT	-
	2010	$F_{1,28} = 3.51$ $P = 0.023$	MO,FA,BW,NP,CC,UN	CC|UN|MO>>FA

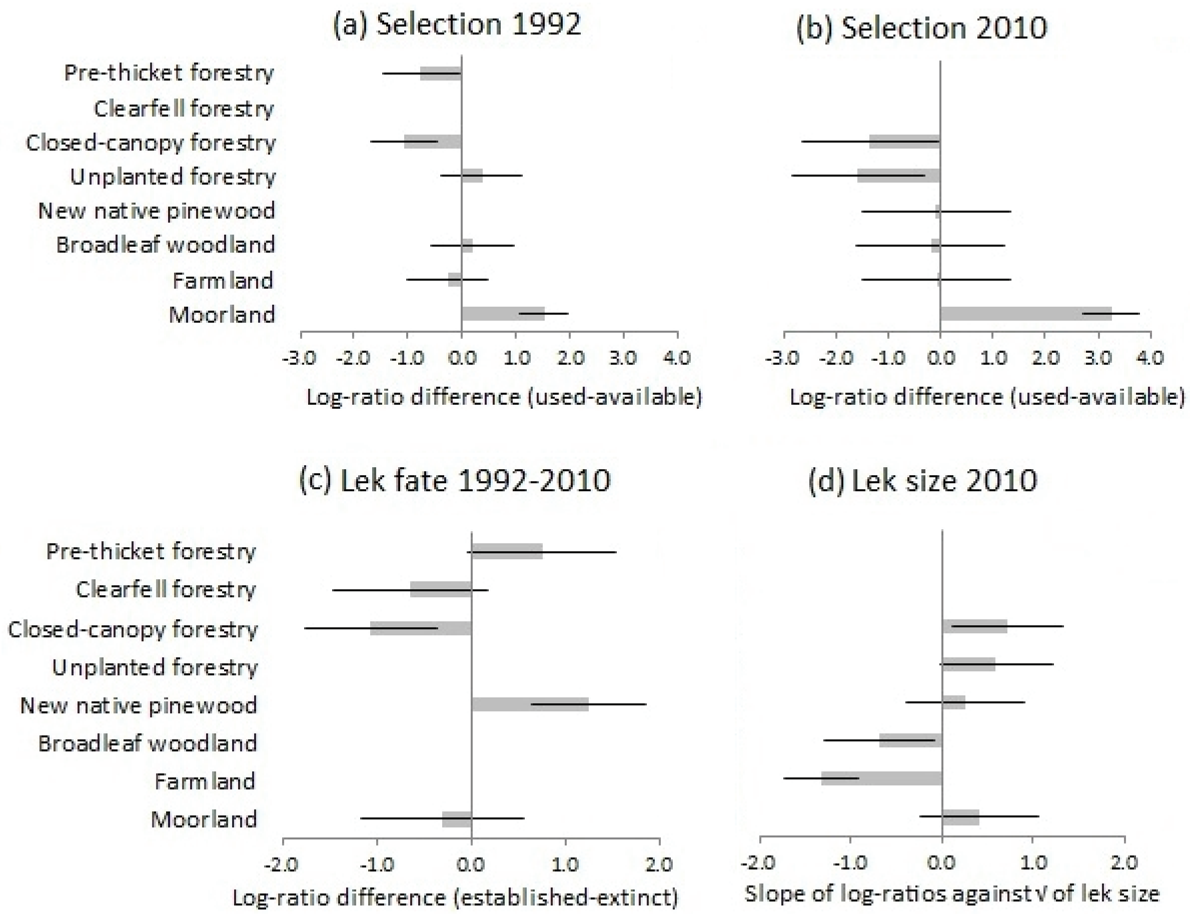


Figure 2.4. Mean difference in log-ratio ([a-b] 'used' minus 'available' for selection in 1992 and 2010, [c] 'established' minus 'extinct' for lek fate between 1992 and 2010) or slope of log-ratio (against the square route of lek size) for each habitat in turn against all other habitats considered (or change in habitat for lek fate). Whiskers represent between-habitats standard errors of differences (a, b, d) or slope (c). Habitats without bars or whiskers were excluded from analyses but are retained on axes for comparison. These plots show both the ranking of the habitats (higher values are more selected, associated more with establishment of leks, or associated with bigger leks), and the relative confidence of that rank (larger whiskers mean we can be less sure about the placement of that habitat. Pairwise differences (Table 2.3) were assessed using non-parametric statistical tests, so are not directly comparable with the whiskers shown.

Leks that became extinct, those that were maintained and those that were established between 1992 and 2010 displayed different habitat change within a 1 km radius (Table 2.4). Established leks showed a more positive change in new native pinewood and a less positive change in clear-fell and closed-canopy forestry than extinct leks (Table 2.3). The rankings of the habitats from compositional analyses are shown in Figure 2.4 c.

Table 2.4 - Replacement table for habitats within lek radii in the Tay study area showing the percentage area replaced by one habitat with another for lek sites that went extinct, were maintained, or were established between 1992 and 2010. Changes in habitats are shown in bold. Habitat codes are as follows: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, UN = unplanted forestry, CC = closed-canopy forestry, CF = clearfell forestry, PT = pre-thicket forestry. For clarity zeroes have been replaced by '-'.

		1992								
2010 fate		**MO**	**FA**	**BW**	**NP**	**UN**	**CC**	**CF**	**PT**	***2010 total***
Extinct	MO	39.9	-	-	-	-	-	-	-	*39.9*
	FA	-	10.2	-	-	-	-	-	-	*10.2*
	BW	-	-	7.5	-	-	-	-	-	*7.5*
	NP	**5.2**	-	-	-	-	-	-	-	*5.2*
	UN	-	-	-	-	6.2	-	-	-	*6.2*
	CC	-	-	-	-	-	9.4	-	**20.0**	*29.4*
	CF	-	-	-	-	-	**0.6**	-	-	*0.6*
	PT	-	-	-	-	-	**0.9**	-	-	*0.9*
	1992 total	*45.1*	*10.2*	*7.5*	-	*6.2*	*10.9*	-	*20.0*	
Maintained	MO	65.6	-	-	-	-	-	-	-	*65.6*
	FA	-	6.9	-	-	-	-	-	-	*6.9*
	BW	-	-	5.5	-	-	-	-	-	*5.5*
	NP	**13.1**	-	-	-	-	-	-	-	*13.1*
	UN	-	-	-	-	1.4	-	-	-	*1.4*
	CC	-	-	-	-	-	2.6	-	**4.5**	*7.1*
	CF	-	-	-	-	-	**0.3**	-	-	*0.3*
	PT	-	-	-	-	-	**0.1**	-	-	*0.1*
	1992 total	*78.7*	*6.9*	*5.5*	-	*1.4*	*3.0*	-	*4.5*	
Established	MO	65.0	-	-	-	-	-	-	-	*65.0*
	FA	-	12.0	-	-	-	-	-	-	*12.0*
	BW	-	-	4.3	-	-	-	-	-	*4.3*
	NP	**10.5**	-	-	-	-	-	-	-	*10.5*
	UN	-	-	-	-	1.2	-	-	-	*1.2*
	CC	-	-	-	-	-	4.0	-	**2.8**	*6.8*
	CF	-	-	-	-	-	**0.1**	-	-	*0.1*
	PT	-	-	-	-	-	**0.1**	-	-	*0.1*
	1992 total	*75.5*	*12.0*	*4.3*	-	*1.2*	*4.2*	-	*2.8*	

We found a significant relationship between lek size and habitat composition in the Tay region in 2010 but not in 1992 (Table 2.4). Farmland was significantly more negatively related to lek size than the amount of moorland, closed-canopy and unplanted forestry, but not broadleaf woodland and new native pinewood. The rankings of the habitats from compositional analyses can be seen in Figure 2.4 d. The small standard error for farmland suggests we can have confidence in its low ranking and, therefore, that it has the most negative relationship with lek size.

2.3.3 Between-region comparison

Management of habitats within 1 km of leks differed among the four regions (Table 2.5). There was no significant relationship between lek size and habitat composition in 2007 for Inverness ($F_{1,49}$ = 0.30, P = 0.884), Argyll ($F_{1,17}$ = 1.05, P = 0.347) or Galloway ($F_{1,24}$ = 1.50, P = 0.182). The coefficient of variation (CV) in habitats around leks across regions was lowest for moorland (0.19) than any other habitats (the range of CV for other habitats was 0.51-1.55) (Table 2.5). When unplanted forestry (small areas of previous moorland now surrounded by forestry) was combined with moorland, the CV was lower (0.07). Composition of young forest components varied quite widely between regions (CV for new native pinewood 0.91, CV for pre-thicket forestry 0.95). Regions with high pre-thicket forestry around leks, however, tended to have less new native pinewood and when the two habitats were considered together as 'total young forest', CV was 0.22.

Table 2.5 - Habitats around leks used in the study. For the Tay region, data were within 1 km radii around leks in 1992 and 2010. For the Argyll, Galloway and Inverness districts, data were available for within 1 km radii around leks only for 2007, when the National Forest Estate inventory of lek sites was taken. Habitats represent the percentage present in each given area (± SE). 'CV' is the coefficient of variation across regions (2010 for Tay, 2007 for all other regions). 'Arg.' = Argyll, 'Gall.' = Galloway, 'Inv.' = Inverness.

	Region and year					
Data	**Tay '92**	**Tay '10**	**Arg. '07**	**Gall. '07**	**Inv. '07**	**CV**
No. of leks	45	30	19	26	51	-
No. of males	354	306	95	135	438	-
Males per lek	7.9	10.2	5.0	5.2	8.6	0.35
Moorland	56±4	67±4	43±8	50±7	58±4	0.19
Farmland	9±2	9±2	2±2	0	2±1	1.55
Broadleaf woodland	7±1	5±1	6±2	1±0	5±1	0.52
New native pinewood	0	11±4	3±1	0	12±3	0.91
Unplanted forestry	5±1	1±0	16±4	12±3	6±1	0.75
Closed-canopy forestry	8±2	6±2	17±5	25±4	14±2	0.51
Clearfell forestry	0	0	3±1	3±1	1±0	0.86
Pre-thicket forestry	15±3	0	10±3	9±2	2±1	0.95
Moorland + unplanted	60±4	68±4	58±4	61±5	64±3	0.07
Pre-thicket forestry + new native pinewood	15±3	11±4	13±3	9±2	15±3	0.22

2.4 Discussion

2.4.1 Spatial distribution relative to leks

The majority of both male and female activity and nest sites were within 1.5 km of lek sites. However, the space use per unit area around a lek showed that a 1 km radius provided a more efficient measure of habitat use since it included the optimum balance (for females and nests, and spring-summer males) of those areas used and not used by black grouse. In females for example, although a 1.5 km radius included 86% more activity, it had to include 125% more area so is likely to include a large proportion of unused or lesser used land. This suggests that a 1 km radius was optimal for analyses of lek-habitat relationships in our study area. It is possible that patterns of activity around leks are region-specific. For example, while we found that 34% of nests were within 1 km of lek sites, this is lower than 72% of nests within 1 km of lek sites in a northern England population (Warren *et. al.,* 2011). In a Finnish study the mean distance between lek of copulation and the nest was 1.2 km (Alatalo *et. al.,* 1992).

2.4.2 Habitat change and lek distributions in the Tay region

Some habitat changes likely to influence black grouse populations occurred in the Tay study area between 1992 and 2010. Forestry stands matured substantially, with pre-thicket areas decreasing and closed-canopy areas increasing. In addition, the amount of moorland decreased by 4.6% of the study area, replaced by enclosed new native pinewood schemes. The number of lekking males in our study area fell by 14% between 1992 and 2010 (354 to 306), but these males occupied 33% fewer lek sites, thus the average lek size was 29% larger. Underlying this change in numbers of leks was an extinction of 30 out of 45 of the leks, but only an establishment of 15 new leks. This clearly demonstrates a distributional shift within the study area.

In both years there was a high degree of selection by lekking groups for moorland relative to other habitats. However, the extent of this selection had increased over the interval; while moorland had decreased by 4.6% over the period, the area within 1 km of leks had increased by 11%. The amount of new native pinewood that replaced this moorland had increased from 0% to 4.6% of the area and it was present in an average of 11% of habitat within 1 km of leks in 2010. In contrast, the other young forest type, pre-thicket forestry, had fallen both in the area (6.5% to 1.1%) and, disproportionately, within 1 km of leks (15% to 0%). These changes resulted from specific circumstances based on the management history of the Tay region landscape. Forest planted in the 1980s, at a pre-thicket stage in 1992, matured to closed-canopy stands by 2010. Meanwhile, most stands planted in the 1950s-70s had not yet been felled and re-stocked by 2010. The result was a proportionately large area of closed-canopy forestry. Had it not been for government subsidised native pinewood schemes, the area of young forest in the study area would have been extremely low (only 1% of the land was pre-thicket forestry in 2010), assuming lack of such subsidies would not have substantially influenced decisions to plant additional commercial forestry.

Habitats near to leks that were maintained or established between 1992 and 2010 were similar in nature, as was the extent to which they had changed. The area of mature forest had changed little, while the size of reduction in moorland had been matched by the increase in new native pinewood that replaced it. In stark contrast, habitats near to the lek sites that went extinct after 1992 had become more dominated by mature forest while the area of young forest had fallen. Additionally, these sites had much less moorland associated with them. Compositional analyses demonstrated the apparent importance of the change in young forest in the likelihood of a lek site having gone extinct or one having become established over the period. In other words, sites where pre-thicket forestry had matured were more likely to be abandoned while sites where new native pinewood was planted were more likely to have lekking groups establish. This looks to have been the mechanism driving distributional shifts.

Relationships between lek size and habitats around leks were observed in the Tay region in 2010, but not in 1992. The relative proportion of farmland around leks compared to all other habitat except broadleaf woodland was negatively related to lek size. In the Tay radio-tagged population no nests were located on farmland (Chapter 4). A possible explanation is that leks with more farmland adjacent have less suitable nesting habitat nearby, and consequently produce fewer recruits. As local and annual variation in production of offspring in the previous summer can be key to driving black grouse populations and lek numbers (e.g. Alatalo *et. al.,* 1992), this could mean smaller leks in these areas. Such a relationship was not observed in the Argyll, Galloway or Inverness Forest Districts but these areas had lower mean levels of farmland around leks (0-2% compared to 9% in Tay).

2.4.3 Regional similarities in habitats around leks

Ecological relationships can vary by region within the same country (e.g. Whittingham *et. al.,* 2007) so it is important to consider the generality of results across regions. For example willow ptarmigan *L. l. lagopus* occurrence showed a negative relationship with willow thicket fragmentation only where willow was scarce in the landscape (Ehrich *et. al.,* 2012). There was relatively little regional variation in the average cover within 1 km of leks of moorland, moorland combined with unplanted forestry, and young forest (pre-thicket and new native pinewood) combined. These are the primary areas that we would expect breeding to occur (see chapter 4). This average composition within 1 km of leks, of approximately 60-67% moorland habitats (providing nesting, brood-rearing, lekking and feeding), smaller areas (10-14%) of young forest (providing nesting, brood-rearing, shelter and cover from predators) (Table 2.5) could provide an indication of the optimum balance of resource requirements for a black grouse lekking group and associated females in Scotland. Indeed, despite a large distributional shift in the Tay region between 1992 and 2010, lekking groups had maintained a relatively similar composition of these habitat types within 1 km.

2.5 Summary

We used radio-telemetry and lek count data in the Tay region to investigate distributions of black grouse in relation to habitat composition. Most non-lekking activity occurred within 1.5 km of lek sites, including female year-round activity and nesting. Lekking groups in the Tay region strongly selected for moorland areas, a pattern which remained consistent as the availability of moorland habitats decreased between 1992 and 2010. The change in moorland to new native pinewood relative to the change in pre-thicket forestry to closed canopy forestry was significantly greater around leks that became established between 1992 and 2010 than leks that became extinct. This suggests planting of new native forests was linked to new establishment of leks and maturing of pre-thicket forestry was linked to lek extinctions. Black grouse in the Tay region were able to shift distributions over time which is essential given the transitional nature of the habitats they use. We compared habitat composition around leks between this and three other Scottish regions (Argyll, Inverness and Galloway). There was high variation in individual habitats between regions, but moorland and young forest (pre-thicket forestry and new native pinewood) had relatively constant presence around leks across Scotland (averaging 43-67% and 9-15% respectively).

