Provision of habitat for black grouse *Tetrao tetrix* in commercial forest restocks in relation to their management

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Declaration

I wish to submit this thesis for examination in accordance with the Regulations for Higher Degrees by Research. I declare that the thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others in the thesis.

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Jenny Owen

Abstract

As planted forests mature and are clearfelled in patches, second rotation tree crops (restocks) become available to black grouse, a species of conservation concern in the UK. Currently, only a limited amount is known about the resources provided by this habitat to black grouse and their broods. The aims of this study therefore, were to investigate the recovery of field-layer vegetation and the invertebrate population from restock through to canopy closure of planted trees, assess the duration of habitat availability and food resources to black grouse, and understand how forest management could improve provision. Changes to the abundance of predators resulting from habitat management were also considered. The comparative habitat quality of restocks was assessed in a wider landscape context.

Field-layer vegetation in 72 restocks in two afforested areas in the north-east and the south-west of the Scottish Highlands was surveyed. On average, only 60% of ground in restocks was re-planted with second rotation trees, with the remainder left unplanted. Initial vegetation recovery was generally impeded by timber harvest residues (mainly brash), which comprised up to 50% of total ground cover two years after restock. Increased cover of heather *Calluna vulgaris*, often an important component of black grouse habitat, and decreased brash cover were recorded in areas of restocks where first-rotation timber was removed by cable-winch (compared with harvester and forwarder removal) and in planted areas (compared with areas left unplanted). Bilberry *Vaccinium myrtillus* and cotton grass *Eriophorum* spp. occurrence was recorded infrequently irrespective of restock age or management. Heather generally dominated the field-layer six years after restock, reaching a height and density reported to be suitable for black

grouse nesting and brood cover in other studies. The onset of tree canopy closure as early as eight years suggests that suitable black grouse habitat availability in restocks is likely to be severely limited in duration.

Brash removal, or break-up and re-distribution of the brash layer, positively affected the recovery of field-layer vegetation species potentially of use to black grouse. Extending the fallow period prior to restock resulted in an extended period of suitable habitat available to black grouse prior to canopy closure. However, habitat created by extending the fallow period also attracted a higher number of mammalian predators of black grouse. In the longer term, areas of restocks left unplanted should provide a valuable open-ground resource after canopy closure of the planted crop, although results suggest that management to prevent encroachment of naturally regenerating non-native trees is likely to be necessary.

Invertebrate taxa selected by chicks in previous black grouse studies were available in all ages of restock studied. Taxa abundance differed as restocks aged and field-layer vegetation developed, although contrasting habitat preferences of taxa meant that each was affected differently by restock management. No single forest management method positively increased abundance of all taxa. Abundance of Lepidoptera larvae, a key food item for black grouse chicks, was positively related to dwarf shrub cover. An extended fallow period prior to restock should prolong increased larvae availability to chicks.

Provision of preferred field-layer vegetation habitat and invertebrate abundance in restocks was comparable to habitat surrounding leks - areas likely to be occupied and

utilised by black grouse. Restocks had a comparatively low occurrence of key plant species, including bilberry *Vaccinium myrtillus* and cotton grass *Eriophorum* spp. Cover of the dwarf shrub bog myrtle *Myrica gale*, positively associated with Lepidoptera larvae abundance in habitat surrounding leks, was absent from restocks. The abundance of other invertebrate taxa considered was similar between leks and restocks.

Study findings are discussed with reference to black grouse conservation and commercial forestry systems in Europe. Management recommendations to improve habitat for black grouse in second rotation planted forests in Britain are provided.

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1.1.1 Taxonomy & Morphology

The black grouse *Tetrao tetrix* (Linnaeus 1758) is one of 18 species of grouse recognised worldwide (Storch 2007), with four species of the genus *Tetrao* exclusively inhabiting Eurasia. There are currently seven (del Hoyo *et al.* 1994) or eight (Potapov & Flint 1989) recognised subspecies, based upon geographical variations in morphology (colour patterns in males and females). Only the British subspecies *T. t. britannicus* is geographically separate.

The black grouse is a large woodland bird adapted to the cold climes of the boreal forest zone. Birds are sexually dimorphic; males (or 'blackcock') have glossy blue-black plumage with a white wing bar and coverts, distinctive lyre-shaped tail, and red eye comb. Females (or 'greyhen') are cryptically coloured rufous-brown, with a forked tail and pale white wing bar.

1.1.2 Distribution & Conservation Status

Black grouse occupy an extremely large range in Northern Eurasia, distributed continuously across the boreal forest zone from Scandinavia to South Eastern Siberia (Storch 2007) and are also recorded in most western and central European countries (Storch 2000). The population is considered to be stable throughout its contiguous range and listed as 'least concern' in the IUCN Red list (Birdlife International 2009), with estimates of between 2.5-3.2 million pairs in Europe in 2004 (Sim *et al.* 2008). However, negative population trends have been reported from Fennoscandia (Wegge 1983; Helle *et al.* 1987; Linden & Helle 2003) and many European populations have declined rapidly during the past century (Niewold 1990; Hudson & Baines 1993), particularly since the 1970's (Birdlife International 2004). Long-term range contractions and population declines in western and southern areas of the range have resulted in vulnerable, fragmented populations (Bergmann & Klaus 1994; Schmitz 1997).

The dramatic decline of black grouse in Britain is well documented. Widespread across Britain until the 20th century, they were 'commonly found in virtually every English county at the end of the 19th century…' (Gladstone 1924). Their range extended from southern to northern England, most of Wales, throughout mainland Scotland and some of the Inner Hebridies (Johnstone 1967; Holloway 1996). Many populations are now extinct; the current range is restricted to upland areas of Scotland, northern England and Wales. Currently listed as a species of high conservation concern (Gregory *et al.* 2002) and UK BAP priority species (UK Biodiversity Action Plan 2008), numbers continue to decline. The most recent national survey in 2005 estimated 5078 displaying males in Britain (95% CI 3920-6156) (Sim *et al.* 2008), 22% less than the first full national survey conducted 10 years previously (Hancock *et al.* 1999), and 80% less than the 25000 males estimated in the early 1990's (95% CI 13800-36700) (Baines & Hudson 1995). There is considerable regional variation in population fluctuations over the past decade. In Scotland, which holds nearly 70% of the British population, numbers declined significantly by 29% between surveys, with large declines of up to 69% in southern Scotland, and smaller, statistically non-significant declines in north and northeast Scotland (Sim *et al.* 2008). In England, populations declined by 11%, but there is evidence for recent range expansion (Warren & Baines 2008). In Wales, numbers increased by 39% between surveys, although the total population remains small (c. 213 males). In addition to population declines, there is evidence that the 28% contraction in range reported in Britain between the early 1970's and early 90's (Gibbons *et al.* 1993) is continuing in core areas (Sim *et al.* 2008).

1.1.3 Reasons for the decline

Population declines across Europe have been linked with numerous factors, many of which are likely to work in combination, including: increased predation by red fox *Vulpes vulpes*, crows *Corvus* spp. and raptors (Angelstam 1983; Baines 1991b; Baines 1992; Summers *et al.* 2004) modern forestry methods, blanket afforestation and forest maturation (Klaus 1991; Helle & Helle 1991; Kurki *et al.* 2000; Haysom 2001; Pearce-Higgins *et al.* 2007); habitat loss and deterioration through agricultural improvement (Kurki & Linden 1995; Ludwig *et al.* 2009a; Ludwig *et al.* 2009b); decline in chick survival (Baines 1991b; Baines *et al.* 1996); collision with deer fences (Catt *et al.* 1994; Baines & Summers 1997); increased disturbance in breeding and wintering grounds (Miquet 1990; Zeitler & Glanzer 1998; Zeitler 2000; Herzog & Kruger 2003; Arlettaz *et al.* 2007; Patthey *et al.* 2008); overgrazing by sheep *Ovis aries* and red deer *Cervus elaphus* (Baines 1996; Calladine *et al.* 2002); exploitation by hunting (Storch 2007) and climate change (Baines 1991b; Loneux 2003; Summers *et al.* 2004; Ludwig *et al.* 2006). Although black grouse can respond positively to conservation management (Grant *et al.* 2009), many efforts to reverse declines have failed, suggesting that further understanding of mechanisms driving the decline is needed.

1.1.4 Reproduction & survival

Black grouse exhibit a promiscuous mating system whereby males defend small territories on traditional leks in spring, displaying and fighting to mate with females. Females lay a clutch of 5-11 eggs in a shallow ground scrape that hatch around mid-June in Scotland, suggested to coincide with the main peak of preferred invertebrate food for chicks (Baines *et al.* 1996), and need to raise 1.5-2 young per year to maintain a stable population (Baines 1996). Declines in chick survival are thought to have contributed to decreases in breeding success of up to 60% across Europe in the latter part of the 20th century (Baines 1991b), although some populations still appear to have good breeding success (Baines 1991a; Baines 1996), and juvenile and adult survival may contribute more to observed declines instead (Baines *et al.* 2000).

1.1.5 Habitat & diet

Black grouse are a relatively sedentary woodland species, found in a wide variety of habitats across their range. In the natural boreal forest, where low temperatures predominate, they inhabit the forest edge and early successional stages of forest regeneration created following wild-fire, disease or storms. Outwith the boreal forest, they utilise structurally similar transitional habitats, such as young open woodland, often with a large deciduous component (Seiskari 1962; Swenson & Angelstam 1993); ancient pinewoods (Summers *et al.* 2004) with open glades maintained by browsers; pine or spruce bogs (Angelstam & Martinsson 1990; Wegge & Kastdalen 2008); intensively managed forests with large-scale clearfelling (Swenson & Angelstam 1993); and newly planted commercial forests (Johnstone 1967; Cayford 1990a). The presence of trees is generally believed to be essential for black grouse (Johnsgard 1983), although some populations in northern England exist in relatively treeless areas. Black grouse prefer areas with young or stunted trees, although tree density is more important than tree age or height, due to the shading out of important ericaceous plants upon canopy closure (Cayford *et al.* 1989)

In Britain, black grouse mainly inhabit the upland moorland transitional zone, where native woodland, agricultural land or exotic commercial tree plantations border heather *Calluna vulgaris* moors. This may create a positive 'edge effect' attractive to black grouse where the boundary of the two habitats is richer than either habitat on its own (Odum 1959), but may also have negative consequences for other species, or no effect at all (Avery 1989). In addition to *Calluna* moorland, black grouse require a diverse mosaic of habitats depending on seasonal requirements, including forests with an understory of dwarf shrubs such as bilberry *Vaccinium myrtillus*, wet moors with cottongrass *Eriophorum* spp., forest bogs rich in invertebrates, and mature deciduous trees, particularly birch *Betula* spp., from which catkins and twigs are eaten when snow covers the ground (Baines 1995). Chicks feed almost exclusively on invertebrates during the first 2 to 3 weeks after hatching, before changing to a predominantly herbivorous diet (Kastdalen & Wegge 1985; Picozzi 1986; Cayford *et al.* 1989; Cayford 1990b; Wegge & Kastdalen 2008). A wide range of beetles, spiders and other arthropods are consumed according to abundance and local availability, but dietary studies have revealed ants, Lepidoptera larvae and sawfly larvae as some of the most favoured items taken by black grouse chicks (Picozzi 1986; Cayford *et al.* 1989; Starling-Westerberg 2001).

The quality, size and distribution of suitable forest habitat patches explain most of the variation in spatial and temporal differences in black grouse abundance (Angelstam &

Martinsson 1990; Storch 2007). Results from British radio telemetry studies suggest that for an area to be occupied, black grouse need an adequate winter food source, a protein and energy rich food source for hens in spring, and insect-rich, tall vegetation for chicks, within a home range of 300-500 ha per lekking group (Picozzi & Hepburn 1984; Cayford 1990b). In Sweden, variation in the density of males attending leks strongly correlated with the number and size of raised bog, clearcut and young forest habitats, with the presence of these preferred habitats explaining 84% of the variation in abundance (Angelstam 1983).

1.1.6 Breeding habitat

Females tend to nest within 1 km of the lek they are mated on (Picozzi 1986) and rear young in tall, dense vegetation (Borset & Krafft 1973; Bernard 1982; Parr & Watson 1988). However, some authors have found no relationship between habitat type or cover and nesting success (Storaas & Wegge 1987), whereas others found that black grouse nested more successfully in younger forest classes, but irrespective of the degree of nesting cover (Brittas & Willebrand 1991). Rate of vegetation growth and levels of primary production are also important to black grouse (Angelstam 1983). In mature, native Scots pinewood *Pinus sylvestris* at Abernethy in Scotland, where vegetation was released from heavy grazing by culling red deer and removing sheep, Watson and Moss (2008) reported the number of cocks at leks were more closely associated with the rate of growth in height of the recovering field layer than with breeding success the previous year. As vegetation matured and growth slowed, black grouse numbers declined. Possible explanations suggested included that vegetation in the early stages of growth was more nutritious for black grouse, increasing bird condition for breeding, or that improved vegetation structure or increased invertebrate density for chicks was provided by a young, fast-growing sward than a mature or heavily grazed one.

1.2 Background to the Present Study: Commercial forestry and Black Grouse Habitat

1.2.1 Forestry in Britain during the last century

Britain's forests have experienced considerable change during the 20th century, most significantly in the extent of forest cover, but also species composition. Heavy demands for timber from Britain's forests followed the outbreak of World War in 1914 as imports could no longer be relied upon, and the Forestry Commission was established in 1919 to rebuild and maintain a strategic British timber reserve. Following extensive harvesting during both World Wars, major re-forestation occurred across Britain from the 1950's, with non-native conifers planted on existing and newly acquired sites, often as extensive plantations on marginal upland agricultural land (Mason 2007). Developments in silvicultural techniques allowed establishment of fast-growing, high-volume producing forests on sites not previously considered suitable for trees. The rapid expansion of afforestation slowed only in the 1980's with the reduction of financial incentives (Foot 2003), by which time a fast-growing, even-aged forest resource was well established across the British uplands.

The forest area of Great Britain has more than doubled since 1947, now covering 3 million hectares, or 12% of the land area (Forestry Commission 2009a). In 2005, the Forestry Commission reported over 16% of Scotland's land as forested, nearly 70% of this with conifers (Smith & Gilbert 2003), with recommendations for forest cover to expand to 25% by 2050 to help reduce the impact of climate change and to increase Scotland's sustainable timber resource (Forestry Commission 2006). Forest species composition has changed dramatically during the last 50 years with a major shift from Scot's pine *Pinus sylvestris* to non-native Sitka spruce *Picea sitchensis*, now the major commercial timber species (Smith & Gilbert 2003). Most conifer plantations are managed on a rotational clearfell patch system (Hibberd 1991), where four stages of growth are recognised: pre-thicket, thicket, pole (economically mature timber) and clearfell (harvest), creating a patchwork of even-aged stands throughout the forest. Many Sitka spruce plantations are now approaching the end of their first rotation, which is generally 40-60 years in duration (Mason 2007). In 2000, 77% of conifer stands were categorised as ready to harvest within the next 20 years (Mason 2007).

1.2.2 Commercial forestry and upland birds

Black grouse have long been associated with commercial forestry, attracted into plantations by early-successional habitats, and numbers rapidly increase in newly forested areas (Thom 1986). Despite widespread black grouse population declines across the UK, local increases were reported from the 1940's following large-scale afforestation of upland habitats in Scotland and Wales (Mead 2000). However, the benefits of young forest habitats are often short-lived; commercial forest canopies close after little more than a decade and most of the ground vegetation is shaded out (Pearce-Higgins *et al.* 2007), rendering the habitat unsuitable for black grouse. Populations will only persist if trees are widely spaced to allow sufficient light to the understory, or if substantial areas of open, unplanted ground, or margins and corridors remain within the plantation (Cayford *et al.* 1989).

When black grouse density is high in newly planted commercial forests, considerable damage can be caused to young trees by buds and needles being eaten (Johnstone 1967).

In the early part of the 20th century, young plantations were repeatedly targeted by black grouse (Gladstone 1923), with some planting schemes in Scotland abandoned altogether due to severe damage (Gordon 1915). Even as late as the 1960's large populations were damaging new plantings across Scotland; of a questionnaire survey returned from 337 forests in 1963, 20% reported 'appreciable damage' by black grouse (Jenkins 1963). Extermination was advocated within an open season, however even in the 1960's there were so many black grouse present 'it is very difficult to shoot enough to make a significant difference to the population…' (Johnstone 1967).

In addition to black grouse, other birds benefited from the early stages of upland conifer afforestation including short-eared owl *Asio flammeus* (Fuller *et al.* 2007), willow warbler *Phylloscopus tochilus* (Moss 1979), red kite *Milvus milvus* (Newton *et al.* 1996), sparrowhawk *Accipiter nisus* (Moss 1979), hen harrier *Circus cyaneus* (Petty & Anderson 1986), and some song-birds (Bibby *et al.* 1985). Some species are now closely associated with introduced conifers, such as firecrest *Regulus atricapillus*, mainly found in Norway spruce *Picea abies* and Douglas fir *Pseudotsuga menziesii* plantations (Peterken 2001). Other taxa also benefited from the early-successional habitats created by afforestation, such as voles *Microtus* spp., red squirrel *Scirius vulgaris* and invertebrates (Staines 1983; Avery & Leslie 1990; Lurz *et al.* 1995; Evans *et al.* 2006). Rather than being influenced by tree species, many of which are non-native in commercial plantations, black grouse and other birds select habitat based upon structure, productivity and patch patterns (Moss 1978; Angelstam & Martinsson 1990; Fuller 1997; Wilson *et al.* 2006). Research on communities of bird species using plantations suggests that population density and abundance increases when vegetation and tree growth is vigorous (Moss 1979). Bird density in a young spruce plantation in

Sweden was found to be one-ninth of that found in natural forest, with lower species diversity (Nilsson 1979). Bird species diversity in managed boreal forests was greater in older forest stands and mixed tree species, and lower in young forest and clearcuts (Jansson & Andren 2003). British studies have also found greater bird diversity in mature than younger plantations (Moss 1979; Currie & Bamford 1982), and twice as many bird pairs in natural pine stands than planted stands (Newton & Moss 1977).

Although conifer plantations attract a greater range of species at higher densities than open hill-ground (Moss *et al.* 1979), losses of moorland species are considerable; upland waders are thought to have been displaced by afforestation (Stroud *et al.* 1987) and raven *Corvus corax* numbers have been impacted by loss of sheep carrion resulting from afforestation (Marquiss *et al.* 1978). Golden eagle *Aquila chrysaetos* foraging habitat has also been negatively affected resulting in decreased breeding success and population declines (Marquiss *et al.* 1985; Whitfield *et al.* 2001).

Commercial forests also provide habitat for predators of ground-nesting birds, such as red fox and pine marten *Martes martes* (Hewson & Leitch 1983; Kurki *et al.* 1998), and nesting sites for crows (Petty 1985), which were previously limited by the lack of suitable tree nesting sites on moorland (Stroud *et al.* 1987). Fragmented forest (compared with continuous forest) may lead to increased numbers of generalist predators (Thompson 2007) and may also increase their searching efficiency (Storaas *et al.* 1999), potentially reducing black grouse breeding success (Kurki *et al.* 2000). Although there is evidence that predator control can benefit black grouse breeding success and increase their abundance, studies have so far failed to identify significant associations between the presence of gamekeepers and black grouse breeding success or density in Britain (Baines 1996). Indeed, it has been suggested that improving brood cover in black grouse habitats may be a better long-term solution than predator control (Hannon & Martin 2006).

1.2.3 Impacts of forestry

When moorland and heathland are afforested with non-native conifer plantations, major changes to ground vegetation occur (Hill 1979), particularly when grazers are fenced out (Baines 1996). Deep ploughing and drainage used during establishment of forests rapidly dry out soils leading to losses of moisture-loving species (Stroud *et al.* 1987) and existing moorland vegetation is eliminated during early successional stages of tree growth, replaced by woodland ground vegetation (Wallace & Good 1995). When trees close canopy, ground vegetation is shaded out and the forest floor is covered with needle litter until timber harvesting. After clearfell, vegetation species richness often peaks (Ferris *et al.* 2000; Roberts & Zhu 2002; Eycott *et al.* 2006) as soil disturbance and increased light availability allows vigorous growth of open ground colonisers such as rosebay willowherb *Chamaenerion angustifolium* and tufted hair-grass *Deschampsia caespitosa* (Abdy & Mayhead 1992), woodland herbs, and dormant heathland vegetation established from the seed bank (Hill & Stevens 1981; Peterken 2001) or seed rain (Mayer *et al.* 2004). Re-vegetation after clearfell is dependent upon many factors, including soil type, soil fertility, harvesting method, and slope and aspect of the site (Wallace & Good 1995; Ferris *et al.* 2000; Astrom *et al.* 2007). The modern managed forestry system cannot equate to the natural boreal forests (Stroud *et al.* 1987). Non-native coniferous planted forests result in an even-aged structure, changes to forest light regimes, and a lack of graded ecotones (Peterken 2001).

The impact of afforestation on abiotic site factors is complex. Not only are there obvious effects resulting from ground preparation and planting, but unplanted ground and freshwater habitats outside the forest are also affected to varying degrees. Intensive management operations can result in various modifications, including: changes to soil profiles; soil compaction and erosion during and following cultivation, drainage and harvesting; nutrient losses through removal of timber and brash from site and through leaching; and changes to water status and aeration. However, it has been suggested that the impacts of forestry may be balanced by the capacity of sites to recover naturally (Worrell & Hampson 1997).

Afforestation of moorland with conifers has been controversial for many decades, being widely regarded as ecologically damaging (NCC 1986; Lindsay *et al.* 1988). However, it has been suggested that that the effects of intensive agriculture on biodiversity would be far worse than those caused by forestry (Peterken 2001) and that upland afforestation has a net beneficial effect by increasing biodiversity (Garthwaite 1983) and potentially acting as a carbon sink (Zerva & Mencuccini 2005).

1.2.4 Commercial forest restocking

Restocking is the replanting of existing forest areas that have been harvested, usually by clearfell. Between 2008 and 2009, nearly 16 000 ha of forest land was restocked in the UK, 60% in Scotland, of which 85% was with conifers (Forestry Commission 2009). Restocking has increased since the 1970's, whilst new plantings on previously un-afforested ground have decreased (Forestry Commission 2009).

Substantial changes to forest policy have taken effect in recent decades, meaning that restocking of the forest estate is approached differently to the original post-war first-rotation plantations. Plans for current productive forests now incorporate a more diverse range of tree species planned according to soil type and underlying geology, and promote a more varied forest age structure (The UK Forestry Standard 2004). High density plantings of Sitka spruce coupes containing 5-10% open space were common between the 1950's and 1980's to obtain government grants, however, up to 40% of coupes are now left unplanted for conservation and aesthetic value. Open, unplanted ground now amounts to 10% of the total forest area in Scotland (Smith & Gilbert 2003), which is likely to benefit black grouse, particularly breeding hens (Baines *et al.* 2000). Appropriate steps to protect soils and watercourses whilst extracting timber and preparing sites for restocking are now routine (The UK Forestry Standard 2004). Fertilisation of young trees, once an essential requirement for newly established first-rotation upland conifer plantations (Taylor & Worrell 1991) is no longer necessary, as decomposing brash, leaf litter, stumps and roots from the previous crop release nutrients at a critical point of sapling growth on restocks (Smith & McKay 2002). Forestry has progressed significantly since the harsh ploughing, fertilisation and drainage systems of post-war plantations. Well informed decisions on felling and future management of forests are critical to avoid the straight-edged monocultures which previously caused so much controversy (Avery & Leslie 1990). Restocking forests after clearfell can provide the opportunity to adjust forest management practices to the benefit of wildlife, whilst improving the aesthetic value of plantations.