3. INDIVIDUAL-SCALE PATTERNS OF HABITAT USE AND SELECTION

3.1 Introduction

The black grouse is a highly sexually dimorphic species, with large differences in size, plumage and distinct breeding roles (Cramp & Simmons, 1980; Watson & Moss, 2008). Grant & Dawson (2005) hypothesised sex differences in habitat preferences due to these underlying differences but found that evidence for such differences was scarce. Rather they identified a larger base of evidence for seasonal differences, with forest habitats used more in winter.

Sex, season and age differences would be expected as the resource needs of birds, and access to the resources themselves, may vary according to the breeding role of birds, change through the annual cycle and change as a bird ages. Knowledge of these patterns could allow conservationists to design habitat mosaics that provide the optimal combination of habitats for birds of different sexes and ages throughout the annual cycle. Where financial resources are limited, identifying the habitats that are most important for groups considered to be most important in driving demographic change (e.g. females if productivity is low, juveniles if recruitment is low) could make conservation efforts more efficient.

In chapter 2 we identified that mature forestry is avoided relative to moorland within 1 km of leks and that forest maturation tends to lead to local lek extinctions (see also Pearce-Higgins *et. al.,* 2007). Mature forestry therefore may form a spatial restriction to black grouse in a given area, and potentially a barrier for connectivity between populations. It is important, therefore, to consider the extent to which birds move from external open habitats into forests, particularly commercial forests, and what characteristics might influence this movement. Such information could allow forests to be designed with the optimal balance between productivity of timber and accessibility to black grouse.

3.1.1 Objectives

This chapter addresses objective 3 of the first project ("To develop individual based models on use of forest habitats", see Section 1.2). To this end we used black grouse radio-telemetry to address the below sub-objectives:

1) To describe the spatial use of birds, particularly the size of home-ranges of males and females.

2) To test whether birds selected for habitats relative to their availability, and whether this selection varied according to sex, age and season.

3) To investigate the extent to which birds moved into commercial forestry plantations from external open habitats and how movements were influenced by forest structure.

4) To investigate field-layer and tree vegetation at radio-locations of birds.

3.2 Methods

3.2.1 Study sites

Radio-telemetry was carried out in the Tay region (Figure 2.1) and located wholly within the areas considered for lek analyses (Figure 2.2). Specifically, we targeted catching around two large-scale commercial forest areas to examine the response of individual birds to variation in forest structure. These blocks were in the vicinity of Tummel Bridge (56°42’01”N, 04°11’11’’W), with subsequent movements of tagged birds defining the study area limits. The focal forests were the Tummel Forest (study area A: Figure 3.1) and the Talladh-a-Bheithe Forest (study area B: Figure 3.1). Both areas had detailed sub-compartment level GIS data available from Forest Enterprise Scotland which we used to compare planting histories and species composition. The two focal forests were at different stages (A: more than 75% first generation planting 1950s-60s, second generation re-stocking 2000s in 10% of area; B: more than 75% first generation planting 1980s, second generation re-stocking 2000s in 3% of area) (Table 3.1). The study areas cover an altitudinal range of 140-490 m (A) and 200-580 m (B) above mean sea-level.

Table 3.1 - Attributes of the two focal commercial coniferous forests (Tummel and Talladh-a-Bheithe) around which radio-telemetry was targeted. Values rounded to 0% or 0 ha are displayed as '-' for brevity.

Attribute	**Level**	**Tummel**	**Talladh-a-Bheithe**
Area (ha)	-	3,062	1,111
Habitat	Closed-canopy	66%	83%
	Clearfell	5%	-
	Pre-thicket	10%	3%
	Unplanted	19%	13%
Planting decade	pre-1940s	-	-
	1940s	6%	-
	1950s	25%	13%
	1960s	52%	-
	1970s	7%	4%
	1980s	-	79%
	1990s	1%	-
	2000s	9%	4%
Species composition	Scots pine	32%	10%
	Sitka spruce	31%	44%
	Lodgepole pine	19%	27%
	Larch spp.	8%	11%
	Douglas fir *Pseudotsuga menziesii*	5%	7%
	Norway spruce *Picea abies*	4%	1%
	Mixed conifers	1%	-
2nd rotation pre-thicket planting per year prior to project (ha)	2000	4	-
	2001	-	4
	2002	120	-
	2003	82	28
	2004	-	-
	2005	74	-
	2006	-	-
	2007	-	-
	2008	-	-
	2009	22	-
	Total	302	32

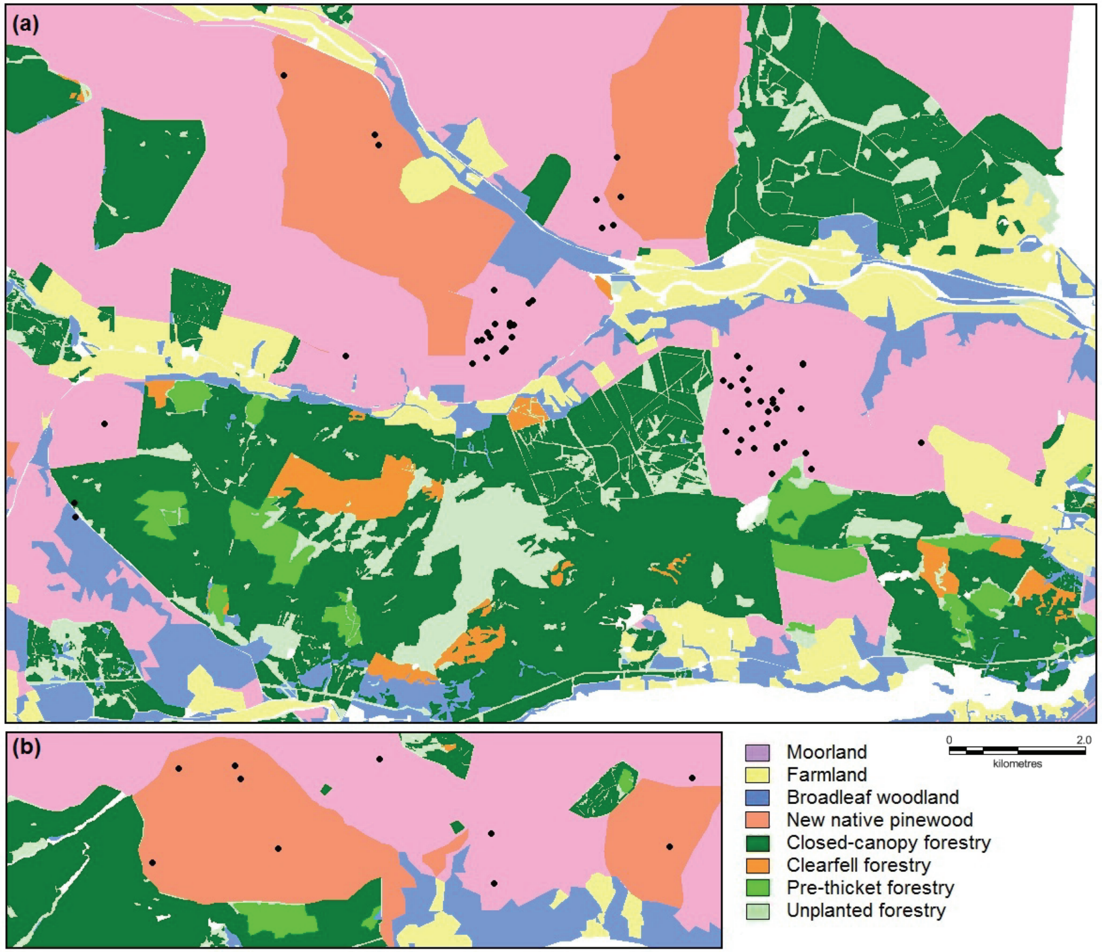


Figure 3.1. Habitat map of study areas with catch locations of 89 birds fitted with radio-collars ('●', some overlain): (a) study area A, (b) study area B. Areas shown represent smallest rectangles containing all subsequent live radio-locations.

3.2.2 Radio-telemetry data

Catching, tagging and weekly tracking of radio-tagged birds is described in Section 2.2.2. At each radio-location we recorded whether a bird was in a tree or on the ground. A 5 m radius circle was centred on each radio-location, within which tree count, average tree height, and most frequent tree species were recorded. A 16 m^2 square ground quadrat (Hill *et. al.,* 2005; Rodwell, 2006) was also centred at each radio-location. Within this we recorded percentage cover, to 5% (see Rodwell, 2006), of a range of taxa within the field/ground layer: heathers (*C. vulgaris* and *Erica* spp.), berries (*Vaccinium* spp. and *Empetrum nigra*), grasses (Poaceae), bog myrtle *Myrica gale*, sedges (Cyperaceae), rushes (Juncaceae), mosses (Bryophyta) and 'others' (all other categories combined). Vegetation height (to nearest 5 cm) was recorded from five points within the quadrat: one at the centre and four randomly selected along each quadrat side.

3.2.3 Describing home-ranges

A home-range (HR) can be defined as a 'repeatedly traversed area where an animal has settled and has a pre-determined probability of occurring during a given period' (Whitaker *et. al.,* 2007). Because radio-tagged birds are not located at all times, it is necessary to infer a home-range or habitat use from these discrete observations. For habitat selection analyses and investigating HR characteristics we described a 100% minimum convex polygon (MCP_{100}) which is the smallest possible polygon containing all radio-locations with external angles greater than 180° (Kenward, 2004). HRs were constructed only where ≥ 10 live radio-locations (Conner, 2001) had been recorded per bird per season and where these spanned ≥ 90 days (half the season). We tested for a significant correlation between the number of radio-locations per bird-season and size of MCP_{100} in order to test if the number of locations recorded had influenced HR size and thus required correcting for (Kenward, 2004). HRs were constructed for autumn-winter and spring summer seasons separately, using the same seasonal divisions described in Section 2.2.2.

3.2.4 Habitat selection analyses

As discussed in Section 2.2.5, direct comparison of mean composition within home-ranges and composition within the study site would be unsuitable for assessing habitat selection. To assess selection we compared use and availability of habitats using compositional analyses (section 2.2.5) at MCP_{100} within study area (called '2nd order selection') and radio-locations themselves within MCP_{100} (called '3rd order selection') (Aebischer *et. al.,* 1993 b; Erickson *et. al.,* 2001), using 'Adehabitat' (Calenge, 2006) within R 2.11.0 (R Core Development Team, 2010). The study area was defined as a larger minimum convex polygon containing each bird-season MCP_{100}, computed separately for study areas A and B. We did not consider '1st order selection' which describes the range of a species within the wider country (e.g. its range within Scotland) (Aebischer *et. al.,* 1993 b). This hierarchical structure reflects the fact that animals make selection behaviours at different spatial scales (e.g. Aldridge *et. al.,* 2012). We carried out analyses for all season-sex-age combinations (eight groups). Within each analysis, habitats not used by at least two birds or available to at least half of birds were excluded. Our test statistic was Wilk's Λ (Aebischer *et. al.,* 1993b). Randomisation tests were used to carry out pairwise tests between habitats at P = 0.050. Selection patterns were visualised in the same manner as lek selection patterns (Section 2.3.5)

3.2.5 Movement from external habitats into forestry

For each radio-location within forestry, we used GIS to measure the minimum linear distance to the boundary between the forestry and the external habitat patch (i.e. non-forestry area, typically moorland or new-native pinewood) on which the bird was found (called 'movement into forestry'). Where the radio-location was in a closed-canopy patch, the minimum distance to the edge of that specific patch (i.e. to the nearest point not considered closed-canopy forestry) was also recorded. We used a non-parametric Wilcoxon rank sum test to test for sex differences in maximum movement into forestry and movement into closed-canopy patches.

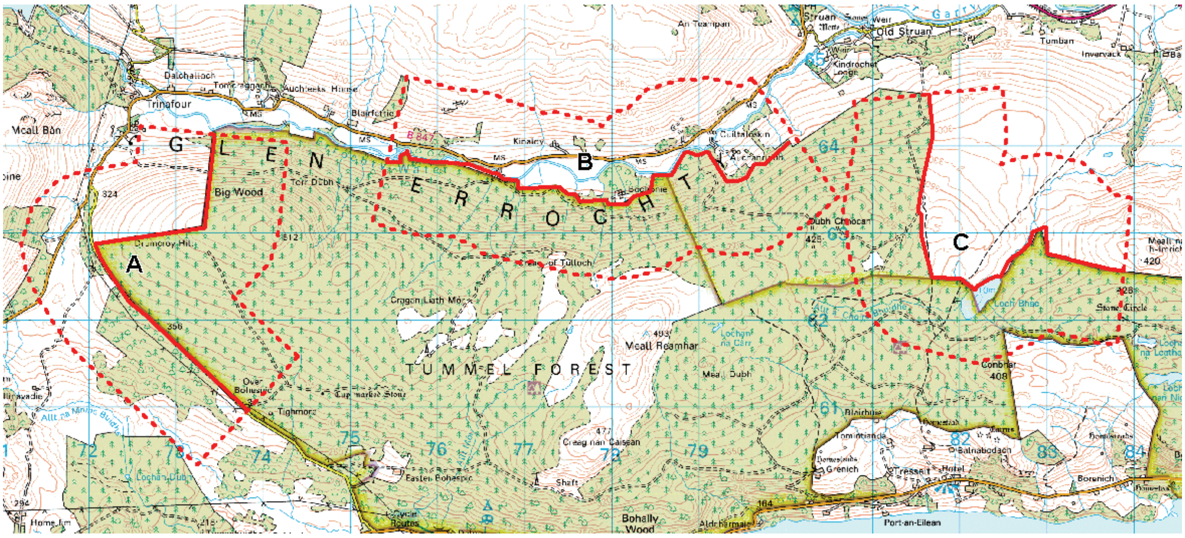
There were four boundary sections within the study area between large-scale forestry and external moorland or new native pinewood patches which contained lek sites, known breeding habitat and where multiple birds were radio-tagged over the course of the project (Figure 3.2). So that we could compare these boundaries directly, we selected the central 5 km length of boundary. The length of 5 km was chosen arbitrarily as containing a large proportion of locations along each boundary. We then created a buffer-zone, perpendicular to the boundary, 0.85 km either side of the boundary itself. This distance represents the radius of a circular area of 228 km^2, the mean MCP_{100} size across all home-ranges in the study, and contains 80% of all movements into forestry in the study (80^{th} percentile of forestry movements = 0.87 km).

Along these boundaries and within their buffer zones we recorded a number of variables that we hypothesised might influence the movement of black grouse into forestry. For the linear feature of the boundary itself we recorded the percentage of non closed-canopy forestry patches (unplanted, pre-thicket or clear-fell) along the interior line as these could alter the connectivity across the boundary. Within the forestry component of the 0.85 km buffer we recorded the percentage cover of each forestry patch-type, as well as the combined percentage of non-closed-canopy patches (i.e. the general 'openness' of the forestry). In addition we recorded the percentage of the closed-canopy component which consisted of larch, as this is potentially important as a source of protein for females prior to breeding (Baines 1990). Finally we recorded three broad measures of bird movement into forestry across these boundaries: the percentage of all radio-locations within the buffer zone that were on the forestry side, the mean distance into the forestry of those locations and the maximum distance into forestry of those locations.

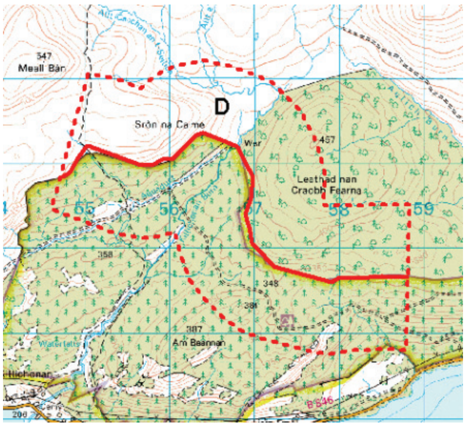
Within each boundary we identified all unplanted patches and larch stands. For these identified patches, we also recorded any use by radio-tagged birds. We used frequency distribution plots to compare the availability of unplanted and larch patch size categories with detected use from radio-telemetry.

3.2.6 Use of forestry at a forest scale: availability of 'open' patches versus use

Within the Tummel Forest as a whole we identified all major unplanted, clearfell and pre-thicket patches ('clearings') using stock-maps and then confirmed categories with ground visits. Two sets of transect surveys were carried out within these patches: a winter set between 8 October and 17 December 2009 and a spring set between 12 April and 18 May 2010. Within any one clearing, transects were 200 m apart running parallel with a clearing edge, with sufficient transects walked to cover every section of a clearing to within 200 m. Transects were walked at a moderate pace by a single observer during daylight hours. When black grouse were flushed, the number and sex of all flushed birds were recorded as well as those habitat data recorded for radio-telemetry flush-points. For these identified patches, we also recorded any use by radio-tagged birds. We used frequency distribution plots to compare frequency of the availability of patches of different types and size categories with detected use during transect surveys.



(a) Tummel Forest (map width 13.5 km)



(b) Talladh-a-Bheithe Forest (map width 5.5 km)

Figure 3.2. Forestry-boundary sections investigated on the (a) Tummel Forest and (b) Talladh-a-Bheithe forest. Each is a 5 km section between inhabited black grouse moorland (large leks present, breeding confirmed) and large-scale forestry. The solid red lines show the boundary section and the dashed red-lines show 0.85 km perpendicular buffers each side of the boundary. Reproduced by permission of Ordnance Survey on behalf of HMSO © Crown copyright and database right 2013. All rights reserved. Ordnance Survey Licence number 100017908.

3.2.7 Vegetation use

We tested for sex, season and sex*season interaction effects between various measures of vegetation use recorded at radio-locations. For single response variable analyses (as opposed to vegetation composition MANOVAs, below) we used generalised linear mixed models (GLMM), with bird ID as a random effect to account for inter-individual variation. We used likelihood ratio tests with the χ^2-distribution or F-distribution as appropriate to compare the full model and simplified versions of the model. First the removal of the interaction term was tested, and then the removal of sex and season. We tested for difference in association with different functional groups (broadleaf/coniferous) and for a larch/non-larch grouping using binomial errors and a logit link function within GLMM. We tested for differences in whether a radio-location was in a tree or on the ground using binomial errors and a logit link function within GLMM, the tree count within 5 m of radio-locations using Poisson errors and a log link function within GLMM, and the average tree height (where trees were present) within 5 m of a radio-location and average vegetation height within quadrats using normal errors with an identity link function within GLMM.

Differences in vegetation composition at radio-locations were investigated using MANOVA, testing for sex, season and sex*season interaction effects. To distinguish occurrences of the presence of vegetation that did not round to a 5% estimate from known absences (0%), we gave the former a value of 1%. Actual estimates of 0% cover were converted to 0.1% to enable log-ratios to be taken (Aebischer *et. al.,* 1993 b).

3.3 Results

3.3.1 Home-range characteristics

From 89 birds radio-tagged, 90 bird-season HRs were estimated from 48 individuals. Sample sizes for HRs by sex, age and season are given in Table 3.2. We found no correlation between number of radio-locations and size of MCP_{100} (r = 0.15, t_{88} = 1.40, P = 0.164). Male black grouse had a mean HR 2.3 times greater than females (males 230 ± 16 SE ha, females 98 ± 16 SE ha; $F_{1,89}$ = 34.6, P < 0.001). We found no significant differences in HR between age, season, or two-way interactions between sex and age, sex and season or age and season (all P > 0.382).

3.3.2 Habitat selection analyses

The majority of sex-age-season habitat selection analyses were significant (Table 3.3), with the exception of female adults in autumn-winter (P = 0.050) and female juveniles in spring-summer (P = 0.134). Pre-thicket and clearfell forestry were generally used very little (Table 3.2). Because less than two individuals had used the habitats, clear-fell was excluded from all group analyses and pre-thicket was excluded from all group analyses except for male and female juveniles in autumn-winter.

The positions of habitats on the selection-avoidance gradient for all groups are shown in Figure 3.3. The top ranking of moorland, with relatively small standard errors (though notably wider in both juvenile and adult females in autumn-winter) is evident as well as the generally high ranking of farmland and broadleaf woodland for males across groups, but generally low ranking or absent (meaning lack of sufficient use to enable analyses) across female groups.

Table 3.2 - Composition within MCP_{100} by season and sex (± SE) and composition of habitats within Tay study area (%). 'Study area refers to two combined MCPs around all individual MCP_{100}s at each study site (8,948 ha). 'Juv.' = juvenile, 'A-w' = autumn-winter, 'S-s' = spring-summer. Habitat codes are: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, UN = unplanted areas within forestry, CC = closed-canopy forestry, FE = clearfell forestry, PT = pre-thicket forestry.

Sex	**Age**	**Seas.**	**n**	**MO**	**FA**	**BW**	**NP**	**UN**	**CC**	**FE**	**PT**
Fem.	Juv.	A-w	11	74±11	2±2	1±0	18±12	2±1	3±1	0	0
		S-s	6	74±13	0	0	21±14	2±1	2±2	0	0
	Adult	A-w	9	45±12	0	0	24±12	1±1	28±12	0	1±1
		S-s	6	67±14	0	1±1	17±7	1+0	14±8	0	0
Male	Juv.	A-w	20	55±8	6+2	8±2	18±6	3±2	9±4	1±0	0
		S-s	11	72±9	10±4	6±2	9±7	1±0	3±2	0	0
	Adult	A-w	15	75±7	13±5	6±2	5±3	0	1±1	0	0
		S-s	12	87±4	10±5	3±1	0	0	0	0	0
Study area				38	9	6	14	5	24	2	2

In four of seven groups that showed significant selection (or margin of significance at P = 0.050), moorland was selected relative to all other habitats, and in two others relative to all but one habitat (Table 3.3). In adult females in spring-summer it was not selected relative to new native pinewood and in juvenile males in spring-summer it was not selected relative to farmland. In adult females in autumn-winter it was not selected relative to new native pinewood, closed canopy or pre-thicket forestry.
Farmland was selected relative to other habitats in all male groups except for juveniles in autumn-winter. In each case farmland was selected relative to all conifer forest habitats (new native pinewood, closed-canopy and unplanted forestry) but not relative to broadleaf woodland. In all male groups broadleaf woodland was selected relative to all forestry habitats (closed-canopy and unplanted), as well as all habitats except moorland in juveniles in autumn-winter and new native pinewood in adults in autumn-winter. In contrast, broadleaf woodland and farmland were not selected relative to any habitats in any female group. Unplanted forestry was selected relative to closed-canopy forestry in both juvenile females in autumn-winter and adult males in autumn-winter, but they were not significantly different in any other groups.

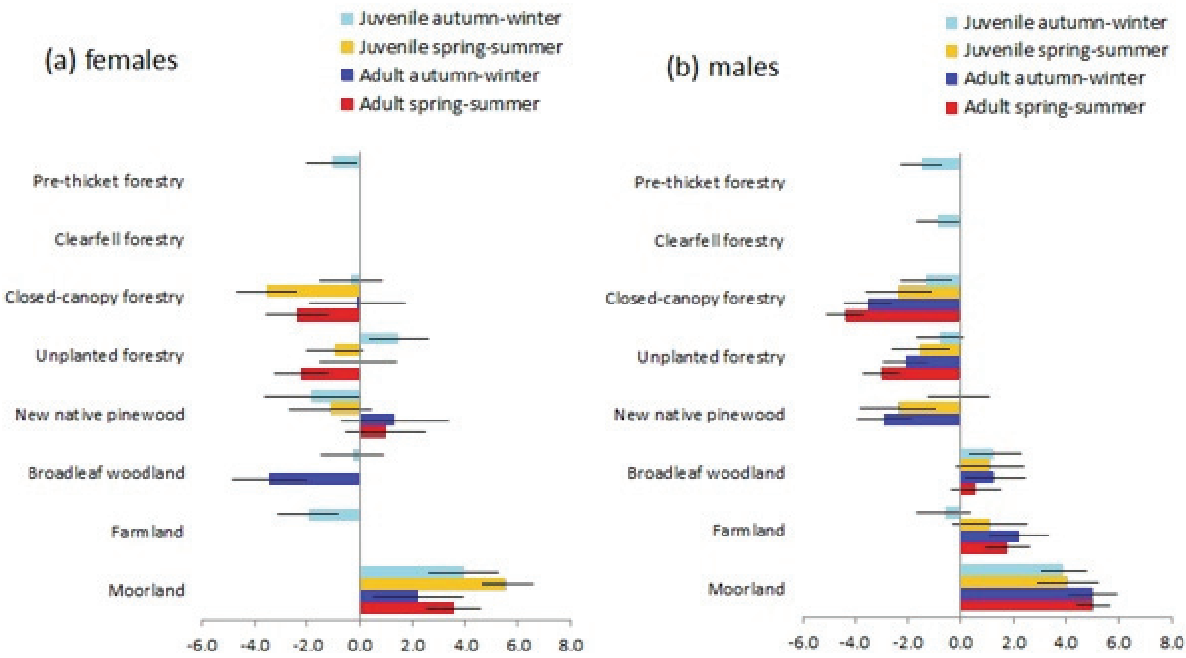


Figure 3.3. Mean difference in log-ratio (used in MCP_{100} minus available in study area) for each habitat in turn against all other habitats considered. Whiskers represent between-habitats standard errors of differences. Habitats without bars or whiskers were excluded from analyses due to lack of use by ≥ 2 birds but are retained on axes for comparison. These plots show both the ranking of the habitats (bars further right are more selected) and the relative confidence of that rank (larger whiskers mean we can be less sure about the relative selection of that habitat). Pairwise differences (Table 3.3) were assessed using non-parametric statistical tests, so are not directly comparable with the whiskers shown.

Table 3.3 - Compositional analyses results for selection of habitats at level II (bird-season MCP_{100} within all birds MCP_{100}). Habitat codes are: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, PT = pre-thicket forestry, CC = closed-canopy forestry, UN = unplanted areas within forestry, FE = clearfell. Habitats were considered for analyses if they were used within ≥ 2 MCP_{100}s. For brevity, a vertical line ('|') indicates where multiple habitats were significantly different (">") to another habitat in pairwise tests. 'Fem.' = female, 'Juv.' = juvenile, 'Seas.' = season, 'A-w' = autumn-winter and 'S-s' = spring-summer.

Sex	Age	Seas.	n	Test	Habitats considered	Pairwise differences
Fem.	Juv.	A-w	11	Λ = 0.11 P = 0.048	MO,FA,BW,NP,UN,CC,PT	MO>[ALL]; UN>CC
		S-s	6	Λ = 0.08 P = 0.134	MO,NP,UN,CC	-
	Ad.	A-w	9	Λ = 0.21 P = 0.050	MO,BW,NP,UN,CC	MO|NP>BW
		S-s	6	Λ = 0.01 P = 0.036	MO,NP,UN,CC	MO>UN|CC
Male	Juv.	A-w	20	Λ = 0.23 P = 0.010	MO,FA,BW,NP,UN,CC,PT,FE	MO>[ALL]; BW>FA|UN|FE|CC|PT
		S-s	11	Λ = 0.22 P = 0.034	MO,FA,BW,NP,UN,CC	MO>BW|UN|CC|NP; FA>NP|UN|CC; BW>UN|CC
	Ad.	A-w	15	Λ = 0.10 P = 0.008	MO,FA,BW,NP,UN,CC	MO>[ALL]; FA|BW>UN|NP|CC; UN>CC
		S-s	12	Λ = 0.03 P = 0.006	MO,FA,BW,UN,CC	MO>[ALL]; FA|BW>UN|CC

In males the position along the selection-avoidance gradient for forestry habitats (closed-canopy and unplanted forestry) appeared to tend towards greater avoidance in juveniles compared to adults and in autumn-winter compared to spring summer (Figure 3.3). In females, however, the patterns were more complex but two are clearest. Firstly, in autumn-winter the difference between moorland and both unplanted and closed canopy forestry are smaller than in spring-summer within age groups. Secondly, the relative difference between moorland and new native pinewood is greater in juveniles than in adults.

3.3.3 Movement from external habitats into forestry

The maximum distance moved into forestry by individuals did not significantly differ with sex (female median of the maximum $distances_{11}$ = 527 m, male median of the maximum $distances_{16}$ = 185 m; W = 65, P = 0.270). Maximum distance moved into closed-canopy patches from patch edge was also not significantly different between males and females (female $median_6$ = 214 m, male $median_{12}$ = 48 m; W = 16, P = 0.067). The cumulative percentages of individuals' maximum movement into forestry reached 78% within 600 m, after which it rose gradually along an asymptote (Figure 3.4).

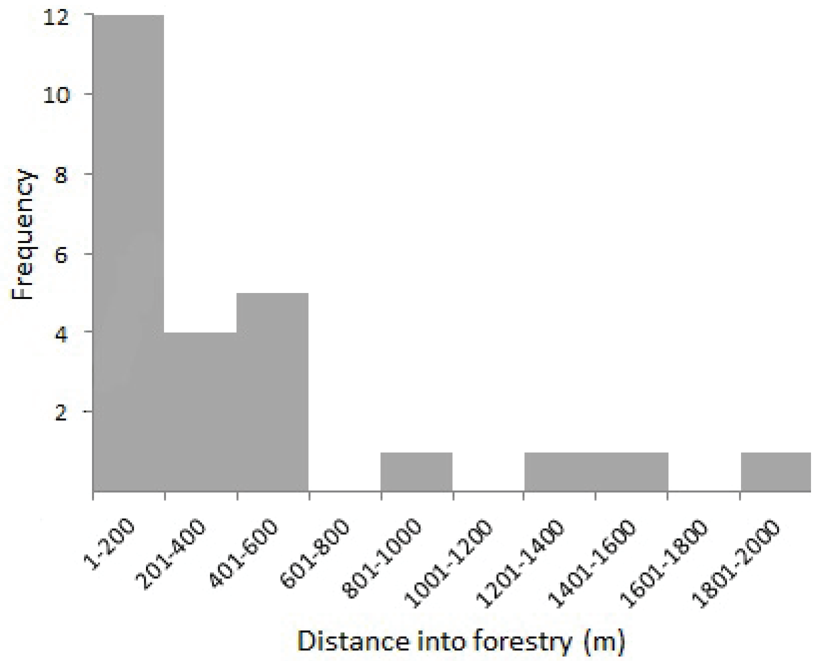


Figure 3.4. Frequency distribution of maximum movements into forestry by 25 individual birds that made maximum movements < 2 km from external habitats into forestry.

Figure 3.5 shows details of the four investigated boundary sections between large-scale forestry and external moorland or new-native pinewood. There are clear differences both in the habitats available along and behind the forestry boundaries and the frequency and extent of movements to within them (Figure 3.5, Table 3.4). The three Tummel Forest boundaries (Figure 3.5 a-c) appeared to show a gradation. Boundary A, bordered by moorland and broadleaf woodland, both extensively used by black grouse, showed very limited movement across (5% of radio-locations, maximum movement into forestry 190 m). It also had a large quantity of closed-canopy habitat (80%) within forestry along the boundary, and incursion only occurred to any degree within patches of larch that met the external edge. Boundary B showed no detected movement across by birds, and was characterised by a band of farmland and broadleaf woodland between moorland and forestry and a relatively large quantity (80%) of closed-canopy cover, little of which was larch (4%), particularly along the external boundary. Finally, Boundary C had a larger quantity of unplanted and pre-thicket areas (33%) than all other boundaries which in large parts were on or connected via wide rides the external moorland edge. Here there was a large degree of movement across the boundary (19% of radio-locations, maximum movement into forestry 824 m), with birds particularly utilising unplanted patches, one large pre-thicket patch on the forest. Where closed-canopy areas were used, generally these were in or close to larch.