1.2.5 Black grouse and restocks

It is unclear whether second rotation restocks provide equally good habitat for black grouse as new plantings, although this seems to be the case for European nightjar *Caprimulgus europaeus* (Ravenscroft 1989), wood lark *Lullula arborea* (Langston *et al.* 2007), short-eared owl (Bibby *et al.* 1985) and tree pipit *Anthus trivialis* (Burton 2007). Ground-nesting hen harrier in Ireland have recently shown preference for nesting in restocks over all other available habitats, although results must be viewed with caution as this relatively new habitat may not prove to be the best choice in the long-term (Wilson *et al.* 2009) . Density and species richness of songbirds in Wales were found to be higher in restocks than newly afforested ground (Currie & Bamford 1981; Leslie 1981), increasing with forest succession (Bibby *et al.* 1985), although comparisons were made between only small numbers of restocks and new planting sites in these studies.

Black grouse were expected to flourish in restocks as they did in newly afforested areas in the 1960's (Watson & Moss 2008), however comparable population increases have not been apparent, possibly indicating that the quality of habitats produced by modern silviculture are not as suitable for black grouse (Hjeljord & Fry 1995), or that other aspects of the forest environment have changed in the intervening period (e.g. increased predator populations). Restocks are evidently used by black grouse in Britain for feeding and roosting (Bibby *et al.* 1985; Cayford 1993) and in one study in Argyll, were found to be occupied as readily as the first rotation of young trees (Haysom 2001). Outwith the UK, black grouse use clearfells or restocks in many areas where modern forestry practices take place (Kolstad *et al.* 1985; Klaus 1991; Brittas & Willebrand 1991; Swenson & Angelstam 1993), having been recorded on leks (Willebrand 1988), nesting in regenerating scrubby vegetation (Sonerud 1988), and recorded in clearfelled areas with young broods, although fresh clearfells are generally avoided (Borset & Krafft 1973; Marcstrom *et al.* 1982). Population increases in Sweden in the 1990's followed large-scale clearfelling, although this was not evident in the Urals, where it may have been prevented by other unknown factors (Watson & Moss 2008). However, the black grouse population decline in Finland appeared wholly independently of changes in forest structure (Helle & Helle 1991), and even where habitat remained intact during the 1990's, widespread European grouse populations mostly declined. This was possibly due to a common factor operating over large-scales and over-riding potential land-use effects, such as weather patterns (Watson & Moss 2008).

There may be a number of reasons for black grouse failing to flourish in restocks. Important vegetation for feeding and cover such as heather and bilberry do not regenerate as readily after clearfelling (Hill & Jones 1978; Kardell 1980; Atlegrim & Sjoberg 1996a; Bergstedt & Milberg 2001; Lakka & Kouki 2009), leading to reduced levels of food for both black grouse and capercaillie *Tetrao urogallus* (Kastdalen & Wegge 1985; Stuen & Spidso 1988; Atlegrim & Sjoberg 1995; Atlegrim & Sjoberg 1996b; Wegge & Kastdalen 2008). Cayford & Hope Jones (1989) suggest that whilst restocks may be of benefit to black grouse in the short-term, low levels of regenerating heather and bilberry make them inferior to new plantings and more permanent semi-natural forest habitats. Invertebrate density is reduced following clearfell (Stuen &

Spidso 1988) and brood habitat quality reduced through drainage of the ground to stimulate wood production in restocks (Cayford & Hope Jones 1989; Wegge *et al.* 1982), possibly affecting chick survival. Drainage of restocks is common-place in second rotation plantings (Morgan & Ireland 2004).

In addition to rapid re-growth of vegetation following clearfell, pre-thicket restocks contain the additional element of brash (tree tops and branches left on site after harvesting) distributed around the site in 'wind rows' or raked into mats (Moffat *et al.* 2006), which aid heavy machinery to cross the site during timber extraction without damaging soils (Wood *et al.* 2003). On steep slopes, brash is removed completely as whole trees are winched to the roadside using a cable crane (Moffat *et al.* 2006), although this can have negative impacts for the following generation of trees (Proe & Dutch 1994; Walmsley *et al.* 2009). The retention of brash on restocks can potentially have negative consequences for black grouse by inhibiting growth of important vegetation species (Abdy & Mayhead 1992), additionally, planted trees can begin to close canopy before brash has degraded enough to allow vegetation to recover or set seed (Watson & Moss 2008). Brash breakdown also enhances the nutrient status of the soil, having negative effects on heather growth. However, brash may have beneficial effects for black grouse, limiting movement of mammalian predators through restocks (Truscott *et al.* 2004), providing refuges and cover for chicks (K. Kortland, pers. comm.), and by increasing the abundance and species diversity of chick food, such as beetles (Michaels & Bornemisszza 1999; Selonen *et al.* 2005; Nitterus & Gunnarsson 2006).

1.3 Thesis objectives

In order to make informed decisions regarding management of second rotation restocks for black grouse and their broods, a thorough assessment of habitat and invertebrate availability in restocks from planting to canopy closure is necessary. The overall objectives of this study were therefore:

1. To investigate the determinants of field-layer vegetation in second rotation restocks, and to understand how forest management could increase suitable habitat for black grouse prior to canopy closure of planted trees.

2. To assess whether management-influenced changes to restock habitat result in changes to abundance of black grouse predators.

3. To quantify abundance of invertebrate food available in restocks to black grouse broods, and to identify management methods that could increase provision in restocks.

4. To assess objectively the ‘quality’ of restocks to black grouse and their broods.

5. To identify implications of the results with respect to forest management and conservation of black grouse in and around Scotland’s plantation forests, and relate findings to other studies in Europe and Scandinavia.

1.4 Thesis structure

Data were collected in the field from two study sites in the Highlands of Scotland in The Trossachs and in Sutherland. Further details of study sites are given in Chapter 2.

Chapter 3 is the first of four data chapters; in this chapter field-layer vegetation is assessed in a chronosequence of second rotation restocks representing sites from re-planting to the onset of canopy closure. Implications of management methods used during restocking upon field-layer vegetation species commonly utilised by black grouse are considered.

Chapter 4 investigates the abundance of invertebrate taxa preferred by black grouse broods available in second rotation restocks from re-planting to canopy closure. Findings are related to field-layer vegetation characteristics, site factors and restock management methods.

Chapter 5 describes changes in field-layer vegetation and invertebrate abundance when the standard fallow period of two years left prior to re-planting in restocks is extended to between three and five years, or further extended to between six and seven years. Consequences of habitat change upon avian and mammalian predator abundance are investigated.

Chapter 6 compares field-layer vegetation and invertebrate abundance in restocks with that in habitat surrounding leks to allow a quantitative, objective assessment of restock ‘quality’ to black grouse and their broods.

Finally, Chapter 7 summarises the main findings presented in the preceding chapters, and provides discussion surrounding the main issues. Management recommendations and suggestions for further research are made.

Chapter 2: Study Areas

Fieldwork was conducted at two sites in the Highlands of Scotland: The Trossachs in the south-west and Sutherland in the north-east (Figure 2.1). Ten commercial forest plantations under clearfell rotation management were used in the study, all with recent records of black grouse using either the forest or forest edge.

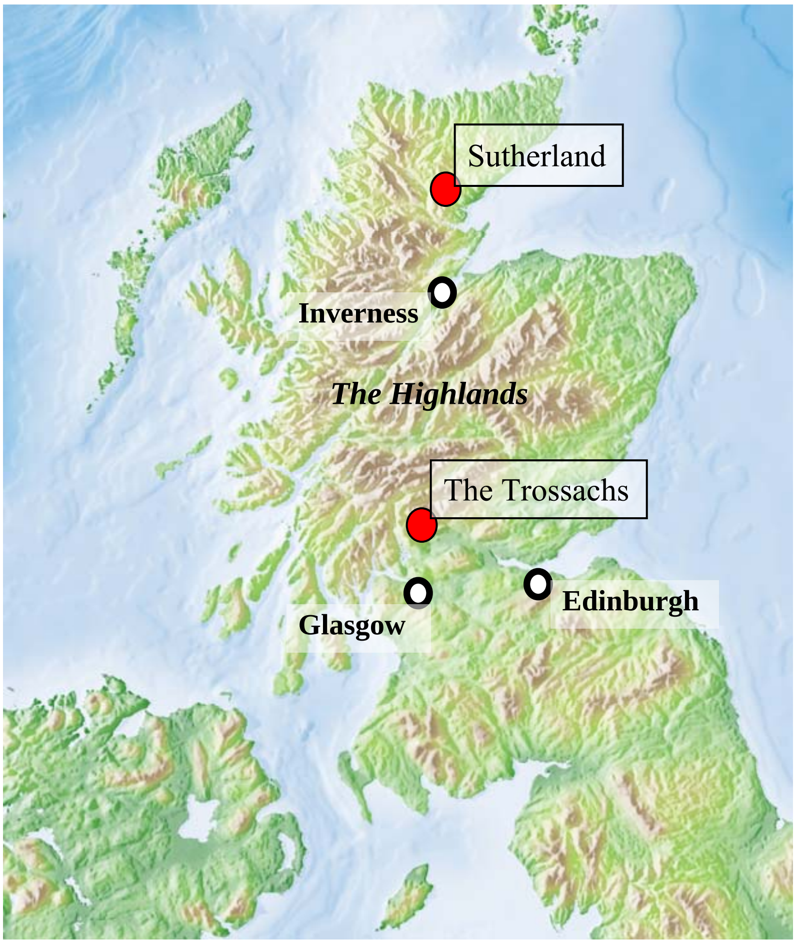

Figure 2.1: Study areas in Scotland: The Trossachs, south-west Highlands, and Sutherland, north-east Highlands.

2.1 The Trossachs

The Trossachs study area was located in Queen Elizabeth Forest Park, part of Loch Lomond and The Trossachs National Park (56º10′ N, 4º23′ W), a 167 km^2 area consisting of three large planted forests owned and managed by the Forestry Commission (Loch Ard, Strathyre and Achray; Figure 2.2). In addition to the planted forest, the study area also contains mountains, moorland, semi-natural forest, rivers and lochs. The climate is cool and humid with an annual mean daily temperature of 4.9ºC minimum and 11.9ºC maximum, with 1344 mm mean annual precipitation [1971-2000 annual means, recorded at Ardtalnaig meteorological station, located approximately 40 km NE of the centre of the study area; Met Office (www.metoffice.gov.uk)]. Underlying geology of the area comprises old, hard Dalradian metamorphic rocks within the Highland complex, more recently sculpted by glaciation to create their current landform. Soils are strongly acidic and generally based from schists, with predominant mineral soils being surface water gleys, iron pans, and wetter areas turning peaty-gleys to deep peat.

2.1.1 Planted conifer forests

Fieldwork was conducted in Loch Ard and Strathyre forests (Figure 2.2), geographically separate by approximately 8 km.

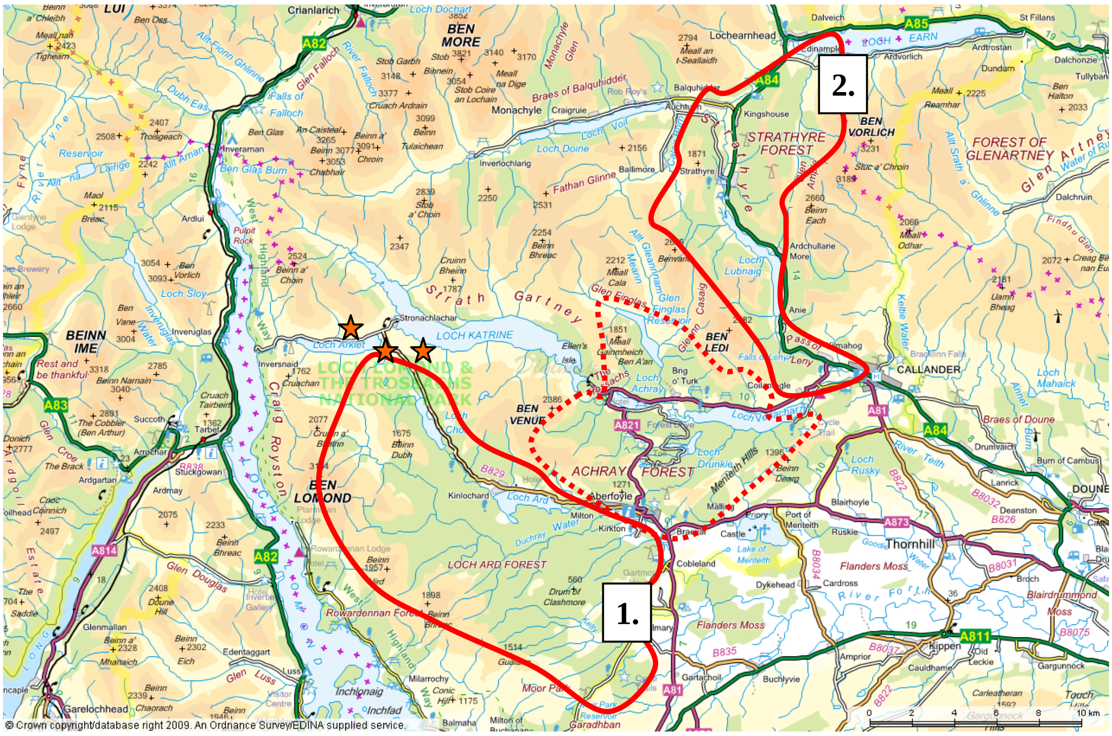

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Figure 2.2: Study sites in Queen Elizabeth Forest Park: 1. Loch Ard forest and 2. Strathyre forest. Achray forest (broken line) was not used in the study due to a lack of suitable restocks. Stars represent black grouse leks used in the study.

Both forests were established between 1920 and 1980, planted mainly on heather moorland, and have been under clearfell and replant silviculture since the 1970s. Sitka spruce *Picea sitchensis* has remained the predominant planted species throughout the first and into the second rotation, currently covering approximately 75% of the forest (Table 2.1). Forest restock plans for forthcoming years aim to broaden species diversity through both restocking and continuous cover management. Both forests are surrounded by mountainous open hillsides containing rough grazing heather moor, with elevations from 0 to 890 m above sea level (a.s.l.). The forest contains a network of tracks restricted to forestry vehicles but open for non-vehicle recreation to the public. Red and roe deer *Capreolus capreolus* utilise the open hill and the forest, although recent culling efforts have reduced the population size. The Forestry Commission operates a fenceless environment in commercial plantations, with the exception of areas where temporary fences are erected to prevent deer browsing of particularly vulnerable stands of trees. Fenced areas in plantations are infrequent, cover small areas (<2 ha) and fences are generally marked with wooden droppers to prevent black grouse collisions.

Forestry Commission staff and forestry contractors regularly report black grouse sightings in and around parts of both plantations, although Loch Ard holds a significantly greater and more stable population. Leks are recorded on forest edges, although in Loch Ard birds also lek on open ground within the forest (Table 2.2). Numbers of lekking males are apparently increasing in Loch Ard forest; however, the Strathyre population has remained small and fragmented over the past decade.

Crows and red fox are routinely controlled by the Forestry Commission, unlike pine marten, numbers of which are increasing. Other potential predators of black grouse adults, eggs and broods, include the wildcat *Felis sylvestris*, stoat *Mustela erminae*, American mink *Mustela vison*, buzzard *Buteo buteo*, goshawk *Accipter gentiles*, hen harrier and golden eagle.

2.1.2 Leks adjacent to plantations

Black grouse leks used in the study are directly adjacent to Loch Ard Forest (Figure 2.2) within the newly designated ‘Greater Trossachs Forest’, a 1400 ha native woodland planting scheme designed to improve landscape and wildlife habitats, particularly for black grouse. Land is owned by Scottish Water but leased and managed by the Forestry Commission. Following the removal of 14 000 sheep between 2003 and 2005, a four year planting programme commenced in 2009, with 460 ha of a planned 800 ha net area of Scots pine and native broadleaves planted to date. All new planting is contained within 32 km of dropper-marked deer fence. Leks are outwith fences, although other newly-established ‘satellite’ leks have increasingly been found close to or within fences over the past two years as the black grouse population increases. Highland cattle have recently been introduced at low density to control and break up rank vegetation which developed as a result of sheep removal and deer population control.

2.2 Sutherland

The Sutherland study area covers approximately 716 km^2, a larger total area than The Trossachs study area, due to the wider geographic spread of study plantations (Figure 2.3). A variety of habitats is encompassed, from lowland sheep pasture to steep-sided gorges, with topography generally flatter and less dramatic than in The Trossachs. Precipitation is low in the north-east Highlands, with 994 mm mean annual precipitation, and an annual mean daily temperature of 3.1ºC minimum and 11.1ºC maximum [1971-2000 annual means, recorded at Kinbrace meteorological station, located approximately 30 km NE of the centre of the study area; Met Office (www.metoffice.gov.uk)]. Soils types in the study area are diverse but generally comprise peaty gleys, peaty podzols, humus iron podzols, with brown earth on some lower slopes.

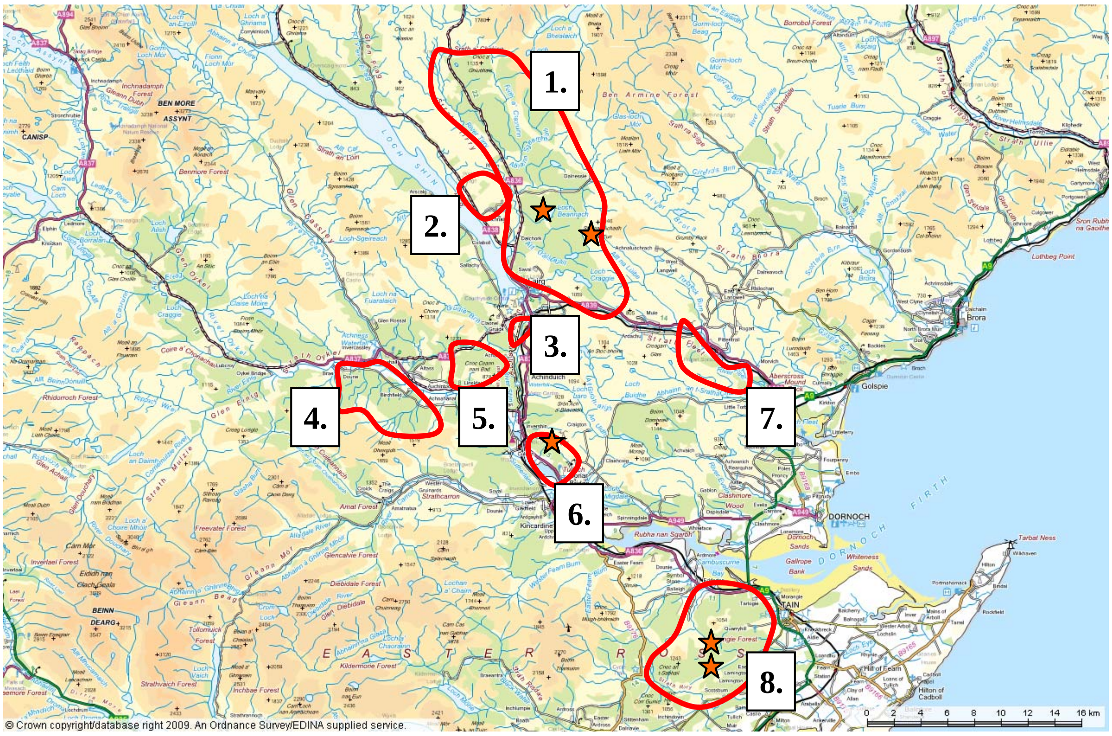

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Figure 2.3: Sutherland study area. Study forests outlined: 1. Dalchork, 2. Shinness, 3. Lairg, 4. Inveroykel, 5. Raemore, 6. Balblair, 7. Rogart, 8. Morangie. Stars denote black grouse leks used in the study.

2.2.1 Planted conifer forests

Fieldwork was undertaken in eight commercial plantations: five owned and managed by the Forestry Commission, the remainder owned privately and managed by independent forestry companies Fountains Forestry Plc. and Scottish Woodlands Ltd. (Table 2.1). All companies use the same timber harvesting and ground preparation methods for restocking, and although the private companies often have much smaller forest areas, these are often adjacent to large Forestry Commission plantations. Forests are geographically separate by at least 8 km, with the exception of Shinness and Dalchork, separated by 2 km of moorland but managed by differing forestry companies.

Landscape is varied, ranging from relatively flat boggy peatlands to hilly areas, with elevations ranging from 0 to 396 m a.s.l.. As in The Trossachs, tree species particularly vulnerable to deer browsing on Forestry Commission land are generally enclosed within temporary deer fences marked with droppers or high-visibility orange barrier netting to prevent bird collisions.

Black grouse have been recorded in or around all forests studied in Sutherland (Table 2.2), with the largest known population in Dalchork. Leks have been recorded either within forests or up to 1 km from the edge, with the exception of Rogart and Inveroykel, where the closest lekking males were 3 km and 5 km respectively. Capercaillie *Tetrao urogallus* are present at relatively high density in areas of thinned commercial woodland in Morangie forest.

Potential predators of black grouse are as recorded for The Trossachs study area, though are not routinely controlled. The deer population is regulated on all Forestry Commission land by regular culling.

2.2.2 Leks adjacent to plantations

Fieldwork was undertaken at five leks in 2009 (Figure 2.3), located within or adjacent to study plantations. Unlike the Trossachs study area, no new planting has occurred near to any of the leks in recent years, apart from routine commercial restocking operations. The black grouse population in the study area is generally low but stable.

Table 2.1: Forest characteristics in the Trossachs and Sutherland study areas.

Study area	Forest name	Managed by	Forest area (ha)	Altitudinal range (m)	Percentage of forest in 2nd rotation	Predominant planted species	Predominant soil types
The Trossachs	Loch Ard	FC	10 000	50-450	50	Sitka spruce	Peaty gleys, intergrade iron-pans, peat, brown forest soils
	Strathyre	FC	4000	100-650	60	Sitka spruce	
Sutherland	Morangie	FC	6100	0-400	5	Scots pine/ lodgepole pine	Peaty gleys, peaty podzols, humus iron podzols, brown earth on lower slopes, shallow peat over boulder clay
	Dalchork	FC	7900	120-370	6	Lodgepole pine/Sitka spruce	
	Lairg	Fountains Forestry	30	70-110	28	Sitka spruce	
	Rogart	Fountains Forestry/FC	300 30	30-290 50-190	17 100	Scots pine	
	Shinness	Scottish Woodlands	60	140-160	40	Scots pine	
	Raemore	FC	1000	60-260	14	Sitka spruce/ lodgepole pine	
	Balblair	FC	300	40-230	51	Scots pine/ Sitka spruce	
	Inveroykel	FC	2700	60-360	10	Sitka spruce/ lodgepole pine	

Table 2.2: Records of black grouse within and around study area forests reported by FC or RSPB staff between 2007 and 2009.