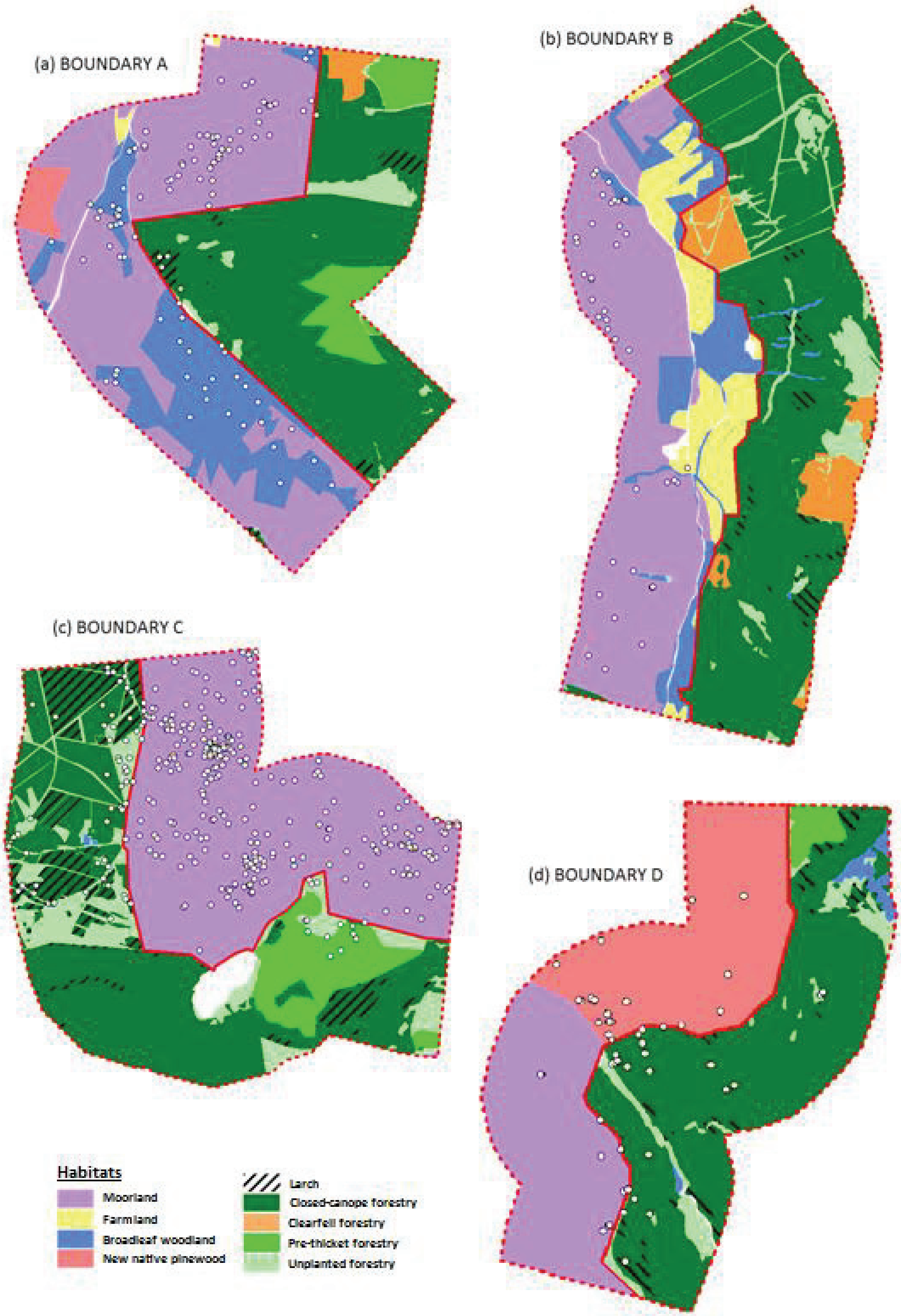


Figure 3.5. Habitat details of moorland-forestry boundary sections and 0.85 km perpendicular buffer sections investigated (locations in Figure 3.2). Radio-locations of birds within these sections are shown as white dots. Note that boundaries B and D have been rotated 90° counter-clockwise for fit.

Table 3.4 - Characteristics of boundary, forestry behind boundary and bird activity across four forestry boundary sections investigated (locations in Figure 3.2).

		Boundary			
Feature	**Characteristic**	**A**	**B**	**C**	**D**
Forest	-	Tummel	Tummel	Tummel	Talladh-a-Bheithe
Boundary	% non-closed-canopy	14%	23%	65%	27%
Forestry composition behind boundary	% unplanted	6%	11%	20%	9%
	% clearfell	3%	9%	0%	0%
	% pre-thicket	12%	0%	13%	4%
	% closed-canopy	80%	80%	33%	13%
	% larch spp.	4%	4%	24%	8%
Bird activity	number of locations	103	47	320	52
	% locations within forestry	5%	0%	19%	42%
	mean distance into forestry (m) ± SE	65±21	0	241±32	203±34
	Maximum distance into forestry (m)	190	0	824	517

Boundary D, on the Talladh-a-Bheithe forest, differed somewhat in terms of usage. Here no usage of the pre-thicket patch on the forest edge was detected, but there were some relatively large movements into non-larch, closed-canopy patches. Quantitative measures of boundary features and bird movements across them are given in Table 3.4. Correlative analyses were not feasible with only four boundaries, but it is of note that Boundary C, with the most larch and most unplanted (20%) patch area, had the highest mean movement beyond the boundary and the highest maximum distance moved beyond the boundary. On the other hand, Boundary D, with the highest percentage of locations within the forestry section, had an intermediate presence of larch and unplanted areas. On boundary D, movements into forestry appeared to be more frequent where the forest bordered new native pinewood than moorland.

Unplanted patches were predominantly less than 2 ha in size across all boundaries. Boundary C had more the most unplanted patches above 2 ha (Figure 3.6). This boundary showed the greatest use of unplanted patches, but greatest use was recorded in the 6-8 ha area band, with little use recorded in patches less than 2 ha. Larch patches were also predominantly less than 2 ha in size, but similar levels of use was recorded across patches of less than 2 ha and 2-4 ha. Patches of 6-8 ha, while low in frequency, showed a relatively high degree of recorded use.

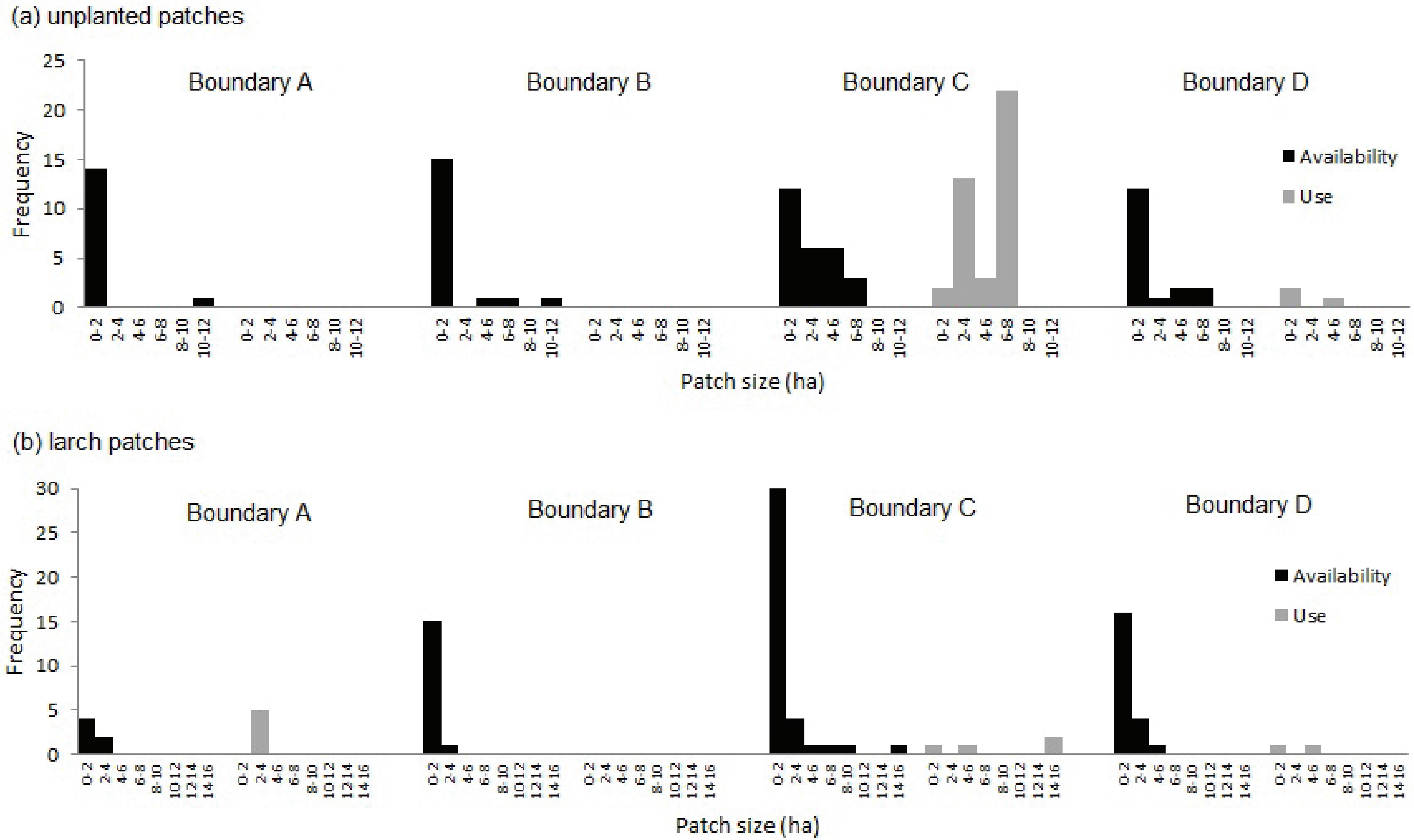


Figure 3.6. Frequency distributions of availability and use of unplanted clearings and closed-canopy larch stands within the four boundary sections studied (see Figures 3.2 and 3.3).

3.3.4 Selection of open and larch patches within forestry

In total, the transect lengths for surveys of unplanted, clear-felled and pre-thicket patches within the Tummel Forest were 46.0 km for the winter set and 40.1 km for the spring set. The numbers of birds flushed were low: seven in the winter and two in the spring. This amounts to one bird observed every 6.5 km for the winter set, and only one bird every 20.1 km for the spring set. A total of 9.2 km^2 of clearings were searched, so densities of birds encountered per area searched were 0.8 birds km^{-2} in winter and 0.2 birds km^{-2} in spring (these are not predicted bird densities as sample sizes preclude distance sampling: Newsom *et al.* 2008). In winter, encounters per area searched by clearing type were: unplanted 0.7 birds km^{-2}, clear-fell 1.0 birds km^{-2} and re-stock 0.0 birds km^{-1}. In spring they were: unplanted 0.5 birds km^{-2}, clear-fell 0.0 birds km^{-2} and re-stock 0.0 birds km^{-2}. The range of clearing sizes in which birds were encountered varied widely, from 9 ha to 234 ha and they were found in both unplanted and clear-fell areas. The frequency of clearing sizes and types quantified and surveyed for the Tummel Forest are shown in Figure 3.7a. Those clearings that were identified ranged in size from 0.3 ha to 233.6 ha, although the size distribution is heavily skewed towards smaller clearings, with 17 (44%) < 10 ha. This frequency distribution is compared with the frequency distribution of clearings being used by the nine birds seen during clearing transect surveys (Figure 3.7b).

3.3.5 Vegetation use

There were significant effects of sex and season in conifer/broadleaf association (χ^2_1 = 5.59, P = 0.018; Figure 3.8c) and there was a significant effect of sex in use of larch/other (χ^2_1 = 6.26, P = 0.012; Figure 3.8a). Females had a higher association with coniferous species than males, in both spring-summer and autumn-winter (Figure 3.8c) and were, on average, six times as likely to be associated with larches as males (Figure 3.8a). There was a significant sex*season interaction with tree count within 5 m of radio-locations (χ^2_1 = 5.11, P = 0.024; Figure 3.8b). Average tree count was similar for males year-round and females in spring-summer, whilst it was almost twice as high for females in autumn-winter (Figure 3.8b). No sex or season effects were detected with average tree height (all P > 0.264) or with location on the ground or in a tree (all P > 0.069). There was a significant effect of sex and season on vegetation height recorded at radio-location (F_1 = 9.96, P = 0.002; Figure 3.8d). The seasonal difference in vegetation height at radio-locations was greater for females than males (Figure 3.8d).

MANOVA revealed a significant sex*season interaction in vegetation composition at ground radio-locations ($F_{1,679}$ = 2.75, P = 0.022). Within individual ANOVAs, there were not any significant sex, or season, effects on berries, bracken, brash or cotton grass (Figure 3.9). Bog myrtle was used more by both sexes in spring-summer at 4-5% cover compared to 1-2% in autumn-winter (P < 0.001). There was also a slightly greater association with mossy areas (P = 0.027) and rushes (P < 0.001) by both sexes in spring-summer. The vegetation groups most strongly represented within quadrats were grasses (group means 18-39%) and heathers (group means 22-38%), both of which had significant interactions between sex and season (both P < 0.001). Grassy areas were used more by both sexes in spring-summer, but this effect was less marked in females than males, who were generally more associated with grassy areas in both seasons. Heathers, in contrast, were used more by females in both seasons, and while their association with heather did not vary much between seasons, it dropped markedly in males between autumn-winter and spring-summer.

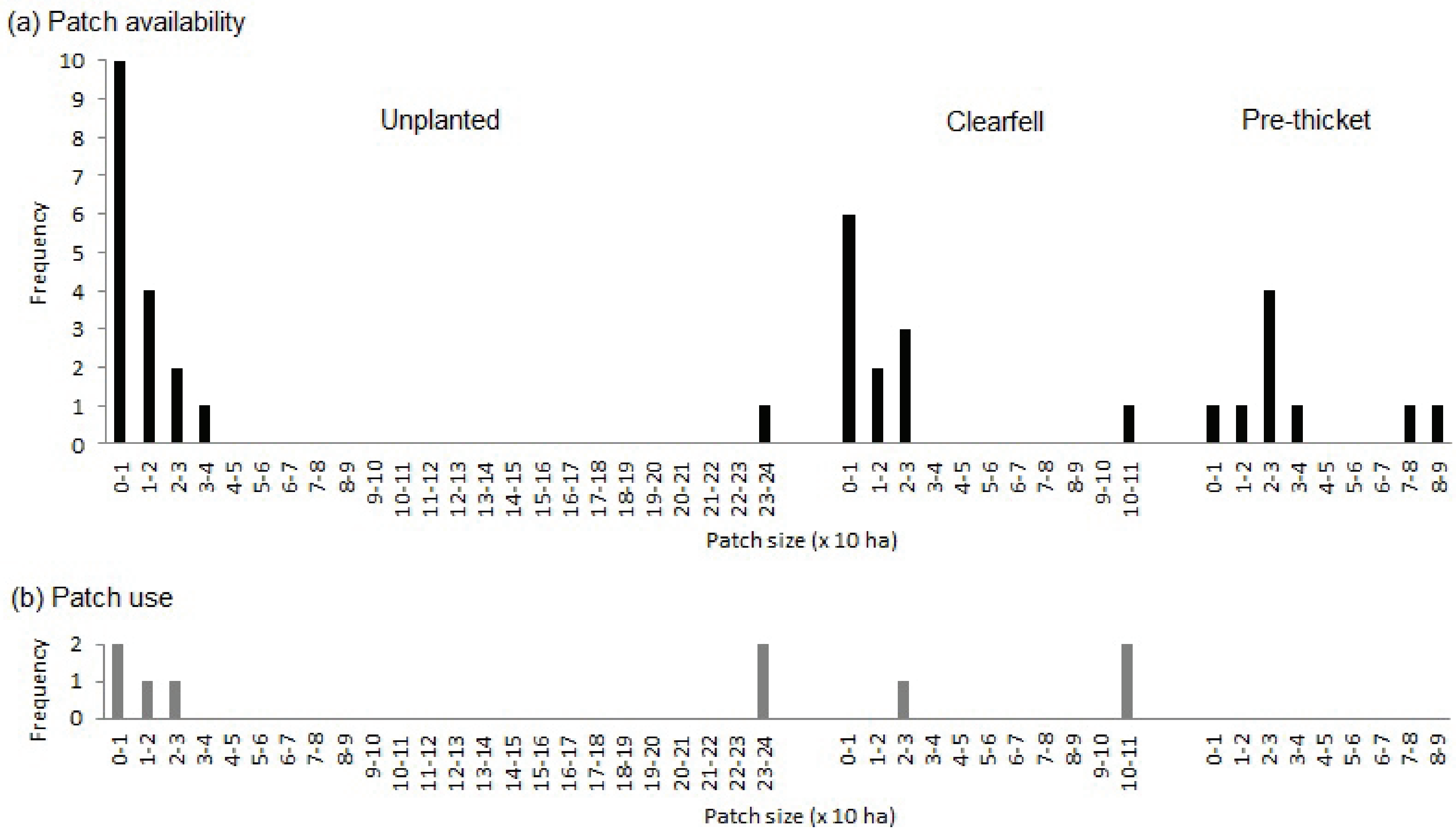


Figure 3.7. Frequency distributions of (a) size of 39 surveyed clearings in Tummel Forest by clearing type and (b) clearing size category of clearings from which each bird was flushed during transect surveys, by clearing type.