Study area	**Forest name**	**Birds recorded within or <1 km from plantation edge since 2007**	**Distance to closest lek**
Trossachs	Loch Ard	Yes	Lekking in open area within plantation
	Strathyre	Yes	<100 m from plantation edge
Sutherland	Morangie	Yes	Lekking in open area within plantation
	Dalchork	Yes	Lekking in open area within plantation
	Lairg	Yes	<2 km from forest edge
	Rogart	No*	<3 km from forest edge
	Shinness	Yes	<1 km from forest edge
	Raemore	Yes	<100 m from forest edge
	Balblair	Yes	<100 m from forest edge
	Inveroykel	Yes	<5 km from forest edge

*area not formally surveyed

Chapter 3: Field-layer habitat availability to black grouse in restocks

3.1 Introduction

Planting of second rotation crops (restocks) in plantations has increased in Britain since the 1950's, with nearly 16 000 ha of forest land restocked between 2008 and 2009, 60% of this in Scotland, of which 85% was conifers (Forestry Commission 2009a). In 2000, 77% of conifer stands were categorised as ready to harvest within the next 20 years (Mason 2007). As forests are restocked, opportunities exist to re-create habitat suitable for black grouse *Tetrao tetrix*, a moorland/forest ecotone species once widespread throughout the lowlands and uplands of Britain, which has declined considerably during the first half of the 20th century (Parslow 1973) and is now a UK BAP priority species (UK Biodiversity Action Plan 2008) and red-list species of conservation concern (Birdlife International 2009). Declines have been due, in part, to degradation and loss of semi-natural habitat, often comprising open mature Scots pine *Pinus sylvestris* forests, birch *Betula* spp. and hazel *Corylus avellana* scrub woodland on moorland fringes. Local population increases and temporary range re-expansion occurred with the commencement of afforestation from the 1950's (Thom 1986) as black grouse adapted well to pre-thicket habitats in young conifer plantations (Avery & Leslie 1990), mostly planted on heavily grazed heather moorland and semi-natural grasslands. However, as plantation trees mature and field-layer vegetation is shaded out, populations once again decline (Pearce-Higgins *et al*. 2007). Outwith remaining semi-natural forest and forest edge habitats, black grouse populations are now mainly associated with commercial forest plantations across much of their Scottish range.

Pre-thicket, second rotation restocks create open space for black grouse in commercial forests, providing a mosaic of different aged habitats as coupes are patch-felled around the forest. However, the development of field-layer vegetation in restocks is likely to differ from that in newly afforested habitats on moorland or grassland. Soil chemistry is altered by the clearfelling process (Adamson *et al*. 1987), by residues from the first-rotation crop, such as needle litter (Hill & Jones 1978) and soils are further compacted by timber extraction machinery (Hutchings *et al*. 2002). By the start of the second rotation, seed banks are depleted (Hill & Stevens 1981) and regeneration of the field-layer and its rate of growth are affected by grazers, particularly deer (Bergquist *et al.* 1999), which were usually fenced out in the first rotation. Heavy grazing can potentially affect black grouse breeding success indirectly, through reduced abundance of key food plants, poorer quality nest cover, and reduced chick survival from decreased invertebrate densities (Baines 1996). Vegetation recovery may be further restricted by brash cover (tree tops and branches left on-site after harvesting), so that a field-layer of a suitable height and density for black grouse may only be available for a comparatively short time prior to canopy closure (often just 10 to 12 years after planting; Hill *et al*. 1984), after which virtually all vascular plant species under non-native crops such as Sitka spruce can be lost (Hill 1986).

The extent to which field-layer vegetation is used by black grouse for food and cover is relatively well-documented. Habitat requirements include a field-layer with variable height and density, usually rich in dwarf shrubs such as heather or bilberry *Vaccinium myrtillus*, boggy areas with *Eriophorum* spp. and damp flushes containing sedges *Carex* spp. and rushes *Juncus* spp. (Baines 1995; Picozzi & Hepburn 1984; Cayford 1990b)

Starling-Westerberg 2001; Baines 1994, Niewold 1990; Parr and Watson 1988). Previous research has suggested that first-rotation plantations can provide some of these types of habitat, providing food, nesting habitat, open areas for lekking and shelter in mature trees (Haysom 2001, Picozzi 1986; Baines *et al*. 2000; Cayford 1990b).

To date, no detailed assessment of habitat availability to black grouse within second rotations has been made, nor any attempt to investigate methods to improve or temporally increase availability of suitable habitat conditions. Previous research suggests that black grouse are well adapted for the modern clearfell system used in Fennoscandia, particularly if good pre-thicket shrub habitat is available (Borset & Krafft 1973; Swenson & Angelstam 1993), and that use of second rotation restocks by black grouse in Scotland may be to the same extent as first-rotation plantings (Haysom 2001). This study also found that greater availability of pre-thicket habitat in commercial plantations was associated with both an increased likelihood of a black grouse lek being present and with larger lek size. Additionally, larger clearfell patches were more likely to contain a black grouse lek, up to a maximum of 200 ha.

Through detailed studies of field-layer recovery from planting through to canopy closure, this chapter evaluates habitat quality and availability to black grouse in second rotation restocks. The effect of forest management upon the plant community as a whole is described, and key species of interest to black grouse (*Calluna vulgaris*, *Vaccinium myrtillus*, and *Eriophorum* spp.*)* are examined in more detail to determine if forest management can increase the quality and the length of time that suitable habitat is available. Two management methods are considered: i) the timber extraction method (Extraction Type) used to remove harvested trees from site during clearfell, and ii) whether areas were replanted with trees or left unplanted (Planting Type), the latter of which may prolong the availability of field-layer vegetation to black grouse in restocks upon canopy closure of the planted crop. In 2004, The Forestry Commission, the UK Government's forestry service, set a target of 10 to 20% of open space to be left in newly planted forests to encourage development of wildlife habitats (The UK Forestry Standard 2004). Whilst no specific guidance is given for open space in restocked forests, design principles are 'no less than for new woodlands', and targeted action to aid black grouse recovery in Scotland's forests forms part of the Scottish Forest Strategy (Forestry Commission 2006). The value of this prescription in creating or maintaining black grouse habitats in commercial forests in Scotland has not yet been assessed.

3.2 Methods

3.2.1 Study area

The study was conducted in eight commercial forest plantations in Highland Scotland - two in Queen Elizabeth Forest Park, a 167 km^2 area in The Trossachs, planted mainly with Sitka spruce *Picea sitchensis*, and six in Sutherland, a less productive forest area planted predominantly with Sitka spruce and lodgepole pine *Pinus contorta*, spread over a 716 km^2 area (see Chapter 2). Extensive clearfell and second rotation planting programmes are ongoing in both areas. The topography of Trossachs plantations is relatively steep and high, whereas plantations in Sutherland are flatter and restocks are generally located at lower altitude (Table 3.1)

Table 3.1: Characteristics of restocks in The Trossachs and Sutherland study areas.

Study area	No. of restocks	No .of transects	Mean altitude m a.s.l. (range)	Mean size ha (range)
Trossachs	36	337	254.1 (80-580)	28 (3-57)
Sutherland	13	104	142.3 (50-213)	16.6 (6.1-30)

Black grouse leks have been recorded within 1 km from the edge of study plantations within the past three years, with two exceptions, where the closest lekking males were recorded less than 2 km and 3 km from the edge. As the main aim of the study was to assess habitat availability to black grouse in restocks rather than habitat usage, black grouse were not systematically searched for.

3.2.2 Forestry terminology

'Felling year' is the year that first-rotation trees are clearfelled within a forest coupe, which is followed by an 18-month to two-year fallow period. A 'restock' is a clearfelled forest coupe re-planted with second rotation trees. 'Years since restock' is the number of years elapsed since these trees were planted, hence does not take into account the fallow period, during which field-layer vegetation is scarce and unlikely to be of use to black grouse.

3.2.3 Field data collection

3.2.3.1 Restock selection

Fieldwork took place in 49 restocks where mature un-thinned, spruce or pine stands had been clearfelled then restocked between 0 and 10 years previously. This type of retrospective chronosequence approach, comparing similar sites from different dates, is widely used in ecological and forest research (Hill 1986; Walker *et al*. 2010) particularly when long-term experimental studies are not possible.

Only restocks in a location likely to be used by black grouse were selected for the study. Black grouse are generally birds of the forest edge (Watson & Moss 2008) and in commercial forests prefer areas with 15 to 40% canopy cover, avoiding areas where the canopy cover exceeds 70% (Cayford 1990b). Therefore, selected restocks were those located on the plantation and grassland/moorland edge, or connected to the edge by unplanted or other, pre-thicket, restocks. Habitat within these restocks is likely to differ from restocks within the centre of the plantation, which are further from moorland seed sources. Restocks that did not meet the 'location' criteria described, but where black grouse had been sighted within the last 2 years, were also included.

3.2.3.2 Transect placement in restocks

Habitat data were collected between May and September from 337 transects in 36 Trossachs restocks in 2008, and 104 transects in 13 Sutherland restocks in 2009. Due to the highly heterogeneous habitats in restocks, stratified random sampling was used for transect placement. In The Trossachs, transects were located in restocks according to Planting Type (PT), i.e. replanted with trees (PL) or left unplanted (UNP), and to the method of timber extraction during clearfell: Extraction Type (ET), i.e. removed by mechanical harvester and forwarder (HF), or by cable winch (WI). Therefore, each transect is a combination of either: PL/HF, UNP/HF, PL/WI or UNP/WI. On flatter ground in restocks, timber is felled by 'conventional harvesting'; trees are de-branched in-situ by heavy machinery (harvesters) and stems extracted from site by large, articulated machinery with a load capacity of up to 18 tonnes (forwarders: HF). On ground inaccessible to heavy machinery due to site topography, chainsaws and cable winches are used manually to cut and drag timber across the surface of the site to roadside, where branches are removed (WI). Often, both extraction methods are used within a restock, according to topography, however, in Sutherland, timber was extracted by HF only as ground was relatively flat. Generally, areas of restocks to be left unplanted are designated by planning foresters at the forest design stage, and take into account landscape value, with an avoidance of linear edges that can be created by tree planting, but also leaving areas unplanted near to streams and watercourses, reducing acidification and nitrification. Areas may also be left unplanted at the tree-planting stage where soils may be damaged by heavy machinery and where timber crops are unlikely to grow well, e.g. boggy areas (J. Mulgrew, pers. comm.).

Following a standard 1 to 2 year fallow period, second rotation trees are planted onto machine-excavated soil ‘mounds’ in HF areas to provide well-drained microsites for tree growth. In WI areas inaccessible to excavators, trees are ‘flat-planted’ directly into undisturbed soils, which are generally freer-draining, with a reduced brash cover.

A maximum of 16 transects were placed in each restock, up to 4 transects per Planting Type/Extraction Type combination, i.e. 4 x PL/HF transects, 4 x UNP/HF, 4 x PL/WI and 4 x UNP/WI. Transects were separated by at least 50 m and located no less than 50 m from the restock edge. If restocks were small and 4 transects per combination could not be fitted, the maximum up to 4 were assigned, according to the 50 m distance criterion stated above.

3.2.3.3 Measurement of ground-, field-layer and canopy cover composition

Vegetation composition and tree canopy-cover were recorded at 5 equally spaced sample points along each 20 m transect. At each sample point, a bamboo cane of 1 m length marked at 5 cm intervals was placed horizontally on the ground and percentage composition of all ground-layer, field-layer and tree canopy cover was estimated by eye to the nearest 5%. Percentage cover at each sample point could therefore exceed 100%. Vascular plants were identified to species where possible and mosses to genus. Non-vegetative groups included bare ground, mounds (excavated soil heaps for trees to be planted into), brash (discarded tops and branches from first rotation trees) and needle litter. Height of vegetation, trees and brash at each sample point were also recorded. Three measures of each (to the highest vegetative shoot, tree leaf or brash branch within 20 cm of the cane) were recorded at each sample point, one taken at arms length in front of the recorder when standing on the 20 m transect tape, one to the left and one to the right. The three scores were averaged to produce one height per sample point for each of the following groups: graminoid vegetation, ericaceous heather species, overall maximum vegetation height, brash and tree height. If vegetation, brash or trees were not present at one of the three points, the group was treated as missing when calculating the average (rather than zero). All measurement was to the nearest 5 cm height marker on the cane. Graminoid height did not take into account inflorescences. For trees, height up to 3 m was measured with the marked cane, but above this a visual estimation only was made. The sampling programme in each study area was designed to take into account vegetation growth throughout the four-month sampling period - restocks were sampled in a random order to prevent bias. An index of field-layer density was measured by counting the proportion of 5, 1 cm thick white marks obscured on the bamboo cane by field-layer cover (a single group comprised of vegetation, brash and trees) at 0, 10, 20, 30 and 40 cm height when the cane was placed vertically at each sample point. The proportion of marks covered was estimated by eye when the observer knelt on the ground with the cane at arms length in front. Three density measures were recorded at each sample point and averaged as described above for height measurements. To interpret community composition in relation to soil moisture content, mean cover-weighted Ellenberg indicator values for moisture (Hill *et al.* 1999) were calculated from plant species cover values at each vegetation sample point (Hawkes *et al.* 1997). Mosses were assigned Ellenberg indicator values for moisture (Hill *et al.* 1999) based on expert opinion (N.J. Willby, University of Stirling).

Response variables were tested in relation to temporal variables, management variables, and site factors within restocks (Table 3.2). Data collected at the restock level were provided electronically by FC Forest Districts. Previous first-rotation crop species were determined using original FC planting maps.

Table 3.2: Time (T), management (M), and site (S) variables considered for statistical models to assess field-layer vegetation

Variable	Data type¶	Description	Level of data collection
Restock age	T	Years since restock	Restock
Study area	M	Sutherland or The Trossachs	Study area
Planting Type (PT)	M	Planted with trees (PL) or left unplanted (UNP)	Transect
Restock size	S	Total restock area (ha), includes planted and unplanted	Restock
Open space	S	Total restock area (ha), unplanted only	Restock
Distance to edge	S	Restock edge to nearest plantation edge (m)	Restock
Previous crop	S*	First rotation crop: spruce or pine	Transect
No. of trees#	S	Number of planted trees in a 10 x 10 m square	Transect
MTH#	S	Mean tree height (m) in 10 x 10 m square described above	Transect
Tree cover#	S	Cover (%) by planted trees	Transect
Altitude	S	Average of 5 equidistant points	Transect
Slope#	S	Average of 5 equidistant points	Transect

not included in analyses due to inter-correlation within the Model (see Appendix, Table 1). ¶ indicates how data were represented in statistical models: T - continuous age covariate; M - 2-level management factor; S - continuous site-dependent variable; S* - 2-level site factor.

3.2.4 Statistical analyses

3.2.4.1 Correspondence Analysis

Canonical correspondence analysis (CCA), a constrained, multivariate analysis, was used to relate the general community composition of restocks to known variation in the environment. In CCA, percentage cover transect scores are regressed against environmental variables scores at each ordination point, resulting in axes constrained to be linear combinations of environmental variables (ter Braak 1986). Variables determined by CCA as having a significant effect on species composition were plotted passively onto a DCA (Detrended correspondence analysis) ordination, which allows interpretation of the influences of environmental variables upon species composition.

CANOCO 4.5 (ter Braak and Smilauer 1998) was used for community analysis, with data square-root transformed and rare species (less than 5% cover) down-weighted, and all other parameters set to default. Species occurring only once were not included in analyses. As initial ordinations showed strong differences in restock community composition between the study areas, Trossachs and Sutherland data were analysed separately. Explanatory variables inter-correlated at $r \geq 0.60$ with the main variables of interest in this study, i.e. Planting Type or Extraction Type (which represent fundamental aspects of restock management) were identified and removed, i.e. number of trees, mean tree height, tree cover, and, for Trossachs data only; slope (Appendix Table 1). Monte Carlo tests with 999 unrestricted permutations were used to test significance of environmental variables at the probability level P=0.05.

3.2.4.2 Generalised Linear Mixed-effects Models

Generalised linear mixed-effects models (GLMMs) were used to examine variation in three individual plant species or taxa considered of particular importance to black grouse (*Calluna vulgaris, V. myrtillus* and *Eriophorum* spp.). Mixed effect models account for non-independent errors that may occur due to more than one level in sampling design (Millar & Anderson 2004), i.e. multiple transects in restocks in this case.

3.2.4.2.1 Model building

Two separate analyses were undertaken; i) to assess the effects of conventional harvesting (HF management only) upon field-layer vegetation in restocks in The Trossachs and Sutherland, and ii) to assess the effects of harvesting in restocks with a more varied topography (HF and WI management), for which data for The Trossachs only was available. Details of datasets used are summarised in Appendix Table 2.

Inter-correlated explanatory variables at ≥0.60 were identified and excluded from analyses (for reasons described in 3.2.4.1 above; Appendix Table 1), removing variables correlated with study area, restock age, Planting Type or Extraction Type. Initial investigations were carried out to determine if inclusion of quadratic terms was justified for the following variables: restock age, size, slope, altitude, and amount of structural open space in the restock. In these cases, the quadratic and linear terms of the particular explanatory variable were used in the full analyses if when added to a model that included the linear term, the quadratic term had a significant effect (at $P<0.05$) on the response variable. First-order interactions between restock age and each forest management variable (Planting Type or Extraction Type) were included, whilst restock identity was specified as a random effect. Minimal adequate models were produced by fitting all of the relevant main effects and interactions, and then removing terms according to their level of significance, until only those significant at $P<0.05$ remained. Interaction terms were tested for removal before main effects. Stepwise model selection techniques such as these have been criticised, and alternative approaches based upon the use of information criteria and model averaging have been suggested (Gibson *et al.* 2004; Rushton *et al.* 2004). However, these approaches were not feasible in this study due to a relatively large number of variables to consider in models. Stepwise selection allowed sequential addition and deletion of variables in a biologically meaningful manner. The removal of inter-correlated explanatory variables (outlined above and in 3.2.4.1) helped to minimise problems associated with stepwise approaches.

3.2.4.2.2 Modelling approaches

C. vulgaris cover data contained a high proportion of zeros (absent from 28% of 441 transects) and could not be transformed to a normal distribution. Therefore, data were modelled using the penalized-quasi likelihood (PQL) method (Venables & Ripley 2002) to account for an unknown distribution (cover values not being based upon a set of trials as for true binomial data), using the glmmPQL function in the 'MASS' library of R, version 2.8.1 (R Development Core Team 2008).

Height and structure of ericaceous heather species and graminoids were analysed with a normal error distribution using linear mixed effects models, hence the lme function in the 'nlme' library of R (Pinheiro *et al.* 2007).

Both *V. myrtillus* and *Eriophorum* spp. occurred with a low frequency across transects (absent from 81% and 92% of 441 transects, respectively). Therefore, they were treated as presence or absence data, using the glmer function in the ‘lme4’ library (Bates *et al*. 2008), based on the binomial logistic regression model.

3.3 Results

Thirty-four vascular plant species, 4 graminoid groups identified to genus only (*Agrostis*, *Festuca*, *Holcus* and *Luzula* spp.) and 4 moss genus groups (*Polytrichum*, *Sphagnum*, *Pleurozium* and *Racomitrium* spp.) were recorded in Trossachs restocks. Twenty-five of these species and all of these genera were also recorded in Sutherland restocks, with the addition of *Galium aparine*.

3.3.1 Field-layer composition in restocks

Non-vegetative cover (brash, needles and mounds) dominated following restock and vegetative cover was mostly grasses (Figure 3.1). Ericaceous heather species (*Calluna vulgaris, Erica tetralix* and *E. cinerea*) dominated 6 to 7 years after restock, covering 39% of the field-layer. Graminoids (*Juncus* spp., *Carex* spp. and grasses) were sparse after restock, with maximum cover between 2 and 5 years. *Eriophorum* spp. (*Eriophorum angustifolium* and *E. vaginatum*) and *V. myrtillus*, species occurred infrequently and cover was generally low where present. Planted trees dominated field layer vegetation from years 8 to 9.

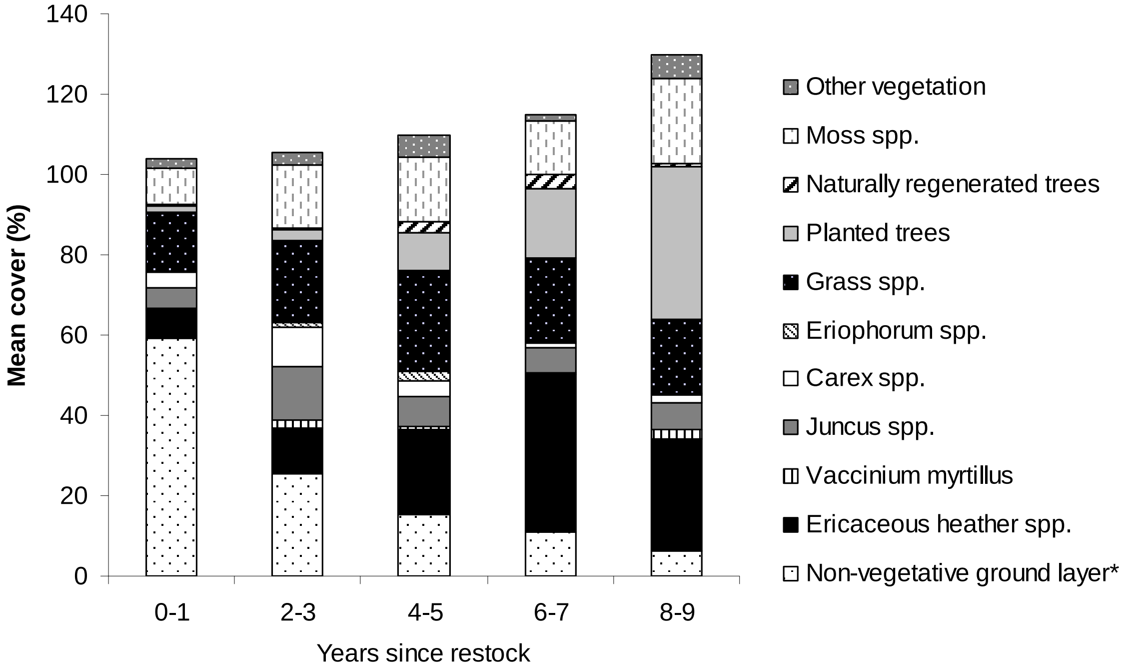


Figure 3.1: Proportion of vegetative and non-vegetative cover between planting and the onset of canopy closure on 441 transects in 49 restocks in The Trossachs and Sutherland. *comprises 78 % brash, 11 % needles and 11 % mounds.

Planted tree cover increased exponentially from restock to over 40% at years 8 to 9 (Figure 3.2a). Tree species mainly comprised non-native spruce (Sitka - 63%, Norway - 7%), as well as pine (Scots - 11%, lodgepole - 6%), and larch (13%).

Naturally regenerated trees were recorded on 94 of 441 transects, comprising birch (53%), Sitka spruce (39%) and western hemlock *Tsuga heterophylla* (8%; Figure 3.2b). Regeneration was locally variable, mainly occurred in areas left unplanted, and on average trees generally covered less than 4% of restock ground.