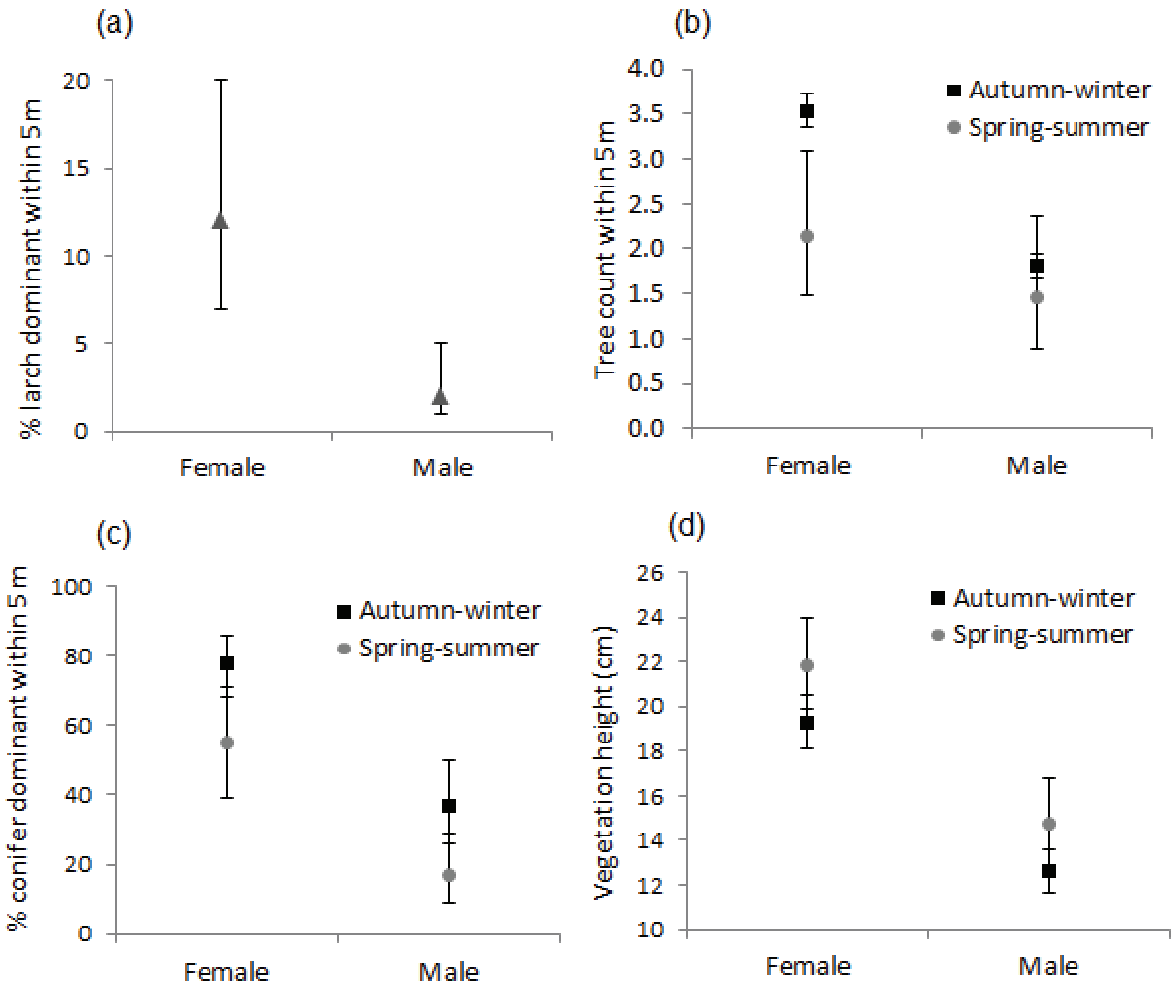


Figure 3.8. Fitted values (± SE) from models of vegetation use by radio-tagged black grouse: (a) percentage of radio-locations with trees present within 5 m that were dominantly (greater than half of individuals) larch species, (b) tree count within 5 m of radio-locations, (c) percentage of radio-locations with trees present within 5 m that were dominantly (greater than half of individuals) conifer species and (d) vegetation height (cm) at radio-locations (ground flushes only).

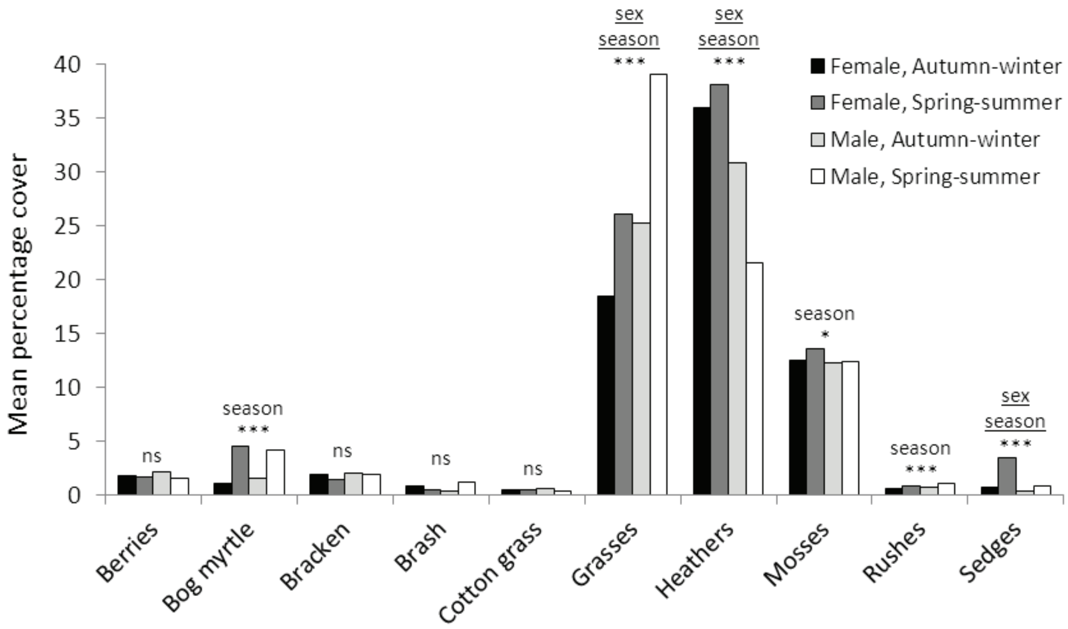


*Figure 3.9. Mean percentage cover at quadrats at ground radio-locations locations by sex and season for various vegetation taxa recorded. MANOVA revealed that there was a significant sex*season interaction in overall vegetation composition ($F_{1,679} = 2.75$, $P = 0.022$). Text above each vegetation set refers to whether sex, season, or sex*season interactions were significant within individual permutational ANOVAs, where 'ns' indicates no significant effects ($P \geq 0.050$), '*' indicates an effect significant at $0.050 > P \geq 0.010$, '***' indicates an effect significant at $P < 0.001$, and underlined text means a significant interaction between sex and season effects. Sample sizes for quadrats are: female autumn-winter 227, female spring-summer 126, male autumn-winter 348, male spring-summer 348.*

3.4 Discussion

3.4.1 Within-population variation in space and habitat use

Cramp & Simmons (1980) describe avoidance of proximity between males and females in winter which could be a function of differential habitat use. Grant & Dawson (2005) suggested sex differences in habitat preferences are expected due to underlying differences in morphology and ecology but that evidence for such differences was scarce. Our results reveal that there is a large amount of within-population variation in the how black grouse utilise space and habitats including sex differences in habitat selection patterns.

In all groups the highest degree of relative selection was for moorland, which matches the lek-scale patterns seen in Chapter 2. The apparent strength and universality of this selection for moorland indicate that it can be used as a benchmark habitat against which to compare relative selection of other habitats between groups. Compared to selection for moorland, the relative importance of forest habitats is not fixed within a population, but appears to differ according the sex and age of a bird and the period in the annual cycle. In males, farmland was generally a highly ranked habitat in selection analyses in contrast to females. The contrasting facts that the area of farmland was negatively associated with lek size (Section 2.4.2) but males selected for this habitat could be explained by the theory that lek populations are driven by female settlement and breeding patterns (Bradbury *et. al.,* 1989). Farmland on the margin of moorland, while not forming good nesting and brood-rearing habitat, was used for a number of leks in the study area, probably because it generally has a short sward. Consistent with this, there was greater association among males with grasses, particularly in spring-summer, and shorter vegetation compared to females.

Both the types used and extent of use of forest habitats varied between males and females. Radio-locations revealed a stronger association with trees among females, particularly in autumn-winter. Within this, females were associated with a majority of coniferous trees and males broad-leaved. Cramp & Simmons (1980) suggest relative use of broadleaf / coniferous species may vary geographically, so the patterns we observed may differ in other regions. Broadleaf woodland was selected relative to commercial forestry habitats in all groups, a pattern not seen in females. Most broad-leaved woodland was birch dominated, the buds of which have been observed as an important food source for black grouse (Baines, 1995). In adult females during autumn-winter commercial forestry habitats were not avoided relative to moorland, in contrast to males. A partial driver behind female use of commercial forestry may be in the use of larch as a source of protein for breeding. Larch, as opposed to cotton grass, has been recorded as a primary protein source in females prior to breeding in some parts of Scotland (Baines, 1995). In our population, females were significantly more associated with larches at radio-locations than males, while association with cotton grass appeared low.

The importance of young forests to the distributional shifts of leks was observed in Chapter 2. During the study period, the cover of pre-thicket forestry was relatively low (2% of radio-telemetry study area) and was virtually unused, so selection patterns could not be properly assessed. Radio-telemetry did, however, highlight that new native pinewood is a relatively important habitat in some groups. New native pinewoods were not significantly selected against relative to moorland in adult females, in contrast to other groups (juvenile females or each male group). Previous studies show that tall ground vegetation is important for black grouse nesting (Baines, 1995) and that breeding females will select scrubby areas in preference to open areas in order to gain cover from aerial predators, even if food resources are lower (Signorell *et. al.,* 2010). Fenced new native pinewoods provide both these structural components. Of 17 nests located in the study (see Chapter 4), four (24%) were in new native pinewoods, despite the habitat making up 5% of the study area. This suggests this habitat may be selected as a preferred nesting habitat, and may drive the detected degree of selection for this habitat in adult females. Females were associated with longer vegetation than males in each season. For breeding, selection for taller vegetation has been linked to better nest concealment and abundance of invertebrates (Baines, 1995), and chick concealment (Baines, 1996).

3.4.2 Forest structure and access

Whilst we saw differences in extent of selection for forestry components between sexes, differences between maximum extent of movement into forestry between males and females were not significant. Movements into forestry could be very large, with a juvenile male moving 6 km into forestry and establishing a winter home range. However, 78% of birds that did use forestry were not recorded further than 0.6 km into forestry and 93% within 2 km.

We were unable to gain much information about selection of open forestry patch sizes relative to their availability, because of low detection of grouse during transect surveys (Figure 3.7). Sample sizes precluded the use of distance sampling to estimate bird densities (60 records has been recommended: Newsom *et. al.,* 2008) and detectability was likely to have been low given spacing of transects and lack of use of dogs. Densities are therefore likely to have been higher than those detected. Birds very often used rides and tracks along the margins of closed-canopy stands which are more difficult to quantify because they form a network across the forest. The radio-tracking and transect results showed that birds used a range of patch sizes available (Figure 3.8b, c). Klaus (1991) suggests that in central Europe the smaller-scale clearings associated with historical alteration of forest habitat had been a positive thing for black grouse, whilst large-scale clearings within modern forestry has been a negative thing. The results of Haysom (2001) in Scotland suggested larger areas of re-stocked pre-thicket forestry were more likely to attract lekking groups.

Patterns seen across the four boundary sections were necessarily only correlational and the low numbers of boundaries exclude robust statistical comparison. But from these preliminary results we can draw hypotheses that could be tested with field trials. The patterns suggest that a moorland-forestry boundary with more unplanted patches, creating an open network into the forest, and with the presence of larches would be linked to greater use of forestry habitats by birds associated with a lek on the external moorland habitat. Excluding track/rides, birds tended to use predominantly larger unplanted patches along boundary sections, with the largest usage recorded in those 6-8 ha in size along Boundary C. Most larch patches with recorded use were 0-4 ha, and use appeared larger in 2-4 ha patches than their relative availability.

The Talladh-a-Bheithe boundary D appeared to show a different pattern to that seen across boundaries A-C on the Tummel forest. In the latter, large contiguous areas with a closed-canopy were avoided, but along boundary D there was movement into such an area. Talladh-a-Bheithe has a younger age-structure, with 79% planted in the 1980s (including the area used along boundary D). Tummel forest, on the other hand, was primarily (77%) planted in the 1950s-60s. It is possible that this could explain some of the difference, although the mechanisms are unclear. Younger areas may have more glades or areas of variable growth that become shaded out at full maturity. Such glades were not quantified in our data. Another difference is that along boundary D there is a large area of new native pinewood along approximately half of the forestry boundary length. It is behind the forestry boundary of this area that the majority of movements, and the most extensive, into forestry were made. New native pinewoods could potentially 'soften' the edge of a forestry area. Therefore two other hypotheses may be constructed: that the presence of new native pinewood along a forestry boundary will lead to greater movement into that forestry, and that closed-canopy stands at 'pole' stage will see more use than those at 'mature' stages.

3.5 Summary

We used radio-telemetry data in the Tay region to investigate individual patterns of habitat use and selection to gain a better understanding of use of forests in relation to other habitats. We compared habitat composition within seasonal home-ranges to available habitats in order to examine selection and its variation with sex and age. Radio-locations were also used to investigate movements from open habitats into commercial forestry and vegetation groups used. For 90 home-ranges identified from 48 individuals there were differences in habitat selection between males and females which varied according to age and season. Moorland was the most highly selected habitat in all groups. In contrast to females, males showed patterns of selection for farmland and broadleaf woodland. Unplanted and closed canopy forestry habitats were generally avoided relative to moorland, but this was not the case in adult females in autumn-winter. New native pinewood was avoided relative to moorland by males in both seasons, but by no females except for juveniles in autumn-winter. It thus appears that in our population females have a stronger association with coniferous forest habitats than males do, and males have a stronger association with broadleaf forest habitats. 78% of those birds that used forestry did not move further than 600 m into the habitat. Movement into forestry appeared greatest where larch and/or substantial unplanted areas (clearings/rides) were present, presenting testable hypotheses for future field trials. Females were associated with taller ground vegetation than males, as well as higher densities of trees and more coniferous species of tree, particularly larch.

4. BREEDING AND SURVIVAL IN RELATION TO HABITAT USE

4.1 Introduction

The demographic parameters productivity, survival and migration ultimately determine local avian population trends (Newton, 1998). Their measurement is essential in bird conservation, for diagnosing causes of population declines (Robinson *et. al.,* 2004) and for testing responses to management (Bolton *et. al.,* 2007). In addition, Jones (2001) asserts the need to consider the adaptive significance of differential habitat use as this may be related to selection patterns. Measuring fitness components of individuals in relation to habitat use might, therefore, reveal the drivers behind these behavioural patterns. Fitness consequences of differential habitats use can act via carry-over effects from one season to the next (Harrison *et. al.,* 2011). This can be a driver of breeding success since birds rely on resources acquired prior to breeding, as well as during breeding, to reproduce (Erikstad, 1985; Guillemain *et. al.,* 2008)

4.1.1 Objectives

This chapter addresses objective 2 of the third project ("To determine whether differential winter habitat use has any carry-over effects in terms of survival or breeding success", see Section 1.2.3). To this end we used survival and productivity data generated from black grouse radio-telemetry to address the sub-objectives below:

1) To estimate survival rates of birds over the course of the project and to examine if these varied with autumn-winter weather conditions.

2) To examine causes of mortality of birds in the study.

3) To quantify breeding success over the course of the project and examine if this varied with habitat use of females in the previous autumn-winter.

4.2 Methods

4.2.1 Meteorological and habitat data

We obtained local meteorological data from a weather station at Dalwhinnie (56°56'24"N, 04°14'20''W) to extract measures of winter severity so that these could be compared to habitat use. This station is situated approximately 15 km NNW from the edge of the radio-telemetry study area at an altitude of 350 m, approximately the mid-point in altitude in our radio-telemetry study areas (range 140-580 m above mean sea level). The autumn-winter weather variables extracted from this weather station were the mean minimum daily air temperature (°C), the mean maximum daily air temperature (°C) (both recorded at 125-200 cm above the ground as standard) and the mean daily minimum grass temperature (°C) (recorded at 5 cm above short turf as standard). We also obtained estimates of minimum snow lie from Met Office maps (www.metoffice.gov.uk). These data were provided in monthly estimates of minimum and maximum snow lie in 5 km UK grid squares. To obtain a seasonal minimum snow lie we summed the minimum values recorded for each month for a 5 km square at the centre of our study area. In addition, we separated the autumn-winter habitat composition within home-ranges (see Section 3.3.2) by year for males and females, to examine if these varied between years.

We used compositional analysis to examine whether certain habitats within autumn-winter home-ranges were more associated with autumn-winter weather variables (mean minimum air temperature, mean minimum grass temperature, minimum snow lie). We carried out analyses for males and females separately. We carried out compositional analyses using the contributed packages 'Adehabitat' (Calenge, 2006), 'Vegan' and 'ImPerm'.

4.2.2 Survival rates

We estimated survival rates by modelling individual encounter histories of birds to death, loss of radio signal or end of study. Consistent with other black grouse survival estimates (Baines *et. al.,* 2007; Warren & Baines, 2002), we excluded the first two weeks following catching and August encounters of all poults. Survival was modelled using the Known Fates model in Programme Mark (White & Burnham, 1999).

Survival rates were estimated on a monthly basis because in our data weekly estimates would have led to high levels of censored data. Due to difficulties in terrain and weather conditions the mean inter-encounter interval was 12 days meaning there were often weeks in which birds were not recorded. In Known Fates models censoring is inflated because if a bird is unrecorded within occasion *n*, it cannot be recorded as having survived or died in the interval between *n-1* and *n*, but nor can it be recorded to have survived or died in the interval between *n* and *n+1*.

For each month a bird was recorded as having survived from the first day of that month to the first day of the next month, having died between the first day and the first day of the following month, or having been censored for that month (not detected in that month, regardless of whether it was found alive in following months). To account for differences in the number of days in each month, intervals were set to the length of each month, and thus model outputs estimated daily survival probabilities (to 7 decimal places). These were raised to the power of 365.25 for annual survival rates, or to 181.25 or 184 for autumn-winter and spring-summer survival estimates respectively.

We considered that survival might vary with sex (male / female), age (juvenile / adult), season (autumn-winter / spring-summer) and year (project year 1 / project year 2 / project year 3). We built 16 Known Fates models that grouped birds by all possible categories and compared them using a small sample Akaike's Information Criterion (AICc) which assesses a model's fit and parsimoniousness (Burnham & Anderson, 2002). Survival rates estimated from the best model, and any models within two AICc units (see Burnham & Anderson, 2002), were presented. We also calculated Akaike's weights (ω_i: a relative weight of evidence for each model) and model likelihood (*L*: a measure of the relative likelihood of the model given the data) (Johnson & Omland, 2004). Akaike's weights are additive and can be summed for all models containing a given variable to estimate the relative importance of that variable.

4.2.3 Causes of mortality

Causes of mortality for radio-tagged birds found dead in this study were categorized as red fox *Vulpes vulpes,* mustelid (family Mustelidae), raptor (order Falconiformes), diseases/starvation or fence strike. Predator identity was identified by examination of recovered carcasses and feathers (Baines *et. al.,* 2007; Thirgood *et. al.,* 1998). Where a whole carcass was found we examined the exterior of the bird for physical injury, and removed the caeca to carry out counts for Strongyle nematode worms *Trichostrongylus tenuis* (Hudson & Newborn, 1995). We also recorded a pectoral muscle score, similar to that used to assess body condition in ringing of live birds (Redfern & Clark, 2001). The score was between 1 and 5, with 1 representing a situation where the sternum feels sharp and pectoral muscle depressed, and 5 where the sternum is barely distinguishable and the muscle feels full and rounded.

4.2.4 Breeding data

In May and June, nest data were recorded for any radio-tagged females and any nests of untagged females found incidentally while tracking. We followed the British Trust for Ornithology's Nest Record Scheme guidelines (Crick *et. al.,* 1999) to minimise disturbance and monitored them according to the procedure of Warren *et al.* (2011). Upon initially flushing a female from a nest, the clutch size was recorded and the length and breadth at the widest point were carefully measured with callipers (instrument precision 0.1 mm) for five eggs selected arbitrarily. Total time at a nest was typically 3-4 minutes and caution was taken not to trample vegetation in the nest vicinity.

Aebischer *et. al.* (1993a) demonstrated that compositional analyses could be used to compare habitat use against fitness traits such as survival probability. We examined if there was any relationship between autumn-winter habitat use (i.e. habitat-type compositions) of breeding females and measures of breeding effort (clutch size, egg volume, and total clutch volume) or success in the following breeding season. Egg volume (V) was estimated using the equation provided by Marjakangas & Tormala (1997) for black grouse $V = 0.51LB^2$, in which L is the egg length and B is the egg breadth. The mean value was taken over all eggs in the clutch. To obtain total clutch volume we multiplied the clutch size by the mean egg volume. Though we could not rule out partial clutch losses reducing clutch size, nests were found on average 1-3 days following start of incubation (the seven successful nests were found on average 24 days before the estimated hatch data, which was compared to an estimated incubation period of 25-27 days from Cramp & Simmons 1980) so we assumed any losses would be minimal. As sample sizes were small (n = 17 nests) we pooled across years. Age of breeding female may have an effect on egg volume and clutch size (Marjakangas & Tormala 1997), so the initial MANOVA contained age and the given breeding parameter plus their interaction. We tested for a significant interaction which would suggest separate analyses were needed for each female age group (juvenile = first breeding year; adult = any subsequent breeding year). If no interaction was detected we retained a non-interactive age factor as the first model term and tested for an effect of the given breeding parameter over this. Hatchability of nests was defined as the proportion of eggs laid in successful nests that hatched.

Following hatching, broods were located using triangulation every 3 - 7 days. Triangulation was used in order to reduce disturbance to chicks. Four points, approximately 10-20 m away from broods, were used to calculate a brood location. At each point a GPS location and a bearing in the direction of the brood was recorded. Nocturnal roosts were located at least 10 days after estimated hatch dates. Roost locations were triangulated in a similar way to day brood locations; however, stakes were placed in the ground and angled in the direction of the brood in order to make locating the site easier when revisited. The survival from hatching until recruitment is considered a critical determinant of population growth in black grouse, and mortality rates are typically highest in the first 10 days (Ludwig *et. al.,* 2010). Survival of broods to 10 days is a relatively simple but important measure to record without extensive disturbance to the brood. It can be determined by a combination of assessing an adult female's behaviour and locating the roost piles of chicks at night roosts. Thus we compared survival of a brood (at least one chick still with a female since brood size was not known accurately) to 10 days across years.

We used data from August catching counts to compare productivity between years and between three of the habitat-types: moorland, new native pine forest and unplanted forestry. Young pre-thicket or clear-felled forestry cannot safely be counted with dogs for comparison because of the presence of large amounts of brash. Counts using pointing dogs are believed to identify most females present in the area counted (Baines 1990). We recorded the number of females seen during these counts and the numbers of chicks seen. From these we estimated the productivity (mean chicks per female). Subject to sampling error, this measure of chicks per female taken in early-mid August is likely to represent an almost absolute measure of productivity across a population if productivity is defined as a measure of young surviving to independence. This is because it is sampled beyond the most vulnerable period (Ludwig *et. al.,* 2010) and is only approximately 1-3 weeks prior to independence (broods were typically observed to break up in late August in this study) (see also Whitaker *et. al.,* 2007, who considered survival to three weeks as “successful” breeding in ruffed grouse *Bonasa umbellus*).

4.3 Results

4.3.1 Habitat use and winter conditions

Winter weather conditions differed substantially over the period of the study (Table 4.1). In terms of all three temperature variables, 2009-10 was the most severe winter and 2011-12 the mildest. Minimum snow lie was similar for 2009-10 and 2010-11 (60 and 56 days respectively) but far lower for 2011-12 (8 days). Annual sample sizes of autumn-winter home-ranges were low, particularly for females. Patterns suggested, however, that males used the highest proportion of broadleaf woodland in the most severe winter and the least in the least severe winter, and showed a similar pattern for closed-canopy forestry. Females used on average 28% of closed-canopy forestry in the most severe winter (though note the large standard error), and then 12% and 10% in the following two winters. Females used, on average, almost no new native pinewood in the most severe winter, 11% in the intermediate winter and 50% in the mildest winter.

Table 4.1 - Weather and home-range (MCP_{100}) habitat composition (percentage area) for the three project autumn-winters (October-March inclusive). All three temperature measures are means of daily recordings at a weather station 15 km from the study site and are given with seasonal standard deviations. Minimum snow lie is the sum of the minimum number of days recorded in each of the six months.

Variable	**2009-10**		**2010-11**		**2011-12**	
Mean min. air temp. (°C)	-3.0±5.4		-0.5±5.5		2.6±0.3	
Mean min. grass temp. (°C)	-2.3±3.4		-1.8±4.1		0.3±4.5	
Minimum snow lie (d)	60		56		8	
Sex	Female	Male	Female	Male	Female	Male
n	4	8	10	14	6	13
Moorland	65±22	54±13	73±11	65±8	38±14	68±8
Farmland	5±5	4±3	0	8±3	0	14±6
Broadleaf	0	13±5	1±0	6±2	0	3±2
New native pinewood	1±1	5±4	11±10	14±7	50±18	14±6
Unplanted forestry	1±0	7±5	3±1	0	1±1	0
Closed-canopy forestry	28±24	16±7	12±6	5±4	10±9	0
Clearfell forestry	0	1±1	0	0	0	1±0
Pre-thicket forestry	0	0	0	0	1±1	0

Compositional analyses revealed significant relationships between autumn-winter habitat composition within home-ranges and mean minimum grass temperature and minimum snow lie in females, and mean minimum air temperature in males (Table 4.2). For example, in females, use of new native pine wood was significantly more positively related to mean minimum grass temperature than all other habitats, and significantly more negatively related to minimum snow lie than closed-canopy forestry, unplanted forestry and farmland, but not to moorland. Compositional analyses plots show the strong relationship between new native pinewood and both these variables (Figure 4.1a, b). In males, use of closed-canopy forestry and broadleaf woodland were significantly more negatively related to mean minimum air temperature than moorland, new native pinewood and farmland (Table 4.2). Closed-canopy forestry was additionally significantly more negatively related to mean minimum air temperature than unplanted forestry. Thus use of closed-canopy forestry and broadleaf woodland was generally greater in more severe winters (males) and use of young new native pinewood greater in mild winters (females).

Table 4.2 - Compositional analyses results for relationship between habitat composition and autumn-winter winter weather variables. Pairwise difference are only shown for significant analyses. Habitat codes are as follows: MO = moorland, FA = farmland, BW = broadleaf woodland, NP = new native pinewood, UN = unplanted forestry, CC = closed-canopy forestry, CF = clearfell forestry, PT = pre-thicket forestry. For brevity, a vertical line ('|') indicates where more than one habitat were significantly different (">>") to another habitat in pairwise tests.

Sex	Variable	n	Test	Habitats considered	Pairwise differences
Fem.	Mean min. air temp.	20	$F_{1,19}$ = 2.56, P = 0.062	MO,FA,NP,UN,CC	-
	Mean min. grass temp.	20	$F_{1,19}$ = 2.99, P = 0.038	MO,FA,NP,UN,CC	NP>>[ALL]
	Min snow lie	20	$F_{1,19}$ = 3.01, P = 0.036	MO,FA,NP,UN,CC	CC|UN|FA>>NP
Male	Mean min. air temp.	35	$F_{1,19}$ = 3.69, P = 0.044	MO,FA,BW,NP,UN,CC	FA|NP|MO>>BW|CC; UN>>CC
	Mean min. grass temp.	35	$F_{1,19}$ = 2.33, P = 0.096	MO,FA,BW,NP,UN,CC	-
	Min snow lie	35	$F_{1,19}$ = 1.84, P = 0.167	MO,FA,BW,NP,UN,CC	-

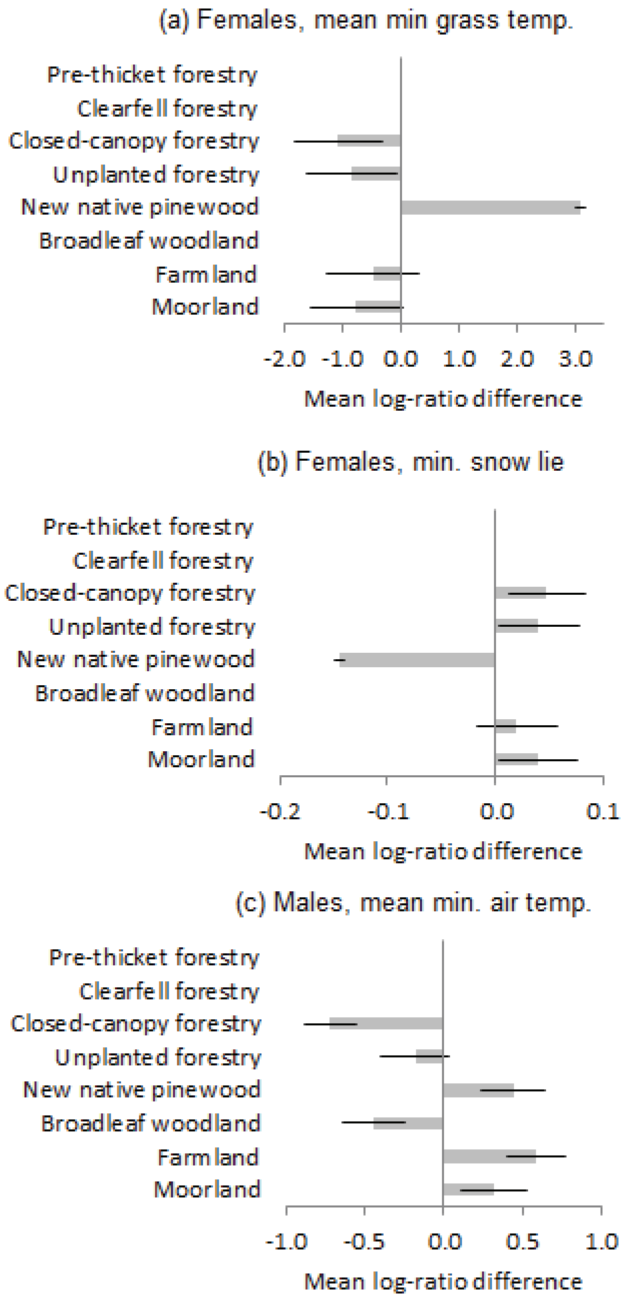


Figure 4.1. Slope of log-ratio (against (a) the mean minimum grass temperature [°C], (b) the minimum snow lie [days], or (c) the mean minimum air temperature [°C]) for each habitat in turn against all other habitats considered. Whiskers represent between-habitats standard errors of slope. Habitats without bars or whiskers were excluded from analyses but are retained on axes for comparison. These plots show both the ranking of the habitats (bars further right are associated with higher temperatures or more snow lie), and the relative confidence of that rank (larger whiskers mean we can be less sure about the placement of that habitat. Pairwise differences (Table 4.2) were assessed using non-parametric statistical tests, so are not directly comparable with the whiskers shown.

4.3.2 Survival rates

Survival analyses were based on 80 birds following exclusions. Nine birds were excluded from the analyses because they either died as a poult in August (three birds), disappeared as a poult in August (five birds) or disappeared within two weeks of handling (one bird) (see Table 4.3 for causes of mortality). Disappearance of poults could be explained by their having been taken underground by mammalian predators, where tags may not be detectable, or by tag malfunctions.

Table 4.3 – Causes of mortality of radio-tagged black grouse in the three project years. Poult mortalities (died before 1 September) are included separately since they were excluded from survival analyses.

Cause	Poult 2009	2009-2010	Poult 2010	2010-2011	Poult 2011	2011-2012	All (%)
Red fox	1	3	-	6	1	8	19 (48%)
Mustelid	-	2	-	1	-	-	3 (8%)
Raptor	-	3	-	6	-	3	12 (30%)
Disease/starvation	-	2	1	-	-	-	3 (8%)
Fence collision	-	1	-	-	1	1	3 (8%)

The best (smallest AICc) model for survival rates contained only age (juvenile/adult) (Tables 4.4 and 4.5). Confidence intervals were wide, but juveniles had an estimated 36% probability of surviving from 1st September to 1st September the following year, while this was almost doubled for adults at 71%. The only other model within two AICc contained age and season groups. This model estimated that juveniles had a 54% probability of surviving from 1 September to 1 March in the following year, and then a 71% chance of surviving their first breeding season until 1 September. Adults, on the other hand, had a higher estimated probability of surviving both seasons: marginally higher between 1 September and 1 March, at 89%, than between 1 March and 1 September at 80%.

4.3.3 Causes of mortality

Forty mortalities of radio-tagged birds were recorded in the course of the study (Table 4.3). Foxes (48%) and raptors (30%) were the most frequent putative predators of black grouse, and both were responsible for mortalities across the period of the project. Mustelids were the identified predator in only 8% of cases. The three fence strikes (8% of all mortalities) were by a male poult in August 2011, a juvenile male in September 2009 and an adult female in September 2011. All three occurred on the boundary between moorland and new native pinewood against unmarked fences. The three instances of disease or starvation (8% of all mortalities) of an adult and two juveniles remain unexplained. The two juveniles had caecal Strongyle worm counts of 0 and the adult female 60. Each had a low chest score, of 1 or 2, suggesting muscle wasting following malnutrition.