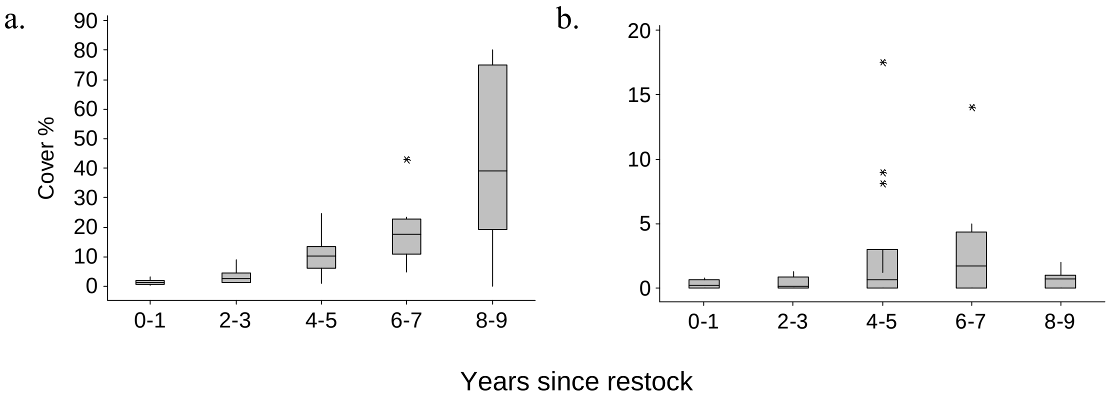


Figure 3.2: Proportion of field-layer cover by a) planted trees and b) naturally regenerated trees on 441 transects in 49 restocks in The Trossachs and Sutherland. Box plots show median (central line), quartiles (box), 5% and 95% centiles (whiskers) and outliers (stars).

3.3.2 Field-layer height and structure

Mean height of ericaceous heather species (*Calluna vulgaris* and *Erica* spp.) reached a maximum of 41.7 cm (± 4.44 cm SE) between 8 and 9 years after restock, whereas graminoids reached a maximum mean height of 64.5cm (± 9.1 cm SE) 6 to 7 years after restock (Figure 3.3).

Graminoids mostly remained above a mean height of 50 cm from restock to the onset of canopy closure between years 8 to 9. Field-layer density increased to year 7, decreasing thereafter (Figure 3.4). Relatively high density estimates, despite sparse vegetative cover from restock to year 1, can be attributed to the extensive cover of brash.

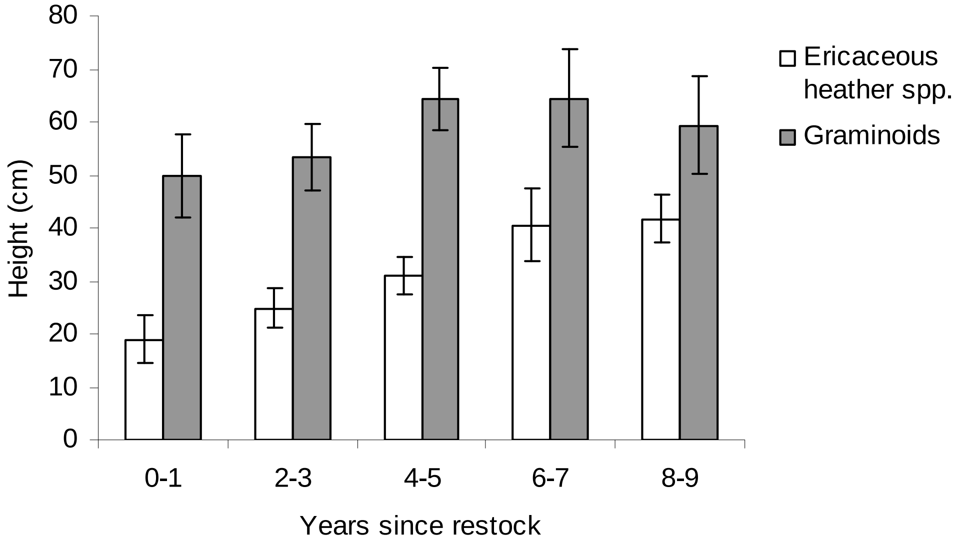


Figure 3.3: Mean height (cm ±1 SE) of ericaceous heather spp. (*Calluna vulgaris, Erica cinerea, E. tetralix*) and graminoids (grasses, *Juncus*, *Carex* and *Eriophorum* spp.) on 441 transects in 49 restocks in The Trossachs and Sutherland.

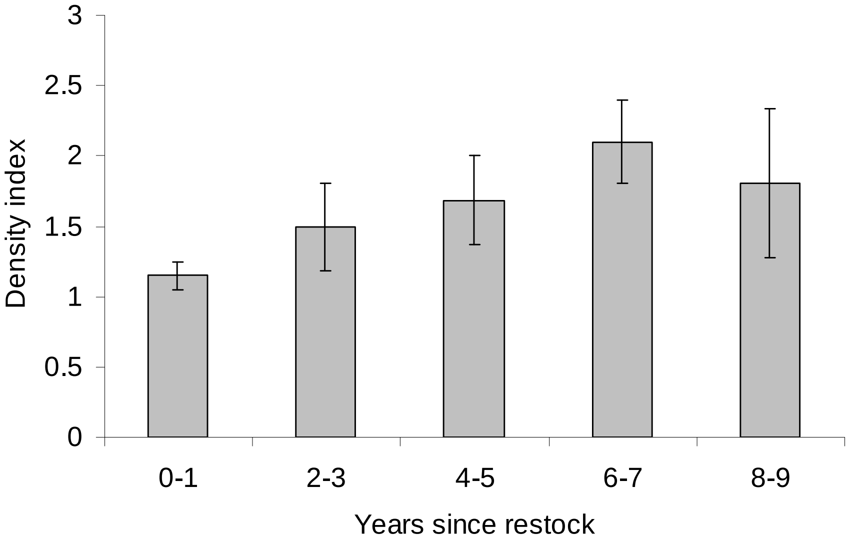


Figure 3.4: Index of field-layer density on 441 transects in 49 restocks in The Trossachs and Sutherland. Bars show mean density (±1 SE) of vegetative and non-vegetative field-layer between 0 and 40cm in height.

Planted tree height increased each year from restock, reaching a mean height of 3.5 m at 8 to 9 years after planting (Figure 3.5a). Mean height of naturally regenerated trees increased at a slower rate, as new annual cohorts of seedlings kept averages low (Figure 3.5b).

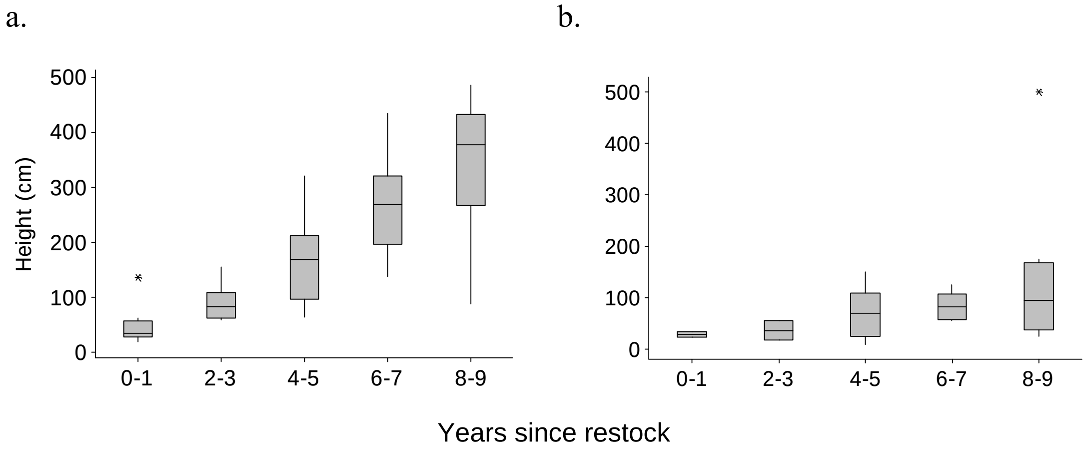


Figure 3.5: Mean height of a) planted trees and b) naturally regenerated trees on 441 transects in 49 restocks in The Trossachs and Sutherland. Box plots show median (central line), quartiles (box), 5% and 95% centiles (whiskers) and outliers (stars).

3.3.3 Ordination analyses of the plant community in restocks

3.3.3.1 Canonical correspondence analysis

In both study areas, restock age exerts the strongest influence upon community composition (axis 1; Table 3.3), explaining 6.2% (Trossachs) and 8.9% (Sutherland) of community variance. A further 3.2% of variation in the Trossachs community is explained by axis 2, which is most strongly correlated with Extraction Type. Axis 2 of the Sutherland data explains 4.7% of the variation, and is most strongly correlated with Planting Type.

Table 3.3: Significant correlations of restock age, management variables and site factors in Trossachs and Sutherland restocks with coefficient axes, tested by canonical correspondence analysis (CCA). Each axis is a linear combination (a multiple regression model) of all explanatory variables. Canonical coefficient columns show which variable(s) are important to explain each axis. Intra-correlation coefficient columns describe the strength of the relationship between environmental variables and the ordination axes.

	Canonical coefficients				Intra-correlation coefficients			
Variable	Trossachs		Sutherland		Trossachs		Sutherland	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.202	0.117	0.255	0.137	-	-	-	-
Restock age^{T,S}	-0.426	0.037	0.509	-0.180	-0.336	-0.055	0.372	-0.101
ET^{T}	0.051	0.215	Na	na	0.062	0.261	na	na
PT^{T,S}	-0.014	0.088	0.028	0.269	0.028	0.069	0.030	0.194
Altitude^{T,S}	0.134	-0.079	0.365	0.221	0.157	-0.102	0.271	0.006
Slope	§	§	-0.006	0.099	§	§	0.054	0.048
Restock size^{T,S}	-0.132	0.077	-0.044	-0.140	-0.087	0.121	-0.072	-0.042
Open space^{T,S}	0.047	-0.078	-0.255	-0.310	0.027	-0.075	-0.031	-0.186
Previous crop^{S}	-0.023	-0.020	0.283	0.047	-0.060	-0.002	-0.093	-0.013
Distance from edge^{S}	-0.012	0.040	-0.308	-0.017	-0.091	0.117	0.112	0.014

For further axes eigenvalues see inset graphs in Figure 3.6. Superscript indicates variable was significant in CCA analyses ($P<0.05$) Trossachs^{T}, Sutherland^{S}. ET refers sto timber Extraction Type (HF or WI). PT refers to Planting Type (PL or UNP). § Slope not included in Trossachs analyses due to inter-correlation with Extraction Type. na: ET variable not considered in Sutherland. See Table 3.2 for further description of variables.

3.3.3.2 Detrended correspondence analysis

DCA ordinations suggest that temporal, management and site factors are associated with field-layer vegetation in each study area differently, but each is generally associated with restock age, the amount of structural open space in the restock, and altitude (Figure 3.6a and 3.6b). Additionally, in Sutherland, the field-layer community is associated with the size of the restock, the distance from the restock to the plantation edge, and the previous tree crop (spruce or pine; Figure 3.6b).

In both study areas, field-layer vegetation is generally species-poor following restocking, particularly in planted HF areas (Figure 3.6a and 3.6b). Cover predominantly consists of brash, needles, bare ground and mounds, with grasses and remnant woodland plants in Sutherland, and mosses in The Trossachs. HF areas are mainly colonised by *Carex, Juncus* and *Eriophorum* spp. in The Trossachs, with a community later dominated by *Molinia caerulea* and heather species. WI areas mostly occur at higher altitude and in smaller restocks than HF areas and are associated with more structural open space, re-colonising quickly with early-successional herbs followed by grasses and *Erica cinerea* prior to canopy closure. Low densities of *Cirsium* spp. and *Sphagnum* spp. occur in Trossachs restocks at the onset of canopy closure, and *Blechnum spicant* and *Pteridium aquilinium* in Sutherland restocks.

3.3.3.3 Influence of topography

In The Trossachs, Extraction Type was strongly associated with the second axis of CCA analyses (Table 3.3) and DCA ordinations (Figure 3.6a). However, the Extraction Type variable may merely be a surrogate for ‘slope’ (which was omitted from analysis due to inter-correlation with Extraction Type), as the timber extraction method used at clearfell is pre-determined by slope. Further investigations of the data using mean weighted Ellenberg moisture indicator values suggest that HF areas contain species indicative of wetter conditions and poorly draining soils (i.e. flatter areas), whereas WI areas contain less moisture-demanding species, indicative of well-drained soils on steeper ground (Figure 3.7). HF areas in Trossachs restocks contain more *V. myrtillus*, *Carex* spp., *Juncus* spp. and *Eriophorum* spp., whereas WI areas contain more grasses and early successional herbs. *C. vulgaris* is more likely to occur in HF areas, whereas *E. tetralix* and *E. cinerea* occur more in HF and more in WI areas, respectively.

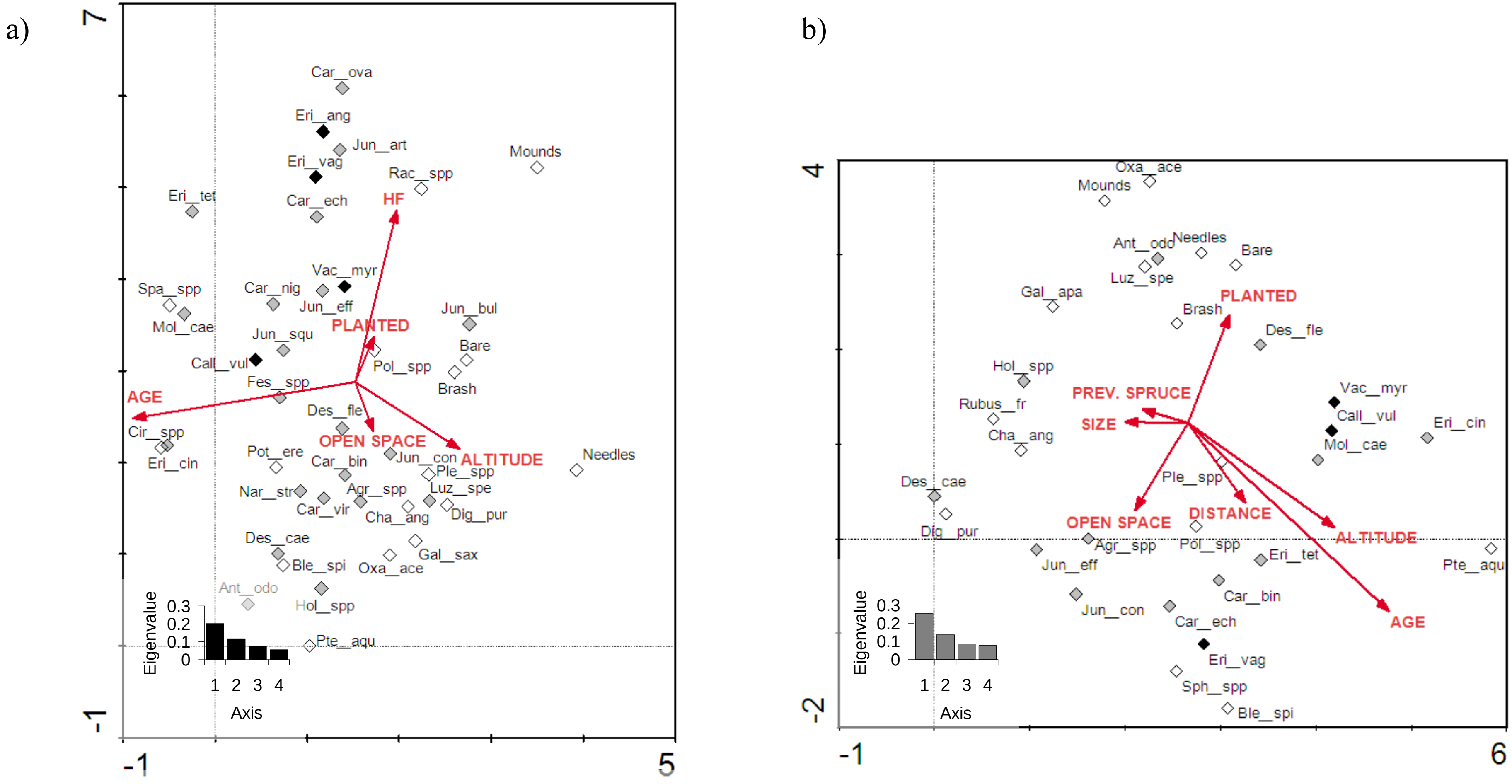


Figure 3.6: DCA ordinations for a) Trossachs restocks (n=36) and b) Sutherland restocks (n=13). Environmental variables are represented by arrows pointing in the direction of maximum change, with longer arrows representing more important variables (Ter Braak 1987). Location of species relative to arrows indicates environmental preferences of those species. Black diamonds represent key vegetation species for black grouse, grey diamonds are species of a genus recorded as used by black grouse, empty diamonds are 'other'. Variables are: restock AGE, restock SIZE, restock ALTITUDE, amount of structural OPEN SPACE left unplanted within the restock, DISTANCE to edge, with 2-level categorical variables represented by: PLANTED (vs. UNP), HF (vs. WI) and PREV.SPRUCE, which denotes the PREVIOUS CROP (spruce vs. pine). Eigenvalues for the first four CCA axes (shown on inset bar charts) are measures of the explanatory power of each axis. See Appendix Table 6 for species list.

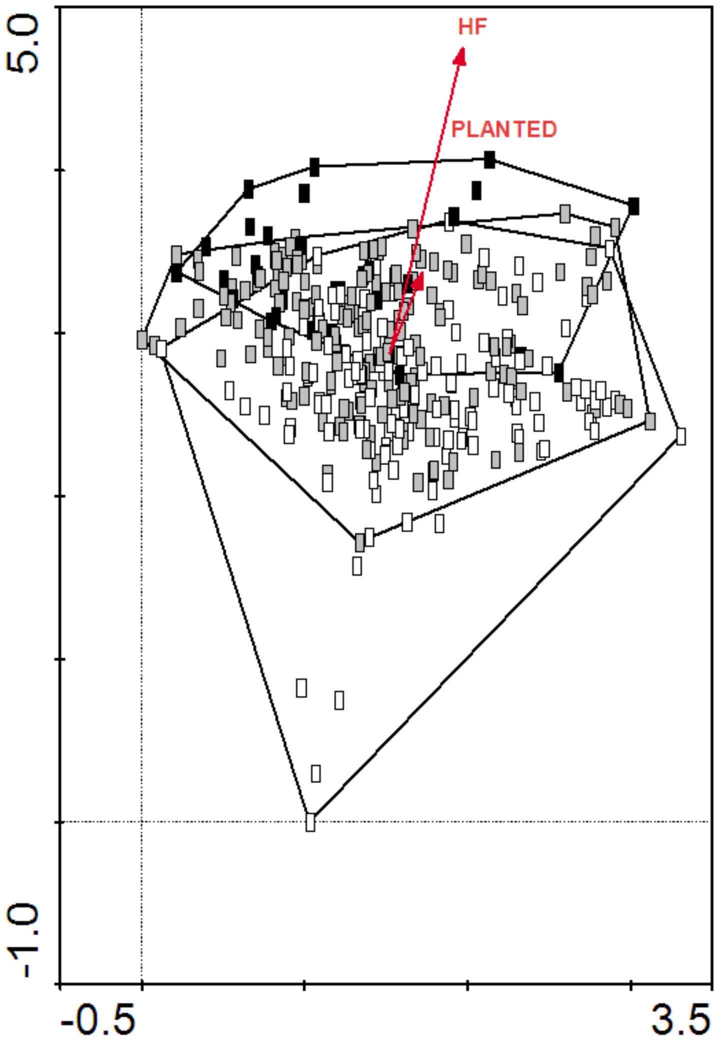


Figure 3.7: Mean weighted Ellenberg moisture values for vascular plants in Trossachs restocks. Each sample point represents a transect. Envelopes enclose transects with similar scores. Wetter communities occur in HF areas towards the top of the diagram (mean weighted Ellenberg indicator values 7.0 to 8.2, black rectangles), mid-range moisture communities in the middle (values 6.0 to 6.9, grey rectangles) and drier communities mainly occur in WI areas towards the bottom of diagram (values 5.0 to 5.9, white rectangles).

3.3.4 GLMM analyses of field-layer species of particular importance to black grouse

3.3.4.1 Conventionally harvested sites

3.3.4.1.1 Development of Calluna vulgaris

Differences in *C. vulgaris* cover in restocks were greatest between study areas; recovery was significantly greater in Sutherland than Trossachs restocks (Table 3.4). Cover increased with restock age and was significantly greater in planted than unplanted areas (Table 3.4; Figure 3.8). The estimated mean cover by year 8 in planted areas reached c.25% and c.42% in Trossachs and Sutherland, respectively, but only c.15% and c.35% in unplanted areas, respectively. *C. vulgaris* cover increased in a curvilinear manner with slope (Table 3.4) to an optimum gradient of 15°.

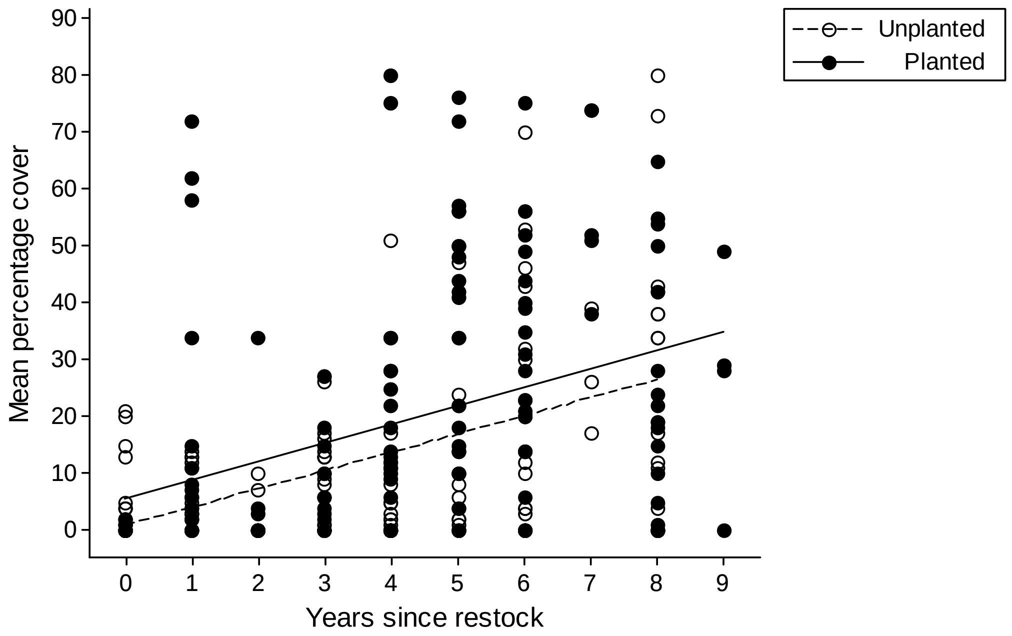


Figure 3.8: *Calluna vulgaris* cover in relation to planting type - Unplanted or Planted (P=0.011; Regression equations: *C. vulgaris* cover = 3.205*Restock age + 0.846 and +3.621*Restock age + 6.560, respectively), on 441 transects in 49 restocks in the Trossachs and Sutherland study areas. See methods for further details relating to Planting Type.

3.3.4.1.2 Influence of brash cover on C. vulgaris *development*

A possible underlying cause for reduced *C. vulgaris* recovery in unplanted areas is brash cover, which is likely to inhibit vegetative growth (Figure 3.9). Brash cover is greater in unplanted areas and greater in Trossachs than in Sutherland restocks, decreasing as restocks age (Table 3.4). Therefore, brash cover was inserted into the final *C. vulgaris* minimum adequate model to determine whether it accounted for further variation in *C. vulgaris* cover, or replaced other effects. As expected, brash cover was negatively correlated with *C. vulgaris* cover when added to the model (t=-2.540, P=0.012), and the inclusion of this effect caused the difference between planted and unplanted areas to become non-significant (t=-1.876, P=0.062). The insertion of brash cover had a small effect only on the study area variable (making it marginally non-significant; t=-1.992, P=0.054), suggesting that whilst brash may have a negative effect on *C. vulgaris* recovery, additional factors probably also account for *C. vulgaris* cover differences between study areas.

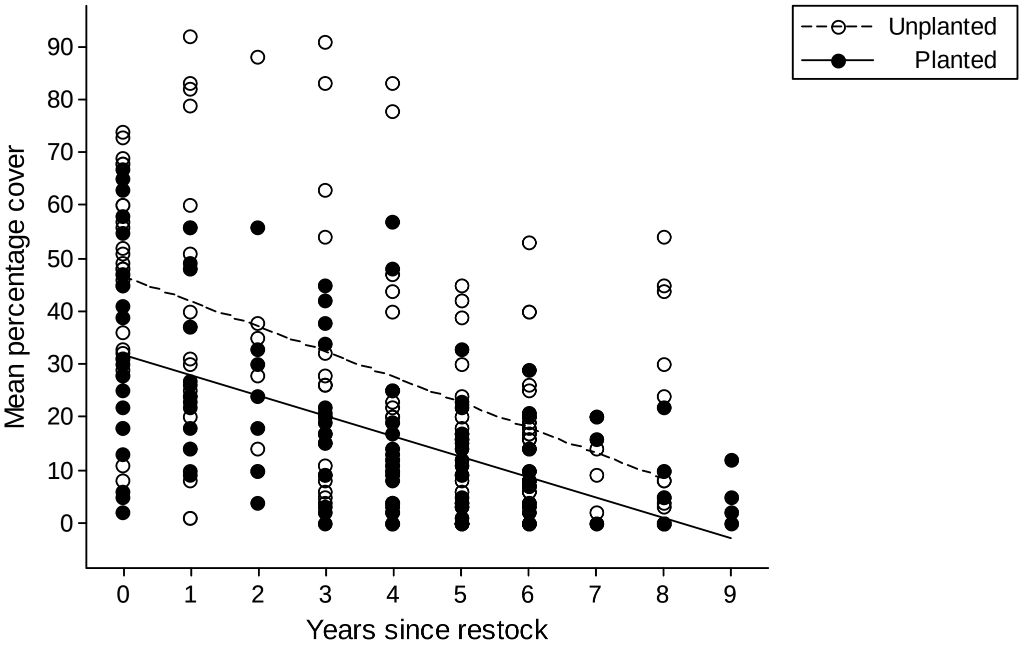


Figure 3.9: Cover of brash in relation to planting type - Unplanted or Planted ($P<0.001$; Regression equations: Brash cover = (-4.764*Restock age + 46.640 and -3.872*Restock age + 31.980, respectively), on 441 transects in 49 restocks in the Trossachs and Sutherland study areas. See methods for further details relating to Planting Type.

3.3.4.1.3 Other taxa examined

As expected from the low occurrence of both *Eriophorum* spp. and *V. myrtillus*, there were few significant effects detected on the likelihood of occurrence for these plant taxa. Both had a greater likelihood of occurrence in Trossachs restocks than Sutherland restocks (z=2.56, $P=0.010$ for *Eriophorum* spp. and z=3.382, $P=0.001$ for *V. myrtillus*), whilst *Eriophorum* spp. occurred more frequently in flatter areas (z=3.700, $P<0.001$ for effect of slope). There was no effect of Planting Type upon probability of occurrence of either species ($P>0.073$ in both cases), and the amount of variation explained by each model was relatively low ($R^2=0.261$ for *V. myrtillus* and $R^2=0.353$ for *Eriophorum* spp.).

It is likely that detectability of differences was hindered by low species occurrence - *V. myrtillus* was present on 15% of transects in planted areas and 34% of transects in unplanted areas of Trossachs restocks, but just 4% of transects in Sutherland, occurring in unplanted areas only. *Eriophorum* spp. occurred on 7% and 12% of transects in Trossachs restocks in planted and unplanted areas, respectively. In Sutherland occurrence was rare, with *Eriophorum* spp. recorded on less than 2% of transects in either Planting Type.

3.3.4.1.4 Vegetation height

Height of ericaceous heather species (*C. vulgaris*, *E. cinerea* and *E. tetralix*) significantly increased with restock age (Table 3.5) but did not exceed 40cm until 6 years after restock. A maximum height of c. 45 cm was reached at the onset of canopy closure. Heather spp. were taller in Sutherland than Trossachs restocks, and taller in planted than unplanted areas, but only by approximately 3.5 cm (Table 3.5).

The height of graminoid vegetation (*Juncus, Carex, Eriophorum* and grass spp.) also increased as restocks aged (Table 3.5). Graminoids were taller in unplanted areas, being on average 9.4 cm taller than in planted areas. As expected from their different life-history strategies, the effects of restock age were less marked on graminoid than on dwarf shrub heights, and overall the explanatory power of the model was considerably lower (Table 3.5).

3.3.4.1.5 Field-layer density

Field-layer density increased with restock age, and was greater in Sutherland restocks (Table 3.5), with these two effects alone accounting for much of the variation in field-layer density and there being no significant differences between planted and unplanted areas (*P*=0.984).

Table 3.4: Minimum adequate GLMM models describing the effects of management and site factors upon cover of *Calluna vulgaris* and brash on 441 transects in 49 restocks in conventionally harvested areas only of Sutherland and Trossachs restocks.

Model	Parameter	Estimate	SE	df	t value	Direction of effect	Statistical test	$R^{2\#}$
Calluna vulgaris cover	Intercept	-3.319	0.448	243	-7.404		glmmPQL	0.539
	Planting Type	-0.359	0.140	243	-2.571**	PL>UNP		
	Study area	-0.748	0.346	38	-2.165*	S>T		
	Restock age	0.286	0.062	38	4.595***	+		
	Slope	0.171	0.045	243	3.825***			
	$Slope^2$	-0.007	0.002	243	-3.460***	∩		
Brash cover	Intercept	-1.102	0.208	245	-5.293		glmmPQL	0.515
	Planting Type	0.734	0.116	245	6.327***	UNP>PL		
	Restock age	-0.272	0.034	38	-7.979***	-		
	Study area	0.529	0.189	38	2.799**	T>S		

Study area (S: Sutherland; T: The Trossachs). Planting Type (UNP: Unplanted; PL: Planted). Positive effects are indicated by + symbols, negative effects by – symbols. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, ∩ represents the type of curve. $^{\#}R^2$ calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. Levels of significance: ****P*<0.001; ** *P*<0.01; * *P*<0.05.

Table 3.5: Minimum adequate GLMM models describing the effects of management and site factors upon height of heather (*C. vulgaris*, *E. cinerea* and *E. tetralix*), graminoid (*Juncus, Carex, Eriophorum* and grass) spp. and field-layer density on 441 transects in 49 restocks in conventionally harvested areas only of Sutherland and Trossachs restocks.

Model	Parameter	Estimate	SE	df	t value	Direction of effect	Statistical test	$R^{2\#}$
Heather spp. height	Intercept	22.791	3.416	137	6.671		lme	0.697
	Restock age	3.103	0.511	35	6.073***	+		
	Planting Type	-3.568	1.391	137	-2.566**	PL>UNP		
	Study area	-7.571	2.753	35	-2.751**	S>T		
Graminoid spp. height	Intercept	44.485	3.672	205	12.115		lme	0.333
	Restock age	1.929	0.719	38	2.684**	+		
	Planting Type	10.491	2.591	205	4.049***	UNP>PL		
Field-layer density	Intercept	1.347	0.126	246	10.720		lme	0.561
	Restock age	0.120	0.020	38	5.978***	+		
	Study area	-0.253	0.115	38	-2.199*	S>T		

Study area (S: Sutherland; T: The Trossachs). Planting Type (UNP: Unplanted; PL: Planted). Positive effects are indicated by + symbols. $^{\#}R^2$ calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. Levels of significance: ****P*<0.001; ** *P*<0.01; * *P*<0.05.

3.3.4.2 Restocks with a more varied topography

3.3.4.2.1 Development of Calluna vulgaris

When considering HF *and* WI areas in Trossachs restocks, *C. vulgaris* cover increased in a curvilinear manner with restock age and was greater in WI areas from restock to the onset of canopy closure (Table 3.6; Figure 3.10). As in the HF only models (Table 3.4), cover was greater in planted than unplanted areas (Table 3.6), but the difference was relatively small (c.5%).

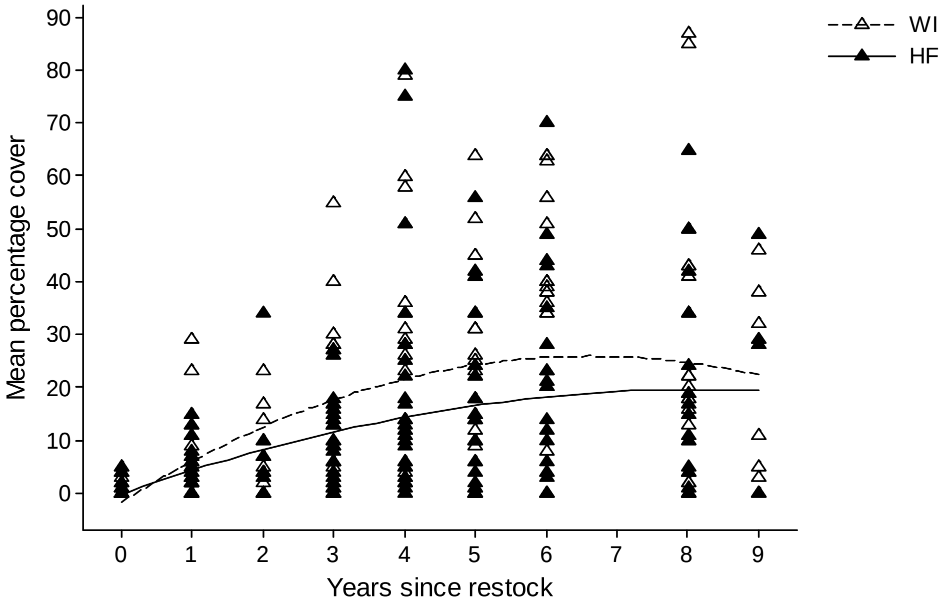


Figure 3.10: Cover of *C. vulgaris* in relation to timber Extraction Type - WI; cable-winch or HF; harvester and forwarder ($P<0.001$; Regression equations: *C. vulgaris* cover = (8.358×Restock age)+(-0.6321×Restock age^2)-1.662, and (4.814×Restock age)+(-0.2913×Restock age^2)-0.255, respectively), on 337 transects in 36 restocks in the Trossachs study area. See methods for further details relating to Extraction Type.

3.3.4.2.2 Influence of brash cover on C. vulgaris *development*

As described for the HF-only model, it was possible that differences in brash cover could explain the observed management effects on *C vulgaris* cover in this model. Therefore, brash cover was again inserted into the final minimum adequate model. As with the HF-only data, there was a strong negative correlation between brash cover and *C. vulgaris* cover (t=-3.556, P=0.001), and this caused Planting Type to be dropped from the model, as it was no longer significant (t=1.498, *P*=0.135). However, Extraction Type remained significant (t=2.802, *P*=0.005), suggesting additional influences upon *C. vulgaris* cover between WI and HF areas over and above the differences in brash cover between the two extraction methods. Differences in slope is a further possible cause of the observed differences between extraction methods (since WI is undertaken on steeper ground), however, there was no significant effect of slope when added to the *C. vulgaris* model (t=1.177, *P*=0.240) and both management factors remain significant, suggesting that greater *C. vulgaris* cover in WI areas is likely to be due to forest management factors, rather than topography alone.

3.3.4.2.3 Other taxa examined

As found previously, few significant effects were detected on likelihood of occurrence of *Eriophorum* spp. and *V. myrtillus* on transects. Only *V. myrtillus* had a greater likelihood of occurrence in unplanted areas of restocks (z=3.891, *P*<0.001), however, the amount of variation explained by the model was low (R^2=0.152). Brash cover did not affect probability of *V. myrtillus* occurrence when added to the final model (z=-0.859, *P*=0.390).

3.3.4.2.4 Vegetation height

In addition to greater *C. vulgaris* cover in planted areas, ericaceous heather species were also 5.4 cm taller (Table 3.7). There was a quadratic relationship between ericaceous heather species height and restock age (Table 3.7), peaking at c.35 cm between 6 and 8 years. Graminoid height also increased in a quadratic manner with restock age, peaking at c.60 cm at year 5, and graminoids were c.8 cm taller in HF than WI areas (Table 3.7). Graminoids were also taller in restocks where the previous first-rotation crop was spruce (Table 3.7), but only by c.4.5 cm. As with the previous graminoid height model (Table 3.5), fit to the data was relatively low (r^2=0. 373).

3.3.4.2.5 Field-layer density

Field-layer density increased in a curvilinear manner with restock age (Table 3.7), peaking between years 6 and 8 at c.60% density. Density was marginally (c.4%) greater in HF areas (Table 3.7).

Table 3.6: Minimum adequate GLMM models describing the effects of management and site factors upon cover of *Calluna vulgaris* and brash on 337 transects in 36 restocks in The Trossachs study area. Restocks had a more varied topography than conventionally harvested areas only, thus different methods of timber extraction (Extraction Type) could be investigated.

Model	Parameter	Estimate	SE	df	t value	Direction of effect	Statistical test	$R^{2\#}$
Calluna vulgaris cover	Intercept	-4.450	0.498	299	-8.940		glmmPQL	0.407
	Planting Type	-0.321	0.129	299	-2.492**	PL>UNP		
	Extraction Type	0.740	0.149	299	4.971***	WI>HF		
	Restock age	1.074	0.246	33	4.372***			
	Restock age^2	-0.081	0.023	33	-3.548***	(		
Brash cover	Intercept	-0.442	0.160	299	-2.771			
	Planting Type	0.645	0.119	299	5.439***	UNP>PL	glmmPQL	0.459
	Extraction Type	-1.045	0.128	299	-8.151***	HF>WI		
	Restock age	-0.228	0.034	34	-8.433***	-		

Planting Type refers to UNP: Unplanted; PL: Planted. Extraction Type refers to HF: timber extraction with mechanical harvester and forwarder; WI: extraction with cable-winch. Negative effects are indicated by – symbols. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, (represents the type of curve. $^{\#}R^2$ calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. Levels of significance: ****P*<0.001; ** *P*<0.01; * *P*<0.05.

Table 3.7: Minimum adequate GLMM models describing the effects of management and site factors upon height of heather (*C. vulgaris*, *E. cinerea* and *E. tetralix*) and graminoid (*Juncus, Carex, Eriophorum* and grass) spp. and field-layer density on 337 transects in 36 restocks in The Trossachs study area. Restocks had a more varied topography than conventionally harvested areas only, thus different methods of timber extraction (Extraction Type) could be investigated.

Model	Parameter	Estimate	SE	df	t value	Direction of effect	Statistical test	$R^{2\#}$
Heather spp. height	Intercept	12.898	4.229	174	3.050		lme	0.641
	Restock age	6.764	1.921	32	3.521*			
	Restock age^2	-0.507	0.197	32	-2.567*	⎛		
	Planting Type	-4.719	1.201	174	-3.931***	PL>UNP		
Graminoid spp. height	Intercept	20.713	7.308	267	2.834		lme	0.373
	Restock age	13.123	2.350	32	5.584***			
	Restock age^2	-1.275	0.255	32	-4.994***	⎛		
	Extraction Type	-6.294	2.442	267	-2.577**	HF>WI		
	Previous crop	11.401	5.343	267	2.134*	Spruce>Pine		
Field-layer density	Intercept	0.950	0.154	300	6.162		lme	0.520
	Restock age	0.282	0.076	33	3.725***			
	Restock age^2	-0.022	0.008	33	-2.684**	⎛		
	Extraction Type	-0.127	0.057	300	-2.237*	HF>WI		

Planting Type refers to UNP: Unplanted; PL: Planted. Extraction Type refers to HF: timber extraction with mechanical harvester and forwarder; WI: extraction with cable-winch. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, ⎛ represents the type of curve. $^{\#}R^2$ calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. Levels of significance: ****P*<0.001; ** *P*<0.01; * *P*<0.05.

3.4 Discussion

Previous research suggests that pre-thicket, second rotation commercial forests may contain habitat suitable for black grouse (Baines *et al*. 2000; Cayford 1990b, Haysom 2001, Borset & Krafft 1973, Picozzi 1986), although availability of this habitat may be limited by forest maturation and canopy closure (Pearce-Higgins *et al*. 2007). Results from this study suggest that commercial forest restocks are potentially useful to black grouse for a limited number of years after re-planting. During this period, field-layer vegetation attains the height and density preferred by black grouse and their broods, however percentage cover of *Calluna vulgaris* can remain relatively low. *C. vulgaris* dominates the field-layer between six to eight years after planting and is greater in planted compared with unplanted areas of restocks. Cover decreases with the onset of canopy closure, which occurs as early as eight years after restock in steeper areas, where brash was mainly removed at clearfell. Forest management can increase temporal availability of this resource to black grouse.

3.4.1 Initial development of field-layer vegetation in restocks

Development of the plant community in restocks is initially slow, restricted by harvesting residue from clearfell. Results show that in the first 2 years following restock, brash forms the main component of the field-layer, with moss, needles from extracted trees and mounds excavated for tree planting. Initial recovery of the field-layer is sparse, comprising heather, grasses, sedges and rushes, which are likely to have regenerated from the seed bank during clearfell and, to a lesser extent, from seed rain blown in from adjacent moorland (Good *et al*. 1990; Hill & Stevens 1981; Abdy & Mayhead 1992). Recovery of the plant community will depend upon soil type (Hill 1986; Wallace & Good 1995, Eycott *et al*. 2006; Hill & Jones 1978), but can also depend on other factors, such as species of the previous tree crop (Hill 1979). Restocks are highly heterogeneous habitats; vegetation development varies not only within the restock but between adjacent restocks, even when on the same soils (Hill & Jones 1978). Furthermore, considerable variation in vegetation biomass can occur between restocks and between years (Örlander *et al.* 1996). These factors make assessment of management prescriptions within restocks difficult, although ordination analyses suggest that development of the field-layer community over time is predominantly determined by the timber extraction method used during clearfell or related topographical factors, and whether trees are planted on the site or not.

3.4.2 Influences of management upon the development of field-layer vegetation

Heather is capable of rapid regeneration following clearfell (Summerhayes & Williams 1926). In this study, *C. vulgaris* was mostly absent at restock, but dominated the field-layer between years six and eight. Heather also reached a mean height generally considered suitable for black grouse nest cover (40 to 55 cm; see Grant & Dawson 2005 for a review) during this period. Heather is an important component of black grouse habitat and its cover provides many benefits, including roosting and nest cover (Parr & Watson 1988). Heather shoots also represent a significant part of the adult diet (Picozzi & Hepburn 1984; Cayford 1990b), particularly in late-autumn and winter (Starling-Westerberg 2001; Baines 1994).

Brash directly suppresses heather growth, firstly by shading, then in later years by soil enrichment from nutrient leaching as brash degrades (Proe *et al.* 1999; Stevens *et al.* 1995; Rosen & Lundmark-Thelin 1987), and brash cover is reported to be the main factor in affecting both numbers and cover of plant species in clearfells (Abdy &

Mayhead 1992). Results from this study demonstrate that for the first two years after planting, approximately 50% of ground cover in restocks was covered by brash; comparatively less than found in other sites two years after clearfell (Abdy & Mayhead 1992; Walmsley *et al.* 2009). Brash cover decreased every year; however, cover remained above 20% up to four years after planting, which is likely to have had a substantial effect on the plant community.

In this study, *C. vulgaris* cover was generally greater and heather grew taller in planted areas of restocks than in unplanted areas, where less brash covered the ground. It is well established that *C. vulgaris* is not a shade-tolerant plant, needing full light and soils with low nutrients (Gimingham, 1972; Iason & Hester 1993, Hester 1987), hence the reduction or removal of brash can positively affect *C. vulgaris* cover (Bergquist *et al.* 1999). During ground preparation for planting in restocks, mounding excavators re-distribute and pile brash, reducing its overall cover, whereas areas left unplanted do not receive this treatment. It is also likely that soil disturbance from heavy machinery created additional regeneration niches for heather.

3.4.3 Field-layer recovery in restocks with a more varied topography

In cable-winched areas of restocks, where brash was mainly removed at clearfell, field-layer vegetation recovered quickly and cover of *C. vulgaris* was greater than in areas where timber was mechanically extracted by harvester and forwarder. Other studies have also reported faster vegetation growth in these areas; as much as 50% greater vegetation biomass can accumulate two to five years after harvesting than on conventionally harvested areas, predominantly due to reduced suppression by brash (Fahey *et al.* 1991). Furthermore, soil nutrients are reduced as four times the quantity of N, P and K is removed in tree biomass from winched areas compared with conventional harvesting (Walmsley 2009). In this study, greater *C. vulgaris* cover in winched areas are likely to have resulted from a reduced brash cover, but analyses suggest that factors additional to this may have contributed. A reduction in soil nutrient status as a result of winched areas usually being on slopes may contribute (Tsui *et al*. 2004), although slope was not found to be a significant additional factor in analyses. The dragging of timber across the site by cable-winch to roadside may prepare soils for improved *C. vulgaris* seedling establishment as the surface layer is effectively scarified, re-distributing needles and seeds near to the surface, and exposing soil underneath to light and rain (Good *et al*. 1990).

However, in winched areas, *C. vulgaris* cover began to decline earlier – just eight years after restock - as cover of planted trees increased and their canopy began to close. Temporal availability of this key heather resource to black grouse is therefore very limited. Heather plants are unlikely to accumulate enough fresh seed within this time period to fully replenish the seed bank prior to canopy closure (Hill & Stevens 1981). As buried heather seed set from several decades of heather growth prior to the first rotation is unlikely to survive beyond the second (Hill & Stevens 1981; Hill 1986), third-rotation restocks may need to rely mostly upon seed rain for heather re-establishment (Eycott *et al*. 2006).