Table 4.4 – Small sample Akaike's Information Criterion (AICc) comparison of models for survival of 80 radio-tagged birds. Models are ranked according to their AICc score (smallest to largest). 'Δ_{AICc}' = the difference between the AICc of a model and the lowest AICc score; ω_i = Akaike's weight, *'k' = number of model parameters estimated; 'L' = likelihood; 'Dev.' = deviance.*

Model	**AICc**	**Δ_{AICc}**	**ω_i**	***L***	**k**	**Dev.**
age	218.64	0.00	0.37	1.00	2	94.04
age*season	220.42	1.77	0.15	0.41	4	91.75
sex*age	221.19	2.54	0.10	0.28	4	92.52
age*year	221.19	2.55	0.10	0.28	6	88.44
sex*age*season	221.73	3.09	0.08	0.21	8	84.86
age*season*year	222.75	4.12	0.05	0.13	12	77.53
year	223.27	4.63	0.04	0.10	3	96.64
null	223.54	4.90	0.03	0.09	1	100.95
season	224.41	5.77	0.02	0.06	2	99.81
sex*season	225.24	6.60	0.01	0.04	4	96.58
sex	225.45	6.80	0.01	0.03	2	100.84
season*year	225.91	7.23	0.01	0.03	6	93.16
sex*year	227.69	9.05	0.00	0.01	6	94.94
sex*age*year	228.08	9.44	0.00	0.01	12	82.86
sex*season*year	230.69	12.05	0.00	0.00	12	85.47
sex*age*season*year	233.66	15.02	0.00	0.00	24	62.56

*Table 4.5 – Survival estimates with 95% confidence intervals (CI) for the top two ranked models in AICc comparison (Table 4.4) (both AICc < 2). Survival rates for the 'age' model are annual survival estimates between 1 September to 1 September, while those for the 'age*season' model are six month survival estimates between 1 September and 28 (or 29) February inclusive (autumn-winter) and 1 March to 31 August inclusive (spring-summer).*

Model	**Group**	**Survival rates (95% CI)**
age	juveniles (all year)	0.36 (0.21-0.51)
	adults (all year)	0.71 (0.47-0.86)
age*season	juveniles autumn-winter	0.54 (0.37-0.68)
	juveniles spring-summer	0.71 (0.47-0.86)
	adult autumn-winter	0.89 (0.63-0.97)
	adult spring-summer	0.80 (0.55-0.92)

4.3.4 Breeding success and breeding habitats

Seventeen nests were located during the study, one of which was found incidentally and was not of a radio-tagged female (Table 4.6). Eight of the nests of radio-tagged females were by juveniles (first breeding attempt) and eight by adults. Four of the 17 nests were in new native pinewood, all at the base of a Scots pine (1-3 m tall), while the remaining 13 were on moorland and not within 5 m of any trees. Two of the new native pinewood nests were juveniles and two were adults, and similarly on moorland four were juveniles and four were adults (the un-aged bird was also on moorland).

Table 4.6 - Nest and brood measures recorded in three project breeding seasons and all seasons combined. The number of females followed through 10 days after hatching is lower than the number of hatched nests because one female (2010) was untagged, and two females (2012) disappeared following hatching (tag not heard in study area).

Parameter	2010	2011	2012	All
Number of nests	2	8	7	17
Clutch size	7.5±0.5	7.3±0.3	7.6±0.4	7.4±0.2
Successful nests (proportion)	2 (1.00)	5 (0.63)	5 (0.71)	12 (0.71)
Hatchability of successful nests	1.00	0.87±0.04	0.93±0.02	0.92±0.02
Chicks hatched/♀ success only	7.5±0.5	6.4±0.4	7.2±0.4	6.9±0.3
Chicks hatched/♀ including failures	7.5±0.5	4.0±1.2	5.3±1.4	4.9±0.9
Number of females followed through 10 days after hatching	1	5	3	9
Brood (≥ 1 chick) alive at 10 days (proportion)	0 (0.00)	2 (0.40)	3 (1.00)	5 (0.56)

Sample sizes were too low for rigorous comparison between years. Clutch size was not significantly different between juveniles and adults ($F_{1,12}$ = 1.02, P = 0.334) and averaged 7.4 ± 0.2 SE. Twelve of 17 nests hatched chicks, but there was no significant difference in the success rate between juveniles and adults ($F_{1,12}$ = 0.25, P = 0.746). Four nests were predated by mammals and one nest failed when the incubating juvenile female was predated by a large mustelid, the carcass being found by the nest and all but one egg having been removed. Successful nests had a hatchability of 0.92 ± 0.02 SE. On average females hatched 4.9 ± 0.9 SE chicks, inclusive of failures.

Of nine females which hatched a brood and could be followed across the first 10 days, three lost their brood (Table 4.6). In addition, three hatched broods could not be tracked because the hen did not have a tag or due to tag failures/disappearances). For juvenile females, two out of five lost their broods before 10 days, while for adults one out of four lost their brood. It was not known how broods were lost. Productivity, as measured by the number of chicks/female in August, varied significantly between years ($F_{3,16}$ = 9.86, P = 0.001) , being as high as 2.5 and as low as 0.8, averaging 1.8 ±0.4 SE across years (Table 4.7).

Twelve females had full autumn-winter home-ranges and subsequent breeding data, six juveniles and six adults. Three habitat-types (farmland, clearfell forestry and pre-thicket forestry) were excluded from home-range analyses because they were not present within those of any of the females with breeding data. We found no significant effect of age on mean egg volume ($F_{1,11}$ = 0.41, P = 0.649), clutch volume ($F_{1,11}$ = 1.02, P = 0.364) or nest success (X^2_1 = 0.93, P = 0.334) so ages were grouped for compositional analyses. MANOVA revealed no relationship between habitat composition and clutch size ($F_{1,12}$ = 1.02, P = 0.342), mean egg volume ($F_{1,11}$ = 0.41, P = 0.657) or clutch volume ($F_{1,11}$ = 1.02, P = 0.375).

Table 4.7 - Measures from brood surveys with pointing dogs carried out in August 2009-2012.

Parameter	**2009**	**2010**	**2011**	**2012**	**All**
Number of females	42	40	53	18	153
Number of sites	7	8	7	3	25
Productivity moorland	2.7±0.3	2.2±0.2	0.9±0.5	1.4±0.1	1.8±0.4
Productivity new native pinewood	2.1±0.3	2.9±0.3	0.8±0.3	-	1.9±0.6
Productivity unplanted forestry	-	-	0	-	0
Productivity all	2.5±0.3	2.5±0.2	0.8±0.3	1.4±0.1	1.8±0.4
Hens/km^2 moorland	4.0±0.8	2.0±0.4	5.7±1.1	5.3±3.5	3.9±0.6
Hens/km^2 new native pinewood	4.9±2.5	2.8±0.5	2.9±0.5	3.1	3.3±0.6
Hens/km^2 unplanted forestry	-	-	1.4	-	1.4
Hens/km^2 all	4.3±0.8	2.3±0.3	3.9±0.8	4.6±2.2	3.6±0.4

4.4 Discussion

4.4.1 Survival and mortality

Seasonal survival rates of juveniles in their first winter from the second ranked model (0.54) were very similar to those recorded in the Scottish Highlands (Strathspey and Deeside) in 2002-2004 (0.56: Baines *et. al.,* 2007). Sample sizes in the latter were low compared to this study, but their estimate of adult survival in winter was similar (1.00) to ours (0.89). However, their combined estimate of spring-summer survival for both juveniles and adults (0.66) was similar to our estimate of 0.71 for juveniles or 0.80 for adults. The product of estimated juvenile autumn-winter survival, first spring-summer survival and adult autumn-winter survival (i.e. the estimated probability of a juvenile on 1 September surviving until 1 March at the beginning of its second breeding season) were similar for both sets of birds (this study: 0.34; Baines *et al.* 2007: 0.37).

Habitat selection patterns can be influenced by weather (see Whitaker *et. al.,* 2006). Our winter data, though only over a 3-year period, showed that habitat composition within home-ranges varied over winter, and that patterns varied in relation to severity of weather in that season. Particularly, use of closed-canopy forestry and broadleaf woodland was generally greater in more severe winters (males) and use of young new native pinewood greater in mild winters (females). Black grouse are known to rely on aerial foraging in trees when snow cover inhibits access to ground vegetation (Cramp & Simmons, 1980; Parr & Watson, 1988) and snow cover was much greater in the first two project winters.

High black grouse mortality can occur where tree cover is limited in prolonged snow (Baines, 1995). Geary *et al.* (2011) found a negative relationship between density of displaying males and average minimum winter temperature two years previously which could be linked to variation in survival. However, in the current study, despite a wide variation in winter conditions, year did not feature in the confidence set of models, and models containing year had a summed ω_i (an estimator of the relative importance of a predictor: Johnson & Omland, 2004) of 20%, compared to 20% for sex, 32% for season and 85% for age (Table 4.4).

One hypothesis to explain this pattern is that the ability to adjust habitat to forest components buffered against variation in survival. While in a mild winter (2011-12) with little snow cover the use of forests appeared low, in more severe winters (2009-2010, 2010-2011), when access to ground foraging was restricted or energetic demands were greater, use of forests was greater. In the severe winter of 2009-10, over which an annual 3% increase in numbers of lekking males was recorded, in northern England, where the mean percentage of forest habitats within 1 km of leks was 0.8%, the number of lekking males decreased by 35% (Warren *et. al.,* 2013). In the English population, the lack of trees for above ground forage and shelter may have meant birds could not adjust habitat use and survival was lower as a result.

Compared to 25 mortalities recorded from radio-telemetry data in the Scottish Highlands (Strathspey and Deeside) 2002-2004 (Baines *et. al.,* 2007), we recorded more than double the proportion of mortalities due to foxes (48% compared to 18%) but a slightly lower proportion due to raptor predation (30% compared to 40%). Mortalities due to fence collisions were also lower in our study (8% compared to 12%). Baines *et al.* (2007) recorded no mustelid or disease/starvation mortalities, while we recorded 8% of mortalities for each. The Tay study area has relatively non-intensive predator removal and it is likely that predator removal is more intense in Strathspey and, particularly, Deeside where intensive driven red grouse shooting is more prevalent, which might explain the difference in the ratio of fox and raptor mortalities. The Perthshire population is also likely to be denser than the populations in Deeside and Strathspey were in the early 2000s (unpubl. data from local black grouse groups). Parasites and pathogens can act in a density dependent manner, as increased populations allow more transmission opportunities (Newton, 1998). Both non-poult disease/starvation mortalities occurred during (December) or following (June) the severe winter of 2009-10 and could be related to direct or carry-over effects of nutritional stress. Considering that in the smaller red grouse a worm burden of 2,000 has been considered as a threshold for detrimental effects on survival (Hudson, 1986), we cannot consider the low worm counts had fatal effects on the birds.

4.4.2 Productivity

Sample sizes of nests, and of broods followed through 10 days after hatching within years were generally low within years, so robust comparison of annual variation of these components was not possible. With years combined, birds hatched on average 4.9 chicks per female while in August we recorded 1.8 chicks per female, though across a different sample of birds. August counts had higher sample sizes of females, and showed wide variation in annual productivity, from 0.8 to 2.5 chicks per hen. Baines *et al.* (2007) found a significant correlation between chicks per female counted in August and percentage change in males at leks in the following year. While our sample size was too small for a correlation test (n = 3 years; 2013 lek data not available yet) variation in productivity did not appear highly linked to variation in lek counts. While the productivity in 2009 and 2010 were recorded as being the same (2.5 chicks per female), the increase in the number of lekking males in the wider region in the following year differed substantially (3% and 51% respectively, unpubl. data from the Perthshire Black Grouse Study Group).

A study in Sweden showed that adult females tended to have larger clutches, higher hatching success and better chick survival than juveniles (Willebrand, 1992) but we did not see this pattern, although our sample sizes were low within years. The proportion of females losing their brood before 10 days was 0.44, which was above the upper end of annual estimates for a Finnish population (0.08-0.36: Ludwig *et. al.,* 2010). Across years, productivity in August counts was similar for broods found on moorland and in new native pinewoods (1.8 and 1.9). However, as discussed in Section 3.5.1, a high percentage of nests (24%) found were located in new native pinewoods relative to its availability in the landscape (5% of total study area).

No carry-over effects on productivity were recorded from winter habitat use within home-ranges on productivity. Such effects have been recorded, for example in black-throated blue warbler *Dendroica caerulescens*, birds tending to use more pine forest than scrub habitat in winter were in better condition for the breeding season (Bearhop *et. al.,* 2004). Carry-over effects are thought to be more common than current literature suggests but there is difficulty in detecting effects because of interactions with density dependent effects on fitness (Harrison *et. al.,* 2011). In addition it may be difficult to elucidate the 'currency' behind carry over effects (e.g. variation in energy supplies or nutrient supplies) or the contributions of intrinsic (individual quality) and extrinsic (habitat quality) effects (Harrison *et. al.,* 2011). While we found no significantly different habitat use between birds in relation to their breeding effort or success, we were unable to account for this range of factors or measure actual body condition at breeding initiation.

4.5 Summary

We used radio-telemetry and August transect-counts with pointing dogs to investigate variation in survival and productivity within the study population. Autumn-winter weather varied significantly over the study period, from severe to mild, and we investigated if meteorological conditions had influenced survival and habitat use, and if winter habitat use had produced carry-over effects on breeding success of females. The biggest driver of survival was age, with annual survival rates estimated at 0.36 in the first year (juveniles) and 0.71 thereafter (adults), while project year did not appear to influence survival. However, habitat use appeared to vary across winters. In males autumn-winter habitat use was significantly related to the mean daily minimum air temperature and in females it was significantly related to minimum days of snow lying and mean daily minimum grass temperature. Overall patterns suggested more use of young forest (new native pinewood) relative to older forest (broadleaf woodland, closed-canopy forestry) in milder conditions. We hypothesise that variation in autumn-winter habitat use to allow more above-ground foraging in trees allows birds to maintain high survival rates in severe winter conditions. Productivity, as measured by August brood transects, varied widely between years, from 0.8 chicks per female to 2.5 chicks per female, but we found no carry over effects of autumn-winter habitat use of females on measures of breeding (egg volume, clutch volume, probability of nest success).

5. CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

5.1 Black grouse and forest habitats: conservation issues

Moorland was the most abundant habitat around leks in both 1992 and 2010 in the Tay region and the most common habitat around lek sites in the Argyll, Galloway and Inverness regions. It was present at higher proportions in those lek sites that were established between 1992 and 2010 than at lek sites that became extinct. At an individual level, in our radio-tagged sample moorland had the highest degree of selection for each sex-age-season group considered, except for juvenile females in autumn-winter.

Black grouse are, however, a species associated with diverse habitat mosaics (Baines *et. al.,* 2000). Where it occupies landscapes with little forest habitat, for example in the north of England, it is possibly sustained by an infrastructure of intensive predator removal, and it may be vulnerable to high mortality in severe winters (Baines, 1994). We observed that year was not a good predictor of survival, and survival rates were not lower in more severe winters, although sample sizes within years may have been too low to distinguish differences. In these more severe winters, males on average used more broadleaf woodland and closed-canopy forestry and females more closed-canopy forestry. A mature forest component of birch and conifer woodland in the landscape may therefore be important for the presence of black grouse populations in Scotland, to buffer against abnormally severe winters. The pattern is complex however, and our lek data showed that the age structure of the forest might influence whether a local population is likely to occur. Leks that became extinct between 1992 and 2010 tended to be in areas where pre-thicket forestry matured, and this effect was probably due to a reduction in the density of breeding hens (Baines *et. al.,* 2000). This could have been a result of recruitment into the local lekking group by young females being low due to the reduction in suitable breeding habitat. In addition, females tend to be relatively site faithful, and it is known that there is a cost involved in selecting a new, relatively unknown, breeding area (Warren *et. al.,* 2011). When pre-thicket forestry matures, hens which have bred there will have to select a new breeding area which may have a negative effect on their survival probability or productivity.

Though moorland was the most prominent habitat, leks across regions had a fairly consistent young forest (i.e. pre-thicket forestry and new native pinewood) component (9-15%). While maturation of pre-thicket forestry was associated with lek extinction, planting of new native pinewoods were associated with lek establishment. Relative selection for new native pinewood by individuals was both group-specific (varied according to age and sex) and context dependent (on time of year and weather conditions). It appeared to be relatively more important in adult females because in in both seasons it was not avoided relative to moorland, and in autumn-winter it was selected relative to broadleaf woodland. Though we did not detect such an effect in our study, adult females tend to breed better than juvenile females and thus may disproportionately influence population change (Caizergues & Ellison, 2000). We also recorded a relatively large proportion of nests in this habitat which may be linked to tall vegetation which provides nesting cover.

This study highlights three important forest habitat components in Scotland that warrant consideration in black grouse conservation efforts: (1) a diverse forest age-structure both over a landscape and at the scale of a lekking group; (2) a diverse species composition (specifically the presence of both broadleaf and coniferous components) at the scale of a lekking group; and (3) substantial moorland areas near to these forest components.

5.1.1 Forest age structure

Black grouse are able to respond to the transitional nature of habitats by shifting distributions over time in a cycle of extinctions and colonisations (Cramp & Simmons, 1980). As young forest matures and populations decline (Baines *et. al.,* 2000; Pearce-Higgins *et. al.,* 2007), over a landscape scale they would ideally be able to colonise new areas of young forest. However, in our Tay region study area, despite forestry being planted over four decades (1950s-80s), the length of the forest cycle meant that in 2010, there was little pre-thicket forest available in the landscape (1%). Pearce-Higgins *et al.* (2007) demonstrated that this likely led to the decline before 2000 in the region and our data showed that this maturation was linked to local lek extinctions. The introduction of subsidies to plant young native forest from 1994 meant that the total area of young forest (i.e. pre-thicket forestry and new native pinewood) in the region was similar in 1992 (7%) and 2010 (6%). Lek establishment was linked to these areas. It does, however, demonstrate that the planting of commercial forestry, even over four decades (which is the approximate time from date of publication to the afforestation target in 2050: Forestry Commission Scotland, 2006) can leave a landscape low in availability of young forest.

New native pinewoods were only selected by adult females in autumn-winter in our study area, but this may be a particularly important group in productivity terms relative to juvenile females. Females in their first breeding season are known to produce fewer young than older females (Brittas & Willebrand, 1991), and also have poorer survival rates (see review by Hannon & Martin, 2006). Females selecting new native pinewoods could provide a mechanism to explain colonisations (i.e. lek establishment) of areas of new native pinewoods that we observed in chapter 2. If females select these areas for foraging, nesting or brood rearing and are more likely to produce recruits for local leks, then leks in these areas are more likely to become established and/or have reduced extinction risk.

The new native pine plantations in the Tay study area varied in age, between approximately 6 years to approximately 15 years old (pers. obs.). The field layer vegetation within them was generally taller and denser than adjacent moorland areas (pers. obs.) with red deer, sheep and cattle having been excluded (but roe deer *Capreolus capreolus* were frequently observed). Reduction in grazing has been shown to have initial benefits in terms of brood-rearing as field-layer vegetation density increases the availability of invertebrate food and cover from predators for chicks, but subsequently growth can be detrimental perhaps as open areas where chicks can dry off become less available (Grant & Dawson, 2005). In some areas tree stands had started to become very dense, equivalent to the onset of canopy-closure in commercial plantations, which is linked to a reduction in female density in commercial plantations (Baines *et. al.,* 2000). It remains unclear whether a similar effect will happen with new native pinewoods which have larger areas of open ground. While the amount of open ground within a commercial plantation can prolong the period of suitability for breeding females, it is still only temporary (Baines *et. al.,* 2000).

5.1.2 Forest species composition

Owen (2011) suggests tree species within forestry are not necessarily important for black grouse, but rather structure and patch patterns should be considered. This may be true in general terms, particularly in young plantations, but in older closed-canopy stands our data suggest that larch component or forest type could be important. In our Tay study population males selected broadleaf woodland relative to forestry habitats (unplanted and closed-canopy) through the year, but this was not the case in females. Where birds were located near to trees, the majority of males were in broadleaf species, and the majority of females in conifer species. The sight of males conspicuously feeding in birch trees can be a common one in black grouse areas (Baines, 1990), but this may not necessarily represent optimal habitat for both sexes at all life stages. Juvenile females in autumn-winter selected for unplanted patches within forestry, and closed-canopy forestry was not avoided by females relative to males. Females showed a much stronger association with coniferous species, particularly with larch. Selection for larch by black grouse has been recognised before (Baines, 1990).

5.1.3 Non-forest habitat: the importance of moorland

An important policy question is where, and on what land-types, new forest should be planted (Towers *et. al.,* 2006). Forestry planted in the 1950s-80s was most often planted on upland moorland or rough grazing areas (Baines *et. al.,* 2000) and much of future new planting may be targeted in these areas. Initial planting of moorland may benefit local black grouse populations and increase local breeding densities, but this effect can be short-lived, diminishing before canopy closure (Baines, 1995; Baines *et. al.,* 2000). Moorland habitats, where most birds do the majority of their feeding through the year and which makes up large areas of nesting and brood-rearing habitat, are important. Our data demonstrated a clear degree of selection for this habitat relative to its availability at both lek and individual scales. The other open habitat, farmland, was present around leks only generally in proportion to its availability, and was associated with smaller lek sizes in the Tay region in 2010. We hypothesise that this is because it represents inferior habitats for females and broods.

The forest cover in the Tay region study area, at 35%, is higher than the national average (18%) and already exceeds the national target (25%). But because intensive farmland and high altitude areas are unlikely to be afforested (Towers *et. al.,* 2006), such marginal, middle altitude upland areas are likely to be disproportionately affected by afforestation policy. The moorland areas in our Tay region study area have relatively low economic value. They are not as intensively used for red grouse shooting as they used to be (this has largely declined in the area) or red deer stalking (much of this occurs on higher ground further from forests). While they have some blanket bog that would gain protection from afforestation (Towers *et. al.,* 2006), large amounts of the dry heath and grass-dominated moorlands could be candidates for subsidised afforestation. It would be potentially damaging in the long term to expand commercial forestry onto moorland areas used by black grouse in areas such as our Tay study area where forestry already covers an area similar to that of moorland. The Scottish Government aims to approximately double new planting rates to 10-15,000 ha (The Scottish Government, 2010), and it may be difficult to do so without encroaching onto open moorland-type habitats used by black grouse.

5.2 Management recommendations

Considering these conservation issues, we would make the following management recommendations:

5.2.1 Conserve large and well connected areas of moorland adjacent to forests

In highly forested areas such as Perthshire (forestry occupies 28% of study area) forestry should ideally remain within its current footprint, and in other areas moorland that supports black grouse leks and breeding females should be avoided for new commercial plantings. Our data suggest that a lekking group might carry out most of their annual activity within approximately 7.1 km^2 (i.e. within 1.5 km of a lek) and most nesting, female activity and male activity in spring-summer occurs within approximately 3.1 km^2 (i.e. within 1 km of a lek). Consistently across regions, an average of two-thirds of the area around leks is moorland-type habitat (i.e. open ericaceous shrub, rough grass or peat moss dominated areas). Thus we would suggest that a lekking group will likely require a continuous moorland area, adjacent to forest habitats, that is at least 5 km^2 (Baines, 1995). Haysom (2001) found that the probability of patch occupation for pre-thicket forestry depended on patch size, being 95% at approximately 3 km^2 and 8 km^2 for first and second rotation patches respectively. Such space-occupancy relationships may exist with moorland habitats. A viable metapopulation in an area, however, would require numerous such areas of moorland, and larger, contiguous, or well connected patches of moorland would be recommended.

5.2.2 *Provide a diverse forest age structure at the scale of lekking groups*

Across regions leks had an average of 9-15% young forest with 1 km of a lek (equivalent to approximately 0.5 km^2). Ensuring that the timing of forest planting or cycles leaves at least this quantity of young forest habitat adjacent to moorland habitats in a landscape could be beneficial. The length of the forestry cycle means that even when staggered over four decades, maturation can virtually eliminate young forest habitats in commercial forest areas. A way of avoiding this might be to stagger targeted afforestation over a longer period than that proposed (i.e. beyond 2050). Manipulation of spatial layout could increase the suitability of forestry over space and over time by increasing the window of availability of young forest and ensuring that such windows do not open and close synchronously across a landscape. The logistics of targeting forest planting to such a degree over such a long period would inevitably be complex. Studies have shown that leaving more open ground between stands can extend the suitability of young forestry to breeding females although not indefinitely (Baines *et. al.,* 2000).

5.2.3 *Provide a diverse range of forest tree taxa at the scale of a lekking group*

Our data show a difference between sexes in the forest type preferred by black grouse. Females showed a greater association with conifer species and males with broadleaf species when individual radio-locations were examined. Within home-ranges, forestry habitats (unplanted and closed-canopy) were not avoided relative to any other habitats by adult females in autumn-winter, while broad-leaved woodland was avoided relative to moorland. In adult males in autumn-winter, forestry habitats were avoided relative to both moorland and broad-leaved woodland. At the scale of a lekking group therefore (i.e. within 1-1.5 km radii of a lek) we recommend both coniferous and broadleaf species are available. Mature commercial coniferous species should ideally contain a component of larch. Planting or natural regeneration of birches on good nesting/brood rearing habitat could be to the long-term detriment to this habitat. This has been observed in our study area, with an area of moorland that, in the early 1990s, was productive brood-rearing habitat. In our August counts in this study (2009-2012) this patch was almost absent of females or broods and has been colonised by birch woodland (unpubl. data). Birch regeneration is known to act as a top-down ecosystem engineer, and reduce heather and bilberry understory (Mitchell *et. al.,* 2007). Broadleaf forests are currently being planted at more than double the rate of conifer forest (Forestry Commission, 2011). Broadleaf woodland was generally present in lower amounts (1-7%) around lek sites than mature coniferous forests (6-25%) and we would recommend that this habitat should be present but may only need to be present at up to 10% near to leks, and should not be encouraged at the expense of open moorland areas used by breeding females.

5.2.4 *Constructively manage the forest edge on moorland boundaries*

Despite any efforts to maintain a diverse age structure in forests, they will inevitably mature in many areas and this will alter their utility to black grouse. Natural events, such as fires and wind-fall are expected to benefit black grouse in forests by creating openings in the canopy where flushes of ground flora may provide food and nesting resources (Klaus, 1991). Modern forestry practice, however, reduces the effects of such disturbance events. Our results suggest that equivalent unplanted areas within forest plantations are selected by juvenile females in autumn-winter relative to closed-canopy forestry, but that there is generally limited movement from external habitats into large-scale forestry. Leaving unplanted patches along forest-moorland edges that incise the forest, connected by wide rides would be beneficial. As suggested by Pearce-Higgins *et. al.,* (2007), spatial and temporal continuity between exterior open habitats, especially moorland, and open habitats within forestry is likely to be important. It would be beneficial to concentrate open areas within 600 m of external moorland habitats to ensure connectivity between the two, while concentrating maximum productivity to the centre of plantations. We also saw relatively limited penetration into closed-canopy stands. Provision of open areas connecting to the external habitats would increase closed-canopy stands' edge/area ratio which, though untested, might improve accessibility.

Our results also suggest that larch is important for females and can provide the primary source of high protein food for building body condition prior to breeding. Larch should be provided along forest boundaries such that small patches are available to multiple lekking groups. An important recommendation lies in the timing of any such manipulation. As Scotland is at a stage where forestry expansion is likely to accelerate (through the Scottish Forestry Strategy: Forestry Commission Scotland, 2006) and many closed-canopy stands are reaching felling age (Mason, 2007), structural changes can be made *a priori* of new or restock planting (i.e. constructively) with costs incurred indirectly via loss of potential future yields, rather than directly via trees being removed at suboptimal times (i.e. destructively).

5.3 Future research needs

Given our findings, we would recommend the following as research priorities for black grouse conservation in Scotland:

5.3.1 To examine effects of forest expansion on population size and distribution

A key research need, outside optimal management of commercial forestry, is to find out the long term effects of new native pine-forests on black grouse populations. These areas are ostensibly attractive to black grouse, containing a mosaic of open patches and trees, but because in our study area they are all less than approximately 15 years old, it is not fully known how black grouse will respond as they mature. It would be useful to investigate how populations within and around these change as they mature, for example by investigating change in size and/or location of leks or density of females and broods in August over time. Specifically we need to investigate whether local black grouse abundance responds to the planting of new native plantations with a similar pattern to that seen within commercial plantations (an initial increase followed by a subsequent fall: Baines *et. al.,* 2000), and whether any pattern is influenced by surrounding landscape factors. Using these data, the likely impact on black grouse populations of different afforestation scenarios, given afforestation aspirations, current forest and constraints to afforestation identified (Towers *et. al.,* 2006) could be modelled. A large number of available GIS datasets could be used to describe the current and potential forest-moorland matrix in Scotland for this purpose.

5.3.2 To test forest-moorland edge modifications

The constructive management recommendations suggested in section 5.2.4 could be tested and fine-tuned with field trials. Our data have presented a number of testable hypotheses with regards to the structure of forestry along moorland boundaries that will lead to increased use by black grouse: (1) a component of larch within the stands, (2) unplanted areas left along and closely behind the forest edge, (3) new native pinewoods between moorland and forest boundaries. Measuring variation in use across different boundaries would most likely require marked individuals which would make trials logistically challenging, but the increasing availability and reducing cost of GPS tags, the data from which can be downloaded remotely, may make such trials feasible in the near future. Because mature stands take decades to establish, it would probably be necessary to use the existing variation in forestry boundary structures present in the landscape. Such a quasi-experimental set-up would need to carefully account for potentially confounding variables.

5.3.3 To investigate the conservation requirements for core moorland habitats

This report has identified the importance of moorland habitats to black grouse for key activities such as lekking and breeding in the Tay region. We can thus hypothesise that a component in conserving black grouse in Scotland is to retain sufficient areas of suitable moorland habitat. Given the political desire to increase the extent of forest in Scotland, it is likely that remaining moorland habitats may be under increasing threat of afforestation. This has the capacity to impact upon black grouse numbers, particularly in southern Scotland where declines have already been greatest and population fragmentation is evident.

A desk based study, using existing lek databases, could consider how the scale and quality of moorland habitats influences black grouse numbers and distribution. These could explore the relationship between extent of moorland and population size, the minimum moorland patch size that will still support a viable lekking system and how the type and intensity of moorland management, including grazing and predator levels, as well as the nature of surrounding habitats, influence these relationships. Additional correlates such as indices of gamekeeper abundance and red grouse shooting bags could be considered as potential predictors of black grouse distribution and abundance.

5.3.4 To test ways to improve brood-rearing habitat quality

This report and other studies reveal that Scottish black grouse distribution and abundance can be influenced by forests in the landscape (e.g. Baines *et. al.,* 2000; Pearce-Higgins *et. al.,* 2007). In particular, young forest can lead to increases in local populations, while maturation across large areas of forest can be detrimental. Open habitats (particularly moorland) and young forests provide key habitats for breeding and lekking. In these the extent of grazing pressure can influence resource provision for breeding females (Calladine *et. al.,* 2002). Over-grazing can restrict the availability of key shrub species that provide high invertebrate biomass and nest sites, while under-grazing can potentially lead to rank vegetation that restricts chick movement.

Given government forest expansion policy, a key research need in black grouse conservation is investigation of the long-term effects of new native forests and their optimal management. Furthermore, if forest expansion reduces the availability of open moorland habitats to black grouse, then remaining unplanted areas (both outside and enclosed by forests) may require better grazing management to provide higher quality habitats and regulate natural regeneration. Cattle grazing or mechanical cutting can alter the structural and species diversity of vegetation. It could potentially benefit black grouse by increasing variation in niches for plants, herbivorous invertebrates and carnivorous invertebrates. A series of trials to test the effects of cattle grazing or mechanical cutting could determine if these had the potential to improve brood habitats and breeding success in these areas.

5.4 Conclusions

Conservation measures for black grouse can be effective, but often their effects have been temporary (Baines *et. al.,* 2000; Grant *et. al.,* 2009). Conservation of the species is complex due to its diverse resource requirements, and further complicated by the large-scale changes that are likely to affect Scotland's forests in the coming decades. Adequate land-management for threatened species depends on understanding how that species uses the landscape (Liu *et. al.,* 2010). Our data provide further information on how black grouse use forest and non-forest habitats. In particular we have added to the evidence regarding the role forest age structure has on distributional shift in the landscape, shed new light on within-population variation in forest resource use, and demonstrated that the degree of connectivity between essential moorland habitats and commercial forestry may be limited and vary according to forest structure. Our data provide a basis for specific recommendations for management of forests for conservation of the species, but also testable hypotheses that will require more rigorous experimental approaches. This study and some important conservation reviews (Baines *et. al.,* 2000; Grant *et. al.,* 2009) point to the need for a balance of habitats. Black grouse conservation requirements should play a role in afforestation targeting decisions and in doing so may deliver additional biodiversity benefits.

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