3.4.4 Recovery of other field-layer taxa important to black grouse

In conventionally harvested areas (timber felling and removal by harvester and forwarder, respectively), field-layer density and graminoid height are greater than in cable-winched areas, providing improved concealment for nesting hens and their broods. Additionally, a wetter plant community establishes in conventionally harvested areas due to topography, potentially providing better brood-rearing habitat likely to contain more invertebrates. Mean graminoid height exceeded 60 cm in most years, greater than the 24 to 40 cm reported as optimal for black grouse brood use (Grant & Dawson 2005), although more recent research in the Highlands of Scotland typically located broods in vegetation taller than this, between 43 cm and 58 cm (RSPB unpubl. data). Tall graminoid and herb vegetation is often utilised by nesting hens and young broods both in Scotland (Parr & Watson 1988; Picozzi & Hepburn 1984) and in Europe (Borset & Krafft 1973; Glanzer 1980; Bernard 1982). Niewold (1990) found that clutches of eggs under taller vegetation (60 to 80 cm in height) seemed to have increased survival compared with clutches under lower vegetation. Tall vegetation provides increased concealment from predators (Baines 1996), and densities of preferred invertebrates are often increased, particularly in wet flushes (Cayford *et al.* 1989; Parr & Watson 1988; Baines *et al.* 1996; Pulliainen 1982; Picozzi & Hepburn 1984; Starling-Westerberg 2001; Niewold 1990). Additionally, tall, rank vegetation provides good winter habitat, although a lack of open areas with shorter vegetation may prevent chicks drying out in wet weather conditions (Warren *et al.* 2003).

Leaving areas of restocks unplanted did not appear to affect the probability of occurrence of *Vaccinium myrtillus* or *Eriophorum* species, other key species preferred by black grouse, although infrequent occurrence and low cover where present meant that analyses had very limited power to detect effects. *V. myrtillus* is a facultative shade plant that commonly occurs in woodland, particularly along edges (Ritchie 1956) - habitat similar to that inhabited by black grouse. It is abundant in the habitat and diet of many black grouse populations (Pulliainen 1982; Picozzi & Hepburn 1984; Cayford

1990b), but scarce in the location of others and hardly found in their diet (Baines 1994; Starling-Westerberg 2001). Clearfelling severely affects *V. myrtillus* by exposing plants to direct sunlight and drought, resulting in reduced growth and poorer quality shoots (Atlegrim & Sjoberg 1996a). Recovery is slower than *C. vulgaris*, which is able to spread more rapidly on bare ground after conifer felling (Watt 1931). If not extensively established before canopy closure, it may be eliminated from future rotations of *Picea* spp. (Hill & Jones 1978). *Eriophorum* species are particularly favoured by feeding hen black grouse in spring (Baines 1994; Niewold 1990; Parr & Watson 1988; Starling-Westerberg 2001; Cayford 1990a), because the flower heads contain high nutritional value (Trinder 1975), so they may be important in determining pre-breeding condition of hens, and subsequent productivity (Watson & Moss 2008). However, occurrence in restocks in this study was very low. Lack of information in the literature regarding *Eriophorum* species growth in clearfelled forestry plantations perhaps points to the relative infrequency of occurrence within this habitat. *Eriophorum* species were found to occur in flatter areas in this study, which is typical of the species, often found in wet acid peaty habitats, such as bogs and marshes (Phillips 1954). Extensive drainage to promote growth of first-rotation crops is likely to have restricted growth of *Eriophorum* species.

3.4.5 Limitations of correlative studies

An inevitable limitation to the study is that, by the very nature of forestry, variables considered are non-independent. For example, where foresters choose to plant trees and leave areas unplanted on a site is not only determined by aesthetic considerations but also by environmental factors including restock topography, hydrology, soil type, etc.. These factors ultimately determine vegetation type that will grow in the restock and the rate of growth. When assessing effects of forest management upon vegetation, the influence of environmental factors is inextricably linked. For example, the method of tree extraction from a harvested forest coupe will influence the recovery of field-layer vegetation as a result of soil disturbance levels, however vegetation recovery will also be influenced by environmental factors such as slope, which will ultimately determine site hydrology, etc.. The gradient of the slope determines the method of tree extraction appropriate for timber harvesting; as variables are correlated, cause and effect become difficult to establish. Conclusions, as with any correlative study, must therefore be drawn with caution.

3.4.6 Management conclusions

As 40% of ground in restocks is (on average) left unplanted, these areas could help to offset the near total loss of field-layer habitat for black grouse upon canopy closure of adjacent trees, whilst maintaining a viable commercial timber crop. Whilst heather cover in these areas is initially limited by brash, the potential longer-term role of unplanted areas in retaining vegetation growth and a seed bank of species preferred by black grouse may be crucial for populations to exist in commercial forestry. Open areas in forestry plantations have been found to have beneficial effects for black grouse: more open space can result in a higher density of hens, a delayed peak in hen density, and an extended period of habitat suitability for black grouse (Baines *et al.* 2000), although can also quickly re-fill with unwanted non-native tree species, which invade some areas densely, but others not at all (Fahey *et al.* 1991; Walmsley 2009).

Further research into vegetation development is necessary to determine guidelines for brash management and the long-term maintenance of unplanted areas in restocks for black grouse. Height and density of mature heather may exceed that preferred by black grouse within just a few years of canopy closure of the planted tree crop, thus management of unplanted areas may be necessary to re-invigorate patches of vegetation growth. Previous studies have shown that black grouse prefer to feed and roost in cut heather moorland strips to those left uncut (Cayford *et al.* 1989), whilst swiping of field-layer vegetation to reduce the height of rank vegetation and stimulate new growth can attract more nesting hens, leading to increased breeding success (Warren *et al.* 2003). Effects of creating additional black grouse habitat in the ecotone between planted and unplanted areas by thinning trees, rather than a hard linear edge, should be also investigated. Appropriate consideration must be made for topography and requirements of the current timber crop however, as effects of wind-throw must be taken into account when thinning (Mason & Quine 1995). In addition to topographical constraints, geographical location must be taken into consideration when making management recommendations for restocks - cover, height and density of field-layer vegetation differed consistently between study areas in this study. A single, broad-scale, country-wide management approach for creating habitat suitable for black grouse in restocks may not be suitable for Scotland's planted forests.

Chapter 4: Invertebrate availability to black grouse in restocks

4.1 Introduction

In the latter part of the twentieth century, a general Europe-wide decline in breeding success of black grouse was reported (Baines 1991b) and there is some evidence that levels of breeding productivity remain low (Baines 1993; Watson & Moss 2008). It seems likely that chick survival is an important factor in determining growth of black grouse populations, with factors affecting survival (e.g. June rainfall) often important in determining breeding productivity (Summers *et al*. 2004; Grant *et al.* 2009). Furthermore, changes in the numbers of lekking males often relate to breeding success in the previous year (Baines *et al*. 2007; Grant *et al.* 2009; RSPB, unpubl. data).

Black grouse chicks feed almost exclusively on invertebrates during the first 2 to 3 weeks after hatching, before progressively switching to a predominantly herbivorous diet (Kastdalen & Wegge 1985; Picozzi 1986; Cayford *et al.* 1989; Cayford 1990b; Wegge & Kastdalen 2008). High chick mortality is sometimes correlated with low invertebrate abundance (Picozzi & Hepburn 1984), and starvation of chicks due to lack of invertebrate prey is an important mortality factor in some populations (Niewold 1990). Higher growth rates of chicks are positively associated with invertebrate availability in red grouse *Lagopus lagopus scoticus* chicks (Park *et al*. 2001).

Broods of black grouse selectively forage in invertebrate-rich habitats (Picozzi & Hepburn 1984) taking a wide range of arthropods according to local availability, although dietary studies have revealed ants and larvae of both Lepidoptera and sawflies to be some of the most frequently taken items (Picozzi 1986; Cayford *et al.* 1989; Starling-Westerberg 2001). Damp grass or rushy mire habitats tend to have a high abundance of these items, and young broods are often found to select these habitats (Niewold 1990; Parr & Watson 1988; Picozzi & Hepburn 1984; Baines *et al.* 1996; Starling-Westerberg 2001).

Studies relating to black grouse chick habitat use and diet within and around commercially planted forests in Britain are rare, yet black grouse are often associated with this habitat (Cayford *et al.* 1989; Haysom 2001). Most dietary studies within commercially managed forests have been conducted in Fennoscandia, where a less intensive form of forest management is practised; clearfelling on the scale typically seen in Britain is rare, seed trees are left to restock felled areas rather than large-scale re-planting, and commercial crops are usually of native origin and slow-growing, compared with non-native, rapidly growing species' such as Sitka spruce *Picea sitchensis* that are commonly planted in Britain.

This objectives of the research presented in this chapter are to determine how the abundance of invertebrate taxa important in the diet of black grouse chicks vary with management in second rotation restocks. The format of the analysis uses a 3-step procedure, which examines how: 1) invertebrate abundance varies in relation to vegetation conditions in restocks; 2) whether restock age, aspects of restock management and site characteristics within restocks appear to contribute to the observed variation (in a similar way to that undertaken for plant taxa – Chapter 3); and 3) whether variation in restock age, management and site conditions can explain the effects of vegetation conditions upon invertebrate abundance.

4.2 Methods

4.2.1 Field data collection

Invertebrate sampling was conducted on 78 transects in 31 restocks in The Trossachs study area in 2008. Transects were chosen from the 337 vegetation sampling transects previously described (Chapter 3, section 3.2.2), randomly selecting one transect per Planting Type (PT)/Extraction Type (ET) combination available within each restock. Invertebrate abundance could therefore be related to vegetation characteristics, forest management factors, and site factors recorded at each transect. Methods for sampling field-layer cover, height and density on transects are described in Chapter 3 (section 3.2.2). Details of datasets used are summarised in Appendix Table 2. All transects were more than 100 m apart and no less than 50 m from the restock edge.

Sampling was conducted between 9 June and 11 July 2008, to coincide with the period when British black grouse chicks are generally hatching and largely dependent upon invertebrate food (Robel 1969a; Starling-Westerberg 2001; Picozzi 1986; Baines *et al.* 1996). In the Trossachs study area, anecdotal records suggest that black grouse chicks mainly hatch from early- to mid-June (D. Anderson, pers. comm.).

Two invertebrate sampling methods were used on each transect in 2008; pitfall trapping primarily assessed epigeal invertebrate abundance, whereas suction sampling assessed the abundance of fauna upon field-layer vegetation (Standen 2000).

4.2.1.1 Pitfall trapping

One pitfall trap (7 cm mouth diameter) was placed at either end of each 20 m transect and invertebrates collected for four consecutive one-week sampling periods. Traps were one-quarter filled with ethylene glycol diluted with water (1/3 v/v; Schmidt *et al.* 2006) and a small amount of surface-tension reducer (dish-washing detergent), with foil lids held 2cm above the ground to prevent flooding by rainwater and capture of non-target species. Catches from traps located along a single transect were pooled and stored in 70% ethanol. In order to avoid repeated measures of invertebrate abundance from the same transect and to reduce the frequency of zero counts in the data, weekly data were pooled for each transect.

Pitfall trap data may best reflect availability of prey for birds (Atlegrim & Sjoberg 1995), since more active invertebrates may be more readily detected by birds. However, data from pitfall traps must be treated with caution (Oxbrough *et al*. 2005). Differences in vegetation structure surrounding traps affects capture rates, making interpretation of absolute abundance data problematic (Melbourne 1999) and unlikely to reflect relative density of the same species on different sites (Briggs 1961). Catches can only be compared reliably if species activity, behaviour and density remain constant across the study area (Downie *et al.* 1996). Taking this into account, the ‘abundance’ term used henceforth refers to the number of invertebrates captured in pitfall traps, and not necessarily abundance *per se*.

4.2.1.2 Suction sampling

Suction sampling was undertaken using a commercially available backpack leaf blower (PB-265ESL; Echo Power Tools Ltd, UK) with a vacuum attachment and comparatively small suction tube of 6.5 cm (compared to 34.3 cm diameter for the D-vac; Dietrick 1961), allowing easy sampling of invertebrates on vegetation between and upon dense brash branches. At full throttle, air tube velocity reached 62 m sec^{-1}, exceeding that required to gain high rates of arthropod extraction (27 m sec^{-1}; Southwood 1978), as well as that reported for similar equipment in other studies (Buffington & Redak 1998; Stewart & Wright 1995). Suction sampling was conducted within two 30 x 30 cm quadrats on each transect, each placed 1 m from the transect ends, to reduce disturbance to pitfall traps. Quadrats were sampled by slowly passing the suction nozzle vertically and horizontally through the vegetation and/or along and between any brash branches, with sampling carried out for 45 s, a period exceeding that considered necessary to capture 90% of the larger invertebrate orders in grasslands, e.g. beetles and arachnids (Brook *et al.* 2008). Each sample was captured in a 30 cm long fine-mesh nylon collection bag inverted into the suction tube (Stewart & Wright 1995), which was emptied into a plastic bag and frozen prior to identification. As with pitfall traps, the two suction catches located along a transect were pooled. Suction sampling was conducted on all transects twice during the study period, in week one and week four, and was undertaken between 09.00 h and 18.30 h on dry days with no more than a light breeze. Captures from each sampling occasion were pooled, for the same reasons that pitfall catches were pooled.

In this initial investigation of invertebrate abundance in restocks, suction sampling was used in preference to sweep net sampling due to the perceived problems of obstruction of vegetation by brash, which is present in all restocks, and commonly snags in nets. However, suction sampling failed to sample Lepidoptera larvae adequately, which are often a major component of the chick diet (Table 4.1). Lepidoptera larvae were recorded in the pitfall catches, but this is not a recognised sampling method for this taxon (Sutherland 1996), and may provide a poor representation of their abundance and/or availability to black grouse chicks. Therefore, sweep netting (a recognised method for sampling Lepidoptera larvae - Sutherland 1996; Haysom and Coulson 1998) and further pitfall trapping were carried out from 7 to 14 June 2009, across 26 of the 78 transects used in 2008, to assess whether the 2008 pitfall data could provide a reliable measure of Lepidoptera larvae abundance. Pitfall trapping was conducted as in 2008, but traps were collected after just one week.

4.2.1.3 Sweep netting

Sweep netting was conducted once along the length of each 20 m transect, sweeping field-layer vegetation to either side a total of 25 times per transect. To overcome the problem of sweep netting in areas with brash, standard sweep net bags were replaced with bags of 45 cm diameter constructed of sailcloth (Kayospruce Ltd, UK), a lightweight, rip-proof fibre previously used for invertebrate sampling in habitats where standard nets are easily damaged (Buffington and Redak 1998).

Counts of Lepidoptera larvae by the two sampling methods were significantly, but relatively weakly, correlated across the 26 transects ($r=0.425$, $P=0.03$; Regression equation: Pitfall captures = 1.60*Sweep net captures+0.378). Thus, analyses of Lepidoptera larval abundance were carried out using the 2008 pitfall trap data, although it is accepted that they were likely to provide a relatively poor assessment of abundance.

4.2.2 Taxa selection and sampling method

Invertebrates were identified to Order following Chinery (1993), with the exception of Hymenoptera, which were further identified to Formicidae (ants), Symphyta (sawfly larvae) and Ichneumonidae (parasitic wasps). Invertebrates measuring ≤2 mm in overall length were considered too small to make an important contribution to black grouse chick diet (Niewold 1990) and are excluded from analyses. Spiders (Araneae) and harvestmen (Opiliones) were not distinguished, but combined and termed ‘arachnids’ for analyses.

Previous data from black grouse chick dietary studies were used to focus statistical analyses upon potentially important invertebrate groups. Invertebrate taxa were included in this study if recorded in at least 5% of crop samples or 5% of faecal samples (percentage composition) in previous studies. This 5% level of selection has been used previously for assigning ‘importance’ of invertebrate taxa groups to birds, because it marks a major discontinuity in the decline in contribution of individual invertebrate taxon to the diet of moorland birds (Buchanan *et al*. 2006). Of the ten invertebrate taxa occurring above this 5% level in previous studies, seven were captured frequently enough in this study to be considered in statistical analyses (Table 4.1).

Most taxa considered for statistical analyses were caught by both pitfall trapping and by suction trapping. As described above, these methods sample different components of the ground and field-layer habitat, and for some taxa are likely to produce different results due to differences in their suitability for sampling those taxa. To avoid producing multiple, and potentially contrasting, abundance measures for the same taxon, the trapping method considered to be most appropriate for each taxon was selected for use in statistical analyses based upon recommendations in Sutherland (1996) and Standen (2000). Therefore, pitfall data were used for beetles, arachnids, and ants (as predominantly active, surface-living taxa on bare ground or low vegetation), whilst suction sampling data were used for true flies and bugs due to their stronger association with field-layer vegetation. As explained previously, analyses of Lepidoptera larvae were also based on pitfall trapping data.

Table 4.1: The contribution (>5%) of invertebrate taxa to the diet of black grouse chicks, as determined by numerical percentage composition in seven study areas. Data are derived from crop or faecal samples. Taxa were included in the present study (bold type) if captured in sufficient quantities for statistical analyses.

Taxon	No. of studies	Reported proportion of diet 5-25%	26-50%	51-75%
Beetles (Coleoptera)	7	1, 2a, 3, 4, 5, 6a, 6b, 6c, 7a, 7b		
Spiders (Araneae)†	1	6a, 6b, 6c		
Harvestmen (Opiliones)†	1	2a		
True flies (Diptera)	4	2b, 4, 5, 6a, 6b, 6c		
True bugs (Hemiptera)	2	1, 5		
Ants (Hymenoptera; Formicidae)	5	2a, 3, 5, 7a, 7b	6a, 6b, 6c	2b
Moth larvae (Lepidoptera)	5	3, 4, 5	2a	1
Sawfly larvae (Hymenoptera: Symphyta)[a]	2	2a, 2b	4	
'Larvae' (moths and sawflies not distinguished)	2	6a, 7b	6b, 6c	
Predatory wasps (Hymenoptera; Ichneumonidae)[b]	2	2b, 4		
Grasshoppers (Orthoptera)[b]	1			7a, 7b

Taxon considered in analyses in this study highlighted in bold type, all adult form unless specified. †Spiders and harvestmen considered in one taxonomic group 'arachnids' in this study. [a]taxon not recorded during this study. [b]not considered in this study due to insufficient captures. Sources: 1 – Niewold (1990). 2 – Cayford *et al.* (1989), study sites: a) Rhyd Wen, b) Penaran. 3 – Borchtchevski (2000). 4 – Starling-Westerberg (2001). 5 – Wegge and Kastdalen (2008). 6 – Picozzi (1986), study sites: a) Birse; b) Etnach, c) Drum. 7 – Ponce (1992), study sites: a) Cervières, b) Frêtes.

4.2.3 Biomass estimate

All invertebrates from the seven taxa selected for statistical analyses were assigned to one of five body length categories; 3-5 mm, 5-10 mm, 10-15 mm, 15-20 mm, >20 mm. Twenty-five individuals from each body length category per taxon were dried in an oven at 60° C for 48 hours, to allow calculation of an average dry weight for each body length category per taxon. Taxon biomass estimates on each transect were then calculated by multiplying the number of individuals captured in each size category by their respective average dry weight, and summing these to give a total biomass estimate for each taxon on each transect. Estimated biomass for each taxon was strongly correlated with abundance data across transects (r=0.69 to 0.92 for all taxon), hence further analyses were conducted on abundance data only.

4.2.4 Statistical analyses

4.2.4.1 Model building

Invertebrate abundance is likely to be affected directly by cover and structure of field-layer vegetation, which in themselves reflect management and site factors operating at a restock site, all underpinned by time since management. As demonstrated in Chapter 3, field-layer vegetation is itself a product of time, management and site factors. Therefore, abundance of each invertebrate taxon was first examined in relation to temporal and management variables, and site factors (Model 1; Table 4.2). Secondly, abundance of each invertebrate taxon was examined in relation to vegetation variables (Model 2; Table 4.2), which were simplified into the two broad plant functional types (PFTs; Wookey *et al.* 2009) that dominated the field-layer (i.e. percentage cover of dwarf shrubs and graminoids), cover of brash, field-layer vegetation height, field-layer density, and Ellenberg moisture score values, which represent a position on a moisture gradient.

Having produced these two models, significant effects from Model 1 were tested for entry to Model 2, to produce a third minimum adequate model (Model 3), which considered the field-layer vegetation, restock age, management variables and site factors. Vegetation variables were removed if the inclusion of significant time, management, or site variables caused them to become non-significant (at $P<0.05$).

To provide a check on whether the order in which models were combined affected the variables retained within Model 3, the process was reversed, i.e. variables from Model 2 were tested for entry into Model 1. In all but one case Model 3 remained unchanged, with the exception being for ants. In this case, two variables of marginal significance (‘open space’ and ‘altitude’) were not selected for entry when the management and environmental variables were added to Model 1.

Table 4.2: Variables considered for statistical models of invertebrate abundance.

Variable	Data type¶	Description	Level of data collection
Model 1. Time (T), management (M), and site (S) variables			
Restock age	T	Years since restock	Restock
Planting Type (PT)	M	Planted with trees (PL) or left unplanted (UNP)	Transect
Extraction Type (ET)	M	First-rotation timber extraction by harvester/forwarder (HF) or by road-side cable-winch (WI)	Transect
Restock size	S	Total restock area (ha), includes planted and unplanted	Restock
Open space	S	Total restock area (ha), unplanted only	Restock
Distance to edge	S	Restock edge to nearest plantation edge (m)	Restock
Previous crop	S*	First rotation crop: spruce or pine	Transect
No. of trees#	S	Number of planted trees in a 10 x 10 m square	Transect
MTH#	S	Mean tree height (m) in 10 x 10 m square described above	Transect
Tree cover#	S	Cover (%) by planted trees	Transect
Altitude	S	Average of 5 equidistant points	Transect
Slope#	S	Average of 5 equidistant points	Transect
Model 2. Vegetation variables			
Moisture score#	C	Mean cover-weighted Ellenberg moisture values	Transect
Vegetation height	C	Maximum height of all vegetation (cm)	Transect
Field-layer density	C	Index (0 to 3) of field-layer density from ground level to 40cm tall, includes vegetation and brash	Transect
Dwarf shrub cover	C	Combined cover (%) of *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, *Vaccinium myrtillus*	Transect
Graminoid cover	C	Combined cover (%) of *Carex, Eriophorum, Juncus, Luzula, Deschampsia, Agrostis, Molinia, Nardus, Festuca* and *Anthoxanthum* spp.)	Transect
Brash cover	C	Cover (%) by brash	Transect

'Moisture score' refers to the mean cover-weighted Ellenberg moisture score (Hill *et al.* 1999) of species recorded along a transect: wetter habitats have a higher score. # not included in analyses due to inter-correlation within the Model (see Appendix, Table 3). ¶ indicates how data were represented in statistical models: C - continuous vegetation variables; T - continuous age covariate; M - 2-level management factor; S - continuous site-dependent variable; S* - 2-level site factor.

4.2.4.2 Statistical analyses

Variables inter-correlated at $r \geq 0.60$ were identified within Model 1 (Appendix Table 3a) and Model 2 (Appendix Table 3b). For Model 1, variables inter-correlated at $r \geq 0.60$ with the effects of main interest in this study, i.e. restock age, Planting Type or Extraction Type (which represent fundamental aspects of restock management) were removed, i.e. number of trees, mean tree height, tree cover and slope. No other variables were inter-correlated within this model. For Model 2, to determine which one of a pair of inter-correlated vegetation variables was included in analyses, univariate correlation tests were run for each invertebrate taxon, with each vegetation variable as the explanatory variable and the taxon as the response variable. For each taxon, the vegetation variable most highly correlated with abundance was used in subsequent analyses, which resulted in the exclusion of the Ellenberg moisture score from Model 2 for all taxa.

Having removed variables inter-correlated at $r \geq 0.60$, minimal adequate models were produced by fitting all of the relevant main effects and interactions of main interest, and then removing terms according to their level of significance, until only those significant at $P<0.05$ remained. Interaction terms were tested for removal before main effects. Quadratic terms of each continuous explanatory variable were also tested, and included if significant at $P<0.05$. First-order interactions between restock age and both Planting Type and Extraction Type were included, as invertebrate abundance response to management is likely to change as restocks age.

Analyses for each invertebrate taxon were undertaken using generalised linear mixed models (GLMMs), specifying restock identity as the random effect. Abundance of flies was analysed with a Poisson error distribution using the 'glmer' function in the 'lme4' library (Bates *et al.* 2008) of R, version 2.8.1 (R Development Core Team 2008). Beetle, arachnid, ant, and true bug abundance data were over-dispersed, hence the 'glmmPQL' function in the 'MASS' library (Venables & Ripley 2002) of R was used specifying 'quasipoisson' errors. This function automatically estimates over-dispersion using a Penalised Quasi-Likelihood method (Zuur *et al.* 2009). Lepidoptera larvae data conformed to a zero-inflated Poisson distribution (Zuur *et al.* 2009), i.e. a higher number of zeros than expected in the dataset for a Poisson distribution, and were over-dispersed, hence the glmmPQL function was also used for this taxon

4.2.4.3 Calculation of R^2 values

The R^2 value produced for each model indicates how much of the variation in the data is explained by the model. For glmer, R^2 values are calculated by (null deviance - residual deviance / null deviance). For glmmPQL, R^2 is calculated by the square of the correlation between the model's predicted values and the observed values.

4.3 Results

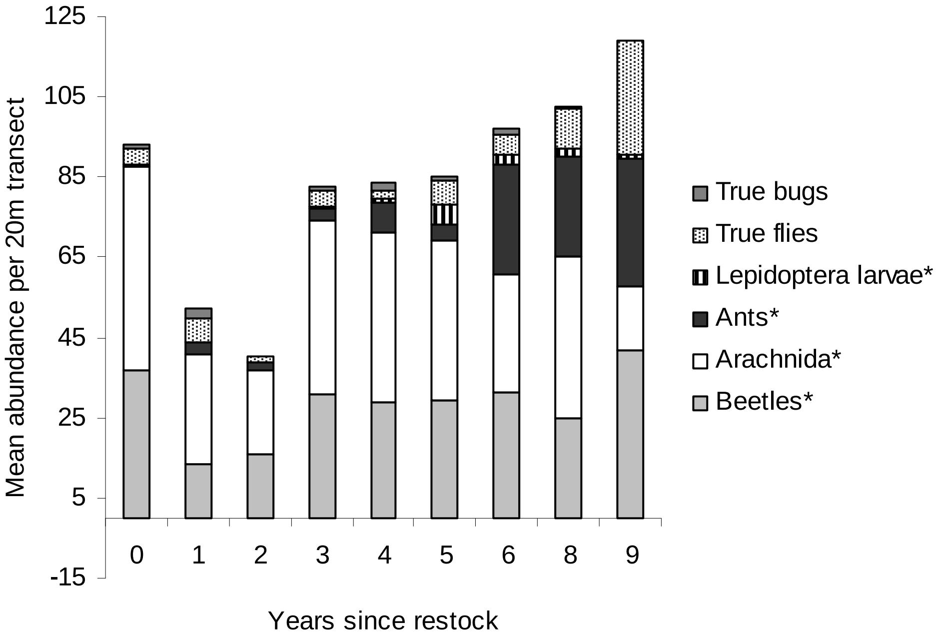
4.3.1 Invertebrate abundance

A total of 13 676 invertebrates were captured during the trapping period in 2008. Of the six taxa considered to be important in the diet of black grouse chicks (Table 4.1), 6888 individuals were recorded in pitfall traps (2986 arachnids, 2341 beetles, 852 ants, 520 true flies, 106 Lepidoptera larvae, and 83 true bugs), and 1186 were recorded in suction traps (693 true bugs, 245 true flies, 140 arachnids, 68 beetles, 39 ants and 1 Lepidoptera larva).

Pitfall trap catches were dominated by open-ground hunters, predominantly beetles, arachnids, and ants (Figure 4.1a), whilst true bugs and true flies dominated suction trap catches (Figure 4.1b). Catches of Lepidoptera larvae were scarce in all restock ages in both years, and predominantly consisted of Northern Winter Moth *Operophtera fagata*. Differences in taxa abundance between trapping methods were most apparent for arachnids; pitfall trap captures generally decreased from restocking to year 9, whereas suction trap captures increased to year 5 then decreased. When considering biomass rather than abundance (Figure 4.2), results suggest that beetles are likely to comprise a substantial proportion of the food available to black grouse in restocks. Biomass of pitfall captured ants is comparatively low compared with abundance in restocks ages 6 to 9 years (Figure 4.2), suggesting that although individuals of this taxon are numerous, they are relatively have a relatively small biomass.

Of the remaining 5602 invertebrates not included in statistical analyses, 2891 were not identified by previous studies as important food items in the black grouse chick diet, including Collembola (91%), Acari (4%), Isopoda (1.5%), Myriapoda (1.5%), adult Lepidoptera, Trichoptera and terrestrial larvae spp. (all <1%). The remaining 2711 individuals were excluded either due to having a body length of ≤2 mm, or comprised too few individuals for analysis, i.e. Ichneumonidae and Orthoptera (two and four individuals, respectively). Symphyta larvae were not recorded at the study site in 2008, or during the 2009 re-survey.

a. Pitfall trap captures



b. Suction trap captures

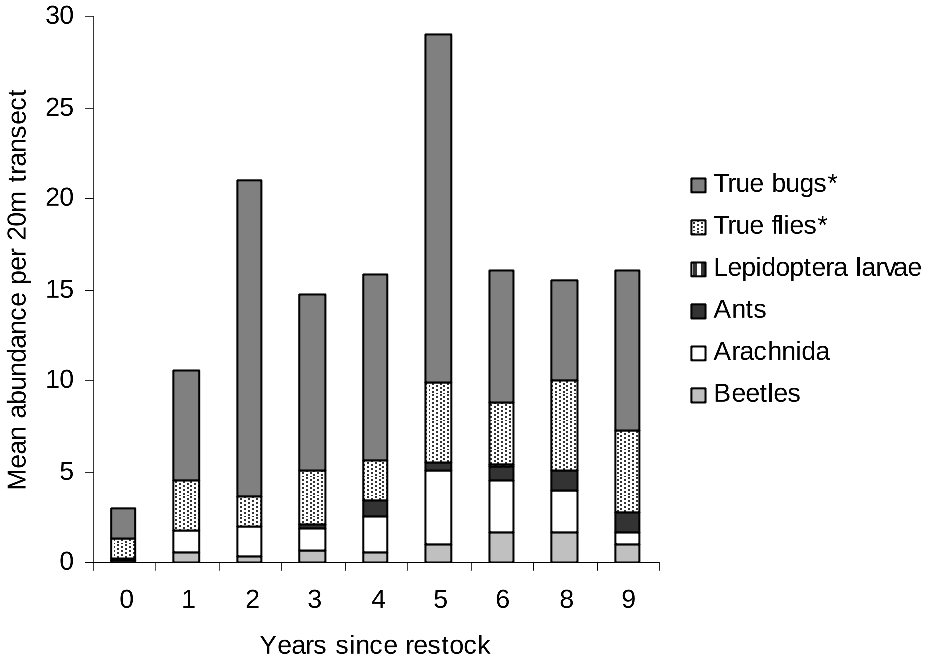
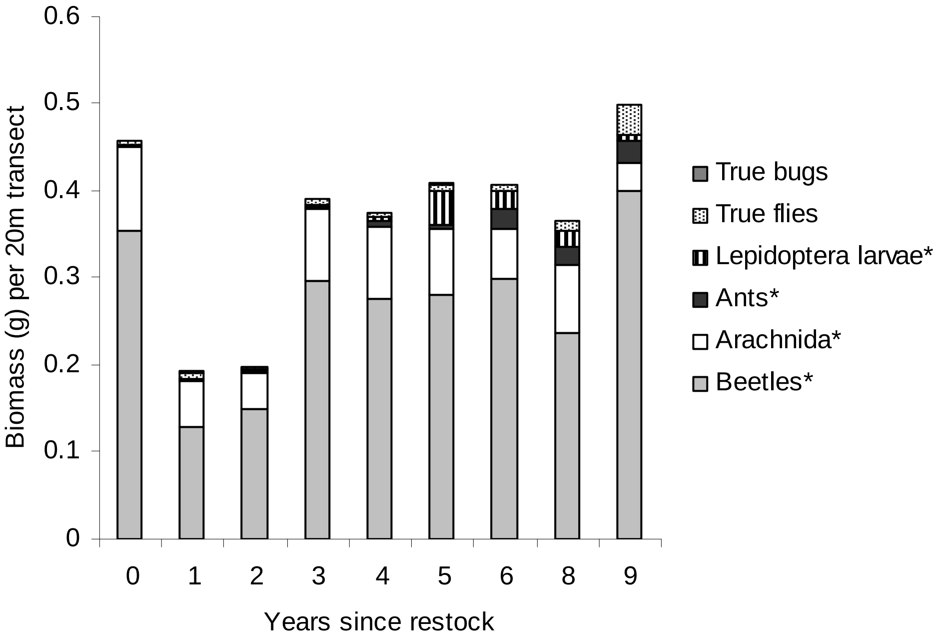


Figure 4.1: Abundance of invertebrate taxa considered to be important in the black grouse chick diet on 78 transects in 31 restocks in The Trossachs study area, captured by a) pitfall trapping (means consist of 4 weeks of pooled data), and b) suction trapping (means comprise 2 sampling occasions, pooled). Note scale differences between graphs. Arachnida group comprise spiders and harvestmen. * Dataset used in statistical analyses.

a. Pitfall trap captures



b. Suction trap captures

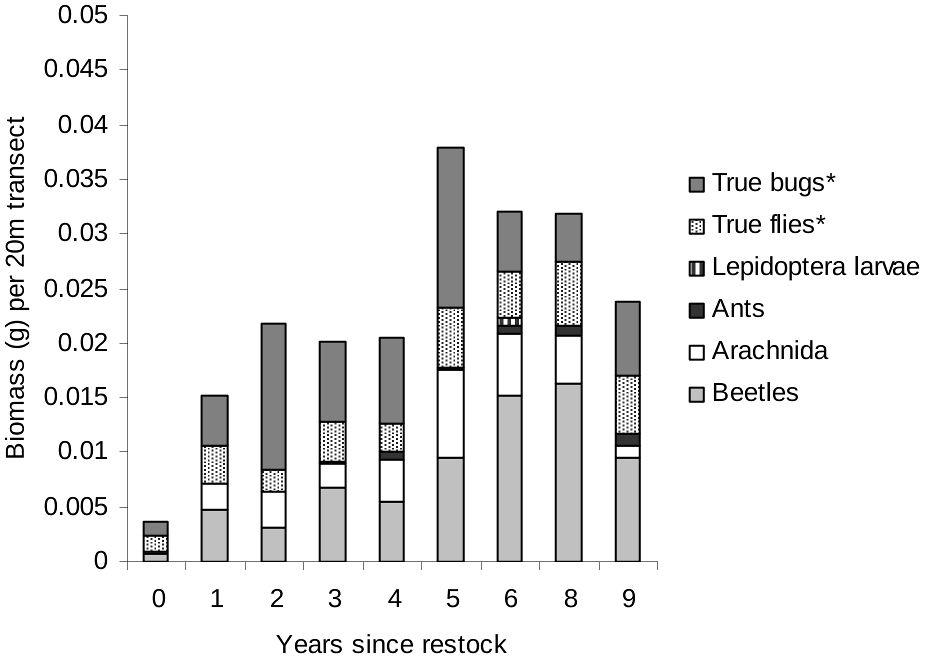


Figure 4.2: Biomass (g) of invertebrate taxa considered to be important in the black grouse chick diet on 78 transects in 31 restocks in The Trossachs study area, captured by a) pitfall trapping (means consist of 4 weeks of pooled data), and b) suction trapping (means comprise 2 sampling occasions, pooled). Note scale differences between graphs. Arachnida group comprise spiders and harvestmen. * Dataset used in statistical analyses.

4.3.2 Performance of statistical models to assess taxa response

Restock age, management and site variables explained between 10 and 67% of the variation in taxa abundance (Model 1; Table 4.3). For four of the six taxa studied, vegetation variables explained between 19 and 63% of the variance in taxon abundance (Model 2; Table 4.4). However, no vegetation effects were retained in the model for beetles and true flies; abundance of these taxa could not be related to differences in field-layer composition, height or structure.

Table 4.3: Taxon response to time, management and site variables (Model 1). Significant relationships listed in order ($P<0.05$; most highly significant first).

Taxon	Model 1 parameter	R^2
Beetles^{P}	ET (WI>HF), Altitude^{+}, Restock age x ET, Restock age^{+}	0.532
Arachnids^{P}	Altitude^{+}	0.582
Ants^{P}	Restock age^{+}, Open space^{-}, Altitude^{-}	0.674
Lepidoptera larvae^{P}	Restock age$^{(}$	0.101
True bugs^{S}	Restock age$^{\cap}$, ET (HF>WI), PT (UNP>PL)	0.452
True flies^{S}	Restock age$^{(}$	0.346

Arachnids group comprises spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap. Positive effects of variables upon taxa abundance are indicated by superscript + symbols, negative effects by – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols $\cap$ and (represent the type of curve. For calculation of R^2 values see methods. ET refers to Extraction Type (HF: harvester/forwarder extraction; WI: cable-winch extraction), PT refers to Planting Type (UNP: Unplanted; PL: Planted). See Table 4.2 for further variable descriptions.

Table 4.4: Taxon response to vegetation variables (Model 2). Significant relationships listed in order ($P<0.05$; most highly significant first).

Taxon	Model 2 parameter	R^2
Beetles^{P}	NA	NA
Arachnids^{P}	Field-layer density^{-}	0.631
Ants^{P}	Dwarf shrub cover$^{\cap}$, Graminoid cover^{-}	0.774
Lepidoptera larvae^{P}	Brash cover^{-}, Graminoid cover^{-}, Vegetation height^{-}	0.194
True bugs^{S}	Brash cover^{-}, Graminoid cover$^{(}$	0.407
True flies^{S}	NA	NA

Arachnids group comprises spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap. Negative effects of variables upon taxa abundance are indicated by superscript – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols $\cap$ and (represent the type of curve. For calculation of R^2 values see methods See Table 4.2 for further variable descriptions. NA denotes no significant variables in model.

When significant vegetation variables from Model 1 were added into Model 2 to create Model 3, explained variation in abundance increased by c. 5% for true bugs, but decreased by 1% for arachnids, and by c. 5% for ants and Lepidoptera larvae, (Table 4.4 and 4.5). R-sq values can decrease in a GLMM because at each stage of the model building procedure, parameters are estimated for both fixed and random effects. The addition of further fixed effects to the model may change the parameter estimates of the random effects. Ultimately, the R^2 value or the 'fit' of the model is only estimated from the fixed parameter estimates of the model. If the parameter estimates of the random effects hardly change then the R-sq value would be expected to increase for a more complex (i.e. larger number of fixed effects) model, but if the random parameter effects change dramatically for this more complex model, then these random terms could then account for an increased amount of the variation, leaving the fixed parameters accounting for less. The R-sq value decreases as it only related to the fit of the fixed effects, and not the fixed and random effects combined. Random parameter estimates can change across models as a result of lack of orthogonality and confounding in the data, such as model variables having different minimum/maximum ranges for different levels of the random effect (restock).

Therefore, Model 3 is reported for all taxa. For beetles and true flies, where a significant response was only recorded in response to time, management and site variables (and not to vegetation variables), Model 1 is reported.

4.3.3 Invertebrate response to habitat variation in restocks

Invertebrate taxa varied in their response to habitat variation in restocks, however, for most taxa, a strong response in abundance was recorded as restocks aged. A positive, linear response between restock age and abundance was recorded for active ground predators caught by pitfall trapping, i.e. ants (Table 4.5; Figure 4.3) and beetles in harvester/forwarder sites (Table 4.5; Figure 4.4). Beetle abundance differed with age according to timber Extraction Type; abundance was 50% greater in cable-winched than harvester/forwarder areas in year zero restocks. Ant abundance was at least three times as high in restocks over six years old than in younger restocks. Abundance of arachnids was not related to restock age, however, abundance declined as field-layer density increased. Ant abundance was negatively related to graminoid cover and positively related to dwarf shrub cover; captures were optimum between c.45% and 55% cover.

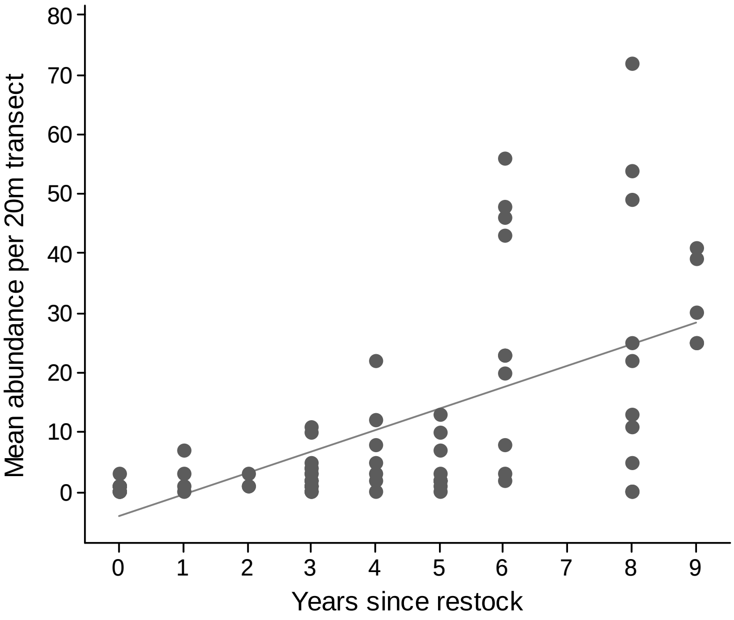


Figure 4.3: Abundance of ants (as measured by pitfall trap catches) in relation to restock age on 78 transects in 31 restocks in The Trossachs study area (*P*<0.001; Regression equation: Ant abundance = 3.61*Restock age-4.07). Mean abundance calculated by summing 2 pitfall traps per transect, with 4 weeks of trapping data pooled.

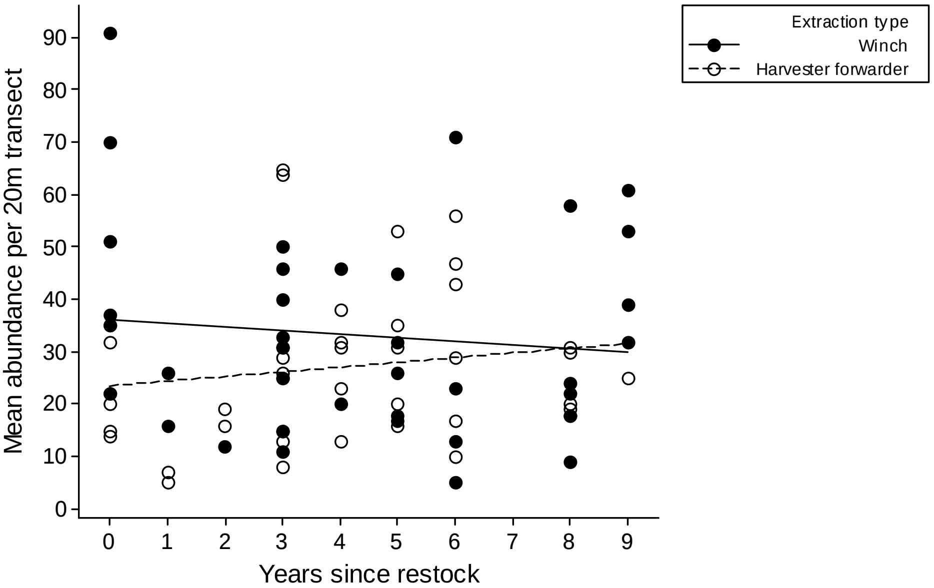


Figure 4.4: Abundance of beetles (as measured by pitfall trap catches) in relation to timber extraction method (Extraction Type) and restock age on 78 transects in 31 restocks in The Trossachs study area (*P*<0.045; Regression equations: Beetle abundance = -0.698*Restock age+36.1 in winch areas, and = 0.897*Restock age+23.5 in harvester forwarder areas). Mean abundance calculated by summing 2 pitfall traps per transect, with 4 weeks of trapping data pooled.

For taxa more associated with the field-layer, i.e. Lepidoptera larvae, true bugs and true flies, a quadratic response in abundance was recorded, such that these taxa increased in abundance during the first four to five years following restocking (Table 4.5; Figure 4.5). Thereafter, abundance either decreased (for true bugs) or levelled off up to the onset of canopy closure at eight years (Lepidoptera larvae and flies; Figure 4.5). The abundance of true bugs was greatest between three and six years after restocking, and was 10 times greater in five year old restocks than newly re-planted restocks. However, the increase in abundance of true flies was marginal only, whilst the apparent increase in Lepidoptera larvae abundance has to be treated with caution given that catches were low in restocks of all ages, but with the highest catch in five year old restocks (Figures 4.1 & 4.5).

No relationship between dwarf shrub cover and Lepidoptera larvae was detected, although there was a negative response of this taxon to areas with taller vegetation and increased cover of graminoids. Abundance of Lepidoptera larvae and true bugs was negatively related to brash cover.

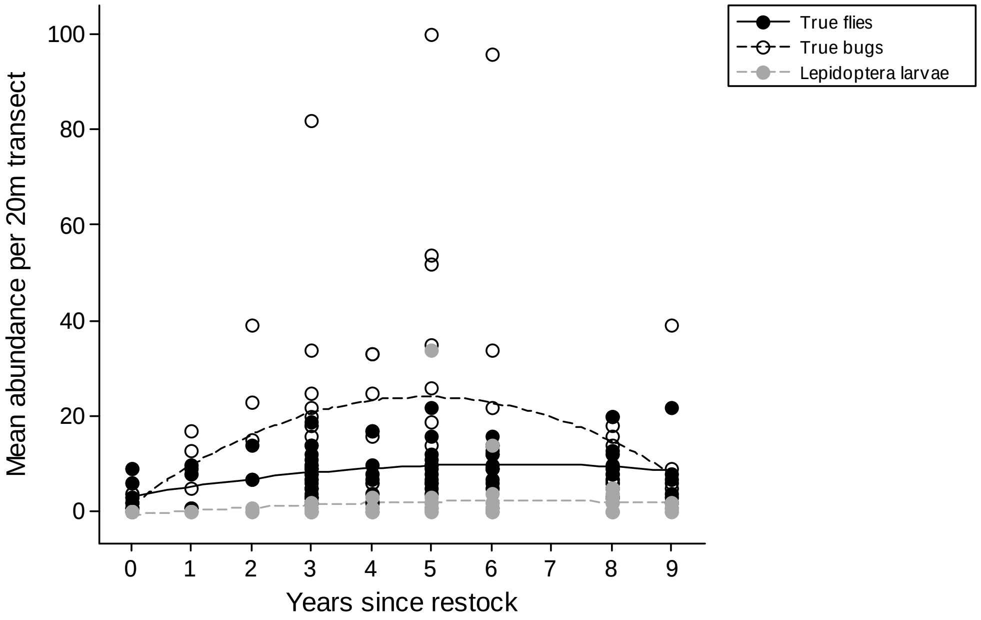


Figure 4.5: Abundance of taxa mainly associated with field-layer vegetation in relation to restock age on 78 transects in 31 restocks in The Trossachs study area. Regression equations: Lepidoptera larvae abundance = (0.894×Restock age)+(-0.069×Restock age^2)-0.641; P=0.012; true bugs abundance = (9.237×Restock age)+(-0.945×Restock age^2)+1.460; P<0.001; true flies abundance = (2.195×Restock age)+(-0.177×Restock age^2)+3.178; P=0.004. Mean abundance calculated by summing 2 suction traps per transect, with 2 occasions of trapping data pooled (for true flies and true bugs) or summing 2 pitfall traps per transect, with 4 weeks of trapping data pooled (for Lepidoptera larvae).

Only true bugs showed a direct response in abundance to both of the main restock managements examined (Planting Type and Extraction Type; Table 4.5). Abundance was c.50% greater in harvester and forwarder (HF) than cable-winched (WI) areas, and c.50% greater in areas left unplanted (UNP) than planted (PL). Addition of the Planting Type variable into Model 3 removed significance of the graminoid cover variable, suggesting that Planting Type explained more variation in the model than graminoid cover (a positive quadratic association; true bug abundance was optimum at c.70 to 90% graminoid cover).

Significantly more beetles and arachnids were found in restocks at higher altitude, (Table 4.5). Restock size, the previous planted (first-rotation) crop, or the distance of a restock from the plantation edge had no discernable effect upon abundance of any taxa.

Table 4.5: Minimum adequate GLMM models describing the abundance of invertebrate taxa preferred by black grouse in relation to significant time, management, site and vegetation variables on 78 transects in 31 restocks in The Trossachs study area. The table reports the overall minimum adequate model (Model 3) constructed by stepwise addition of significant variables from a restock age/management/site variables model (Model 1; Table 4.3) to a vegetation model (Model 2; Table 4.4).

Taxon	Model 3 parameters	Estimate	SE	df	t value	Direction of effect	Statistical test	Model 2 R^2#	Model 3 R^2#
Beetles	Intercept	2.475	0.302	44	8.204		glmmPQL	NA	NA
	Restock age	0.080	0.038	29	2.093*	+			
	ET	0.492	0.189	44	2.609*	WI>HF			
	Restock age x ET	-0.088	0.041	44	-2.156*	§			
	Altitude	0.001	<0.001	44	2.553*	+			
Arachnids	Intercept	3.083	0.295	45	10.447		glmmPQL	0.631	0.621
	Field-layer density	-0.238	0.117	45	-2.034*	-			
	Altitude	0.003	<0.001	45	3.973***	+			
Ants	Intercept	0.307	0.405	44	0.757		glmmPQL	0.774	0.722
	Dwarf shrub cover	0.034	0.011	44	3.241**				
	Dwarf shrub cover^2	-0.001	<0.001	44	-3.095**	∩			
	Graminoid cover	-0.012	0.004	44	-3.050**	-			
	Restock age	0.354	0.065	29	5.469***	+			
Lep. Larvae	Intercept	-3.475	2.307	44	-1.506		glmmPQL	0.194	0.133
	Brash cover	-0.066	0.027	44	-2.480*	-			
	Graminoid cover	-0.014	0.006	44	-2.211*	-			
	Vegetation height	-0.013	0.005	44	-2.371*	-			
	Restock age	1.887	0.809	28	2.332*				
	Restock age^2	-0.149	0.067	28	-2.218*	╭			

Table 4.5: *Continued.*

Taxon	Model 3 parameters	Estimate	SE	df†	t/z value	Direction of effect	Statistical test	Model 2 R^2#	Model 3 R^2#
True bugs	Intercept	2.175	0.529	44	4.110		glmmPQL	0.407	0.459
	Brash cover	-0.031	0.008	44	-3.664***	-			
	Restock age	0.555	0.199	28	2.786**				
	Restock age^2	-0.059	0.019	28	-3.056**	∩			
	PT‡	0.657	0.155	44	4.247***	UNP>PL			
	ET	-0.867	0.177	44	-4.908***	HF>WI			
True flies	Intercept	1.132	0.238	-	4.765		glmer	NA	NA
	Restock age	0.383	0.108	-	3.536***				
	Restock age^2	-0.032	0.011	-	-2.885**	⎛			

Arachnids group comprises spiders and harvestmen. Restock age/management/site variables italicised. ET refers to Extraction Type (HF: harvester/forwarder extraction; WI: cable-winch extraction), PT refers to Planting Type (UNP: Unplanted; PL: Planted). See Table 4.2 for further variable descriptions. Positive effects are indicated by + symbols, negative effects by – symbols. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, symbols ∩ and ⎛ represent the type of curve. § Relationship illustrated by Fig. 4.4. NA indicates no significant Model 2 vegetation variables (Table 4.4) to formulate Model 3. ‡ *PT* replaced the 'graminoid cover' variable. # For calculation of R-sq values refer to methods. † For calculation of parameter estimates using 'glmer', the R statistical programme uses REML (residual maximum likelihood); estimates are not based on observed and expected mean squares or on error strata, hence degrees of freedom are not given (as all F ratios use the same denominator). Levels of significance: *** $P<0.001$; ** $P<0.01$; * $P<0.05$.

4.4 Discussion

Black grouse hens select invertebrate-rich habitats for chick feeding (Baines *et al.* 1996). As in most gallinaceous birds, habitats with sufficient cover to evade predators, but where vegetation is not too dense to impede brood movement are also selected (Bergerud & Gratson, 1988). It has been suggested that one of the most direct management actions for future grouse conservation is the retention or restoration of these brood-rearing habitats (Hannon & Martin 2006). Results from Chapter 3 suggest that second rotation restocks may contain suitable habitat for black grouse and their broods, whilst this chapter indicates that restocks contain invertebrate taxa found important in the diet of black grouse chicks elsewhere. Results suggest that restock age is an important determinant of invertebrate availability to black grouse chicks. Manipulation of forest management methods during the felling and restocking process can alter the vegetative field-layer and affect the abundance of some invertebrate taxa, however, effects which are consistent across the majority of the taxa considered are difficult to discern.

4.4.1 Restocks and Lepidoptera larvae

Several studies investigating the content and composition of black grouse chick crops and droppings report Lepidoptera larvae as one of the most frequently taken food items, which, together with ants and sawfly larvae (the latter of which was not captured in restocks this study), often make up the greatest proportion of the chick diet (see Table 4.1). In terms of energy expenditure for nutritional value return, Lepidoptera larvae are likely to be the most important food source available to chicks, representing a large, protein-rich, easy to catch food item (Starling-Westerberg 2001) when compared with ants, which have a smaller biomass and are probably more difficult to catch.

In this study, Lepidoptera larvae were most abundant five years after restocking, however, catches were infrequent and abundance was low relative to other taxa captured. In Britain, Lepidoptera larvae are closely associated with heather *Calluna vulgaris* moorland (Webb 1989; Fielding 1992; Coulson 1988), however, no relationship between larval abundance and dwarf shrub cover was recorded in our study. Other studies have reported larval density to be greater on taller vegetation and positively associated with the taller ‘building’ and ‘mature’ phases of *Calluna* growth (Haysom & Coulson 1998), however, a negative relationship was recorded with vegetation height in this study.

It is unlikely that pitfall trapping provided reliable estimates of Lepidoptera larvae abundance or reliable associations of this taxon with field-layer vegetation. Whilst pitfall trap and sweep net data from the 2009 re-survey were correlated (albeit weakly), providing a reasonable reflection of abundance, it is likely that associations with field-layer vegetation, hence the effects of different forest management methods, were not adequately assessed, and an effect of dwarf shrub cover on abundance was not detected. Data from pitfall traps are more likely to represent movement of larvae on the ground than their association with food plants, possibly recording movement of larvae when locating suitable pupation sites either in or on top of soils in spring (Skinner 1984). Therefore, significant yet weak relationships between Lepidoptera larvae and field-layer vegetation variables in statistical models in this study must be treated with caution. To gain a more reliable and informative assessment, a more appropriate trapping method (such as sweep netting) should be deployed, which would allow more reliable interpretation of associations and easier comparison with other studies.

Lepidoptera larvae abundance is likely to be highest in restocks with a greater density of suitable host plants, such as bog myrtle *Myrica gale* (Baines *et al.* 1996) or bilberry *Vaccinium myrtillus* (Baines *et al*. 1994; Fielding 1992; Welch *et al.* 1994), however, these were recorded infrequently in restocks. The reduction in quantity of bilberry in clearfelled areas of commercial forests is well-documented in Scandinavia (Atlegrim & Sjoberg 1996a), and can result in a decrease in the abundance of Lepidoptera larvae (Kvasnes & Storaas 2007) and herbivorous insect larvae in general (Atlegrim & Sjoberg 1996b; Lakka & Kouki 2009). Development of suitable field-layer vegetation in restocks is likely to be further impeded by brash cover for a number of years after clearfell. Increased brash cover was negatively associated with larval abundance in this study, as suitable habitat for oviposition by adults and feeding opportunities for larvae were likely to be reduced.

4.4.2 Effect of restock age and management upon invertebrate abundance

The number of years since restocking affected the abundance of all invertebrate taxa, with the exception of arachnids. Since changes in taxa abundance are most likely to be related to changes in field-layer vegetation, information from Chapter 3 is used to aid interpretation of results forthwith.

Invertebrate taxa differed in their response to restock age. Ant abundance increased with restock age; numbers were three times higher in older restocks. Most ants are generalist predators, scavengers and indirect herbivores (Wilson & Hölldobler 2005) and greater abundance in older restocks probably reflects a greater availability of suitable food and habitat resources. Species richness of ants commonly increases from forest planting to c.20 years (see Niemelä 1997 for a review), and subsequent increases in abundance are likely to result. Increased ant abundance in restocks with a moderate dwarf shrub cover and decreased graminoid cover suggests preference for better-developed habitats, compared with more sparsely-vegetated, young restocks. This habitat is further enhanced for ants in restocks with a greater proportion of planted trees (i.e. decreased open space), where a more complex forest habitat is available.

Beetle abundance generally increased with restock age, although levels of abundance differed according to the timber extraction method used at clearfell. In the year following restock, beetle abundance in cable-winched areas was double that recorded in harvester/forwarder extracted areas, although numbers were similar by the onset of canopy closure. The method by which timber is extracted from forest coupes following clearfell affects field-layer re-vegetation and density in restocks; cable-winched areas are largely free from brash after harvesting and generally re-vegetated much faster than harvested/forwarder extracted areas (see Chapter 3). Beetles can take advantage of this early vegetative cover, which seems likely to increase prey abundance, whilst providing cover during hunting.

Increases in the abundance of true bugs and true flies were most prominent in the initial years following restocking; a period when non-vegetative ground cover (composed of brash and needles) had mostly degraded, and re-vegetation of field-layer species commenced (see Chapter 3). Decreases in abundance of Lepidoptera larvae and flies mainly occurred with the onset of canopy closure at around eight years, when tree growth began to out-compete field-layer vegetation. Abundance of true bugs was greatest between three and six years after restocking, a period when cover by graminoid species was optimal, and food resources abundant for this plant-sap feeding group (Brusca & Brusca 2003). Apart from beetles, true bugs were the only taxon to respond to differences between forest management methods in restocks, i.e. Planting Type or Extraction Type. Abundance was significantly lower in planted areas, possibly due to the greater cover of non-native trees and *C. vulgaris* providing less suitable habitat than in unplanted areas. The wetter plant community that established in harvester/forwarder extracted areas, mainly composed of graminoids: *Carex, Juncus* and *Eriophorum* spp and later *Molinia caerulea* (see Chapter 3), also apparently benefit true bugs, which were significantly more abundant in these areas than in cable-winch extracted areas. Cable-winched areas also have a significantly greater cover of *C. vulgaris*, which may out-compete the non-woody vegetation preferred by true bugs. Abundance of true flies was comparatively low, and flies were not found to respond to any variable measured. This could be a consequence of the suction trapping method used; as more mobile species, flies were occasionally observed to fly clear of the suction nozzle whilst (or even before) vegetation was sampled, which is a recognised disadvantage of this method (Sutherland 1996) that may result in a biased sample and an unclear result.

Although overall abundance of arachnids did not change significantly as restocks aged, it is likely that forest specialists replaced open ground specialists as vegetation developed (Oxbrough *et al.* 2005). However, other factors may contribute to this apparent lack of relationship with restock age. Statistical analyses were conducted using pitfall trap data, which was most likely to bias catches towards wolf spiders (Lycosidae) - an active, ground-hunting group - and against less active groups, notably money-spiders (Linyphiidae), which build webs in field-layer vegetation to trap prey (Oxbrough *et al*. 2005; Atlegrim & Sjoberg 1995). By using only pitfall trapping data, and hence sampling mainly the ground-level group, the group most likely to increase with age-related changes to the field-layer was less well represented, reducing the chances of detecting an effect of restock age. For the arachnid group in particular, consideration should be given for the use of both pitfall trapping and suction sampling when assessing abundance in restocks.

Existing studies investigating the response of invertebrate taxa to plantation forest management in Britain mostly focus upon Carabid beetle and spider assemblages - taxa that are easily captured by pitfall traps - which often respond to changes in forest structure, and are taxonomically well-known (Oxbrough *et al*. 2010). In comparison with this study, which focussed upon the period between restock and the onset of canopy closure, previous work has investigated invertebrate response through a complete forest rotation from planting to maturity (e.g. Day & Carthy 1988), or has compared invertebrate response between forest plantations and surrounding habitats (e.g. Butterfield *et al.* 1995). In Fennoscandia, research often focuses upon differences resulting from timber felling type, particularly the comparison between clearfelling, single-tree selective felling, and uncut controls (Atlegrim & Sjoberg 1995; Nitterus *et al.* 2007). Whilst studies describing the recovery of field-layer vegetation within second-rotation forests are relatively common (see Chapter 3), data relating to the response of invertebrates in this habitat are rare.

4.4.3 Invertebrate provision in restocks for black grouse chicks.

This study represents one of the most intensive invertebrate sampling studies covering the most diverse range of invertebrate taxa conducted in second rotation commercial forest restocks to date in the UK. Restocks appear to provide a resource of most invertebrate taxa preferred by black grouse chicks, particularly of true bugs in restocks around five years old and ants six years after restock. Whereas ants are commonly recorded in the diet of black grouse chicks and often occur as a major component, true bugs are recorded in fewer studies, and often represent a relatively minor proportion of the diet (See Table 4.1). Both taxa have a relatively low biomass, hence large numbers are likely to be required to equate to a larger, easy to catch protein-rich meal, such as Lepidoptera larvae.

Previous dietary studies suggest that beetles commonly occur in the diet of chicks, although comprise a relatively small proportion of the overall invertebrates consumed. Beetles are common in second rotation plantations in Britain, where clearfelled areas often result in higher species diversity than closed-canopy areas (Day & Carthy 1988; Butterfield *et al.* 1995). Furthermore, increased structural diversity provided by brash piles in restocks can result in increased abundance of certain taxa, such as spiders (Oxbrough *et al.* 2010), although brash cover was found to be negatively associated with true bug abundance in this study. Indirect effects of brash upon black grouse broods may be important however; roost droppings observed underneath brash piles suggest that black grouse may use brash in restocks for cover (J. Owen, unpublished data), thus the retention of well-distributed brash piles in restocks may provide beneficial shelter and cover prior to the recovery of field-layer vegetation.

If Lepidoptera larvae abundance is low in restocks due to the lack of suitable field-layer vegetation (rather than inadequacies of the sampling method), availability of other invertebrate taxa may be important in providing a food source for chicks. Invertebrate taxa recorded in this study were similar to those recorded in first-rotation forests in Wales (Cayford *et al.* 1989). Analyses of brood droppings from in and around forest plantations suggested that ants and Lepidoptera larvae formed the greatest proportion of chicks' diet, but locally abundant taxa such as harvestmen were also important. Chicks also foraged opportunistically to some degree (Cayford *et al.* 1989), taking a wide range of invertebrate groups, and abundance of taxa differed between study sites. Variation in the abundance of different taxa can be important in determining diet composition; in two study areas in the French Alps, grasshoppers formed a major component of chick diet (Ponce 1992), and Lepidoptera larvae were comparatively rare. However, grasshoppers are not a commonly recorded item in either chick diet or in black grouse habitat in Britain (present study; Picozzi 1986; Cayford *et al*. 1989; Starling-Westerberg 2001; Baines Baines *et al*. 1996; Baines 1996). In addition to Lepidoptera larvae, chicks are reported to favour other slow-moving, soft-bodied invertebrates, such as true bugs (Niewold 1990), and larvae of other species, such as sawflies, which comprised a high proportion of the chick diet on grass-dominated moorland in Northern England (Baines *et al.*1996; Starling-Westerberg 2001).

4.4.4 Management conclusions

Identifying and improving potential areas of brood habitat is likely to be important for maintaining black grouse populations. When suitable habitats are reduced, hens are forced into sub-optimal habitats containing fewer insects in which more chicks starve (Niewold 1990). Willow grouse broods travel further to find food when suitable habitat is limited (Erikstad 1985), and predation risk is increased with the aggregation of broods on small areas of remaining suitable habitat (Kastdalen & Wegge 1985; Lakka & Kouki 2009).

Understanding the factors involved in the development of better brood habitat is necessary so that management resources can be directed appropriately. Whilst there is no clear evidence that the application of one particular forest management method considered (either Planting Type or Extraction Type) results in an increased abundance of all invertebrate taxa in restocks preferred by black grouse, an increased abundance of most taxa was detected in response to restock age. In areas that contain black grouse and where the provision of brood habitat is a priority, restocks of five years or older where planted trees have not yet closed canopy should be made available throughout the second rotation of plantation forests, although this age may vary slightly between FC forest districts across Scotland due to factors such as climate, soils, topography, and tree species planted. Alternatively, the extension of fallow periods before restocking (where appropriate) may increase the duration of suitable habitat to invertebrates, hence prolong optimum taxa abundance prior to canopy closure.

Whilst the size of restocks or their distance from the plantation edge did not appear to be important factors for the invertebrate taxa studied, previous studies suggest that habitat is more likely to be used by black grouse if located on the plantation/moorland edge (Watson & Moss 2008). Whilst somewhat surprising that areas left unplanted provided no greater benefit in terms of increased invertebrate abundance, it is likely that the comparative importance of these areas will become apparent after trees have closed canopy in restocks subject to a two year standard fallow period. As mentioned previously in Chapter 3, correlative studies are subject to limitations due to the difficulty in establishing cause and effect (see 3.4.5). Forest management methods such as leaving areas unplanted influence the recovery of vegetation, which in turn is likely to influence invertebrate abundance. However, which areas are left unplanted in a restock can be a result of site topography, meaning that in a restock on flat ground all unplanted areas may be left in boggy areas, making it difficult to discern the influence of environmental factors upon invertebrate abundance from those resulting solely from forest management.

Comparisons with productive, natural black grouse habitat are necessary to quantify the potential quality and value of restocks to black grouse and their broods within and around commercial forests.

Chapter 5: Potential effects to black grouse from extended fallow periods in restocks

5.1 Introduction

Alternatives to chemical insecticides used for control of pine weevil *Hylobius abietis*, a pest of commercial conifer crops, are currently sought by the Forestry Commission (FC). Whilst permethrin-based insecticides can prevent damage to young trees (Leather *et al*. 1999; Langstrom & Day 2004), and are relatively low cost (von Sydow 1997), growing economic and environmental concerns have resulted in a change of policy aimed at reducing and eventually discontinuing chemical use on the national forest estate. However, without preventative measures to guard against *Hylobius* attack, losses of planted trees average around 50%, and in some cases whole sites can fail without adequate protection (Willoughby *et al.* 2004).

Previous research suggests that planted trees are particularly at risk from *Hylobius* attack up to two years after clearfell (Willoughby *et al.* 2004). *Hylobius* beetles are attracted by volatiles emanating from the resin of freshly cut conifer stumps in newly clearfelled areas, which act as breeding material for the development of eggs through to the pupal stage. The subsequent emergence of adults from stumps can result in widespread damage to newly planted saplings in a restock, as adults feed on the bark. Populations often remain at high levels for four to five years after clearfell, resulting in high tree mortality over a prolonged period (Eidmann 1974; von Sydow 1997; Orlander & Nilsson 1999). One possible alternative to annual prophylactic pesticide use is to increase the current ‘standard’ fallow period between clearfell and restocking; from the current prescription of two years, to between three and five years, thereby allowing the *Hylobius* population to naturally build up, decrease, and stabilise at low levels before restocking commences (Moore 2004; Willoughby *et al.* 2004). Whilst not feasible for all sites due to subsequent increased competition from ground vegetation (Nilsson & Örlander 1999), extended fallow period restocks have been trialled experimentally by FC since the late 1990's to ascertain best practice for weevil control (Heritage & Moore 2001; Willoughby *et al.* 2004). In 2010, recommendations were made to extend fallow periods in restocks within FC forests across Scotland, following publication of successful management trials in the North Highlands Forest District in Sutherland (Forestry Commission 2009b).

Restocks with an extended fallow period could provide a number of benefits to black grouse *Tetrao tetrix*. In addition to semi-natural woodland and moorlands, black grouse use young commercial conifer plantations and the recovering vegetation in pre-thicket clearfells and restocks of the second rotation for feeding, lekking, nesting and brood rearing (Cayford *et al.* 1989; Haysom 2001). However, suitable habitat within commercial plantations is often available for a limited time only prior to tree canopy closure (this study; Pearce-Higgins *et al.* 2007). In second rotation restocks, where there is also an initial period of vegetation development (Chapter 3), extending the fallow period may allow better re-establishment of slower-growing ericaceous and other dwarf shrub species that are of particular importance to black grouse, such as heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus*, and also increase the duration of their availability. This may in turn influence the availability of invertebrate foods for black grouse chicks, as well as having potential effects on the abundance of species that may predate black grouse adults, eggs and chicks. Vegetation development may influence small mammal populations (Sullivan *et al.* 2001; Fernandez *et al.* 1994; Ecke *et al.* 2002) which are likely to be important prey items for a range of avian and mammalian predators, and can affect populations of such predators (Hamerstrom 1979; Hörnfeldt *et al.* 1986). Thus, as large areas of the forest estate remain to be clearfelled over the coming decades (Mason 2007), the practice of extending fallow periods may represent a substantial increase in the amount of potentially useful habitat available to black grouse and their broods, and influence the abundance of invertebrate food items and potential predators.

The objective of this chapter is to assess the influence that extended fallow periods may have upon black grouse and their broods using second rotation restocks, by examination of changes in: 1) field-layer vegetation composition, 2) abundance of invertebrate taxa preferred by black grouse, and 3) predator abundance. Changes are assessed by comparing restocks subject to an extended fallow period with restocks subject to a standard fallow period in the same geographical area, allowing quantification of potential benefits to black grouse.

5.2 Methods

5.2.1 Field data collection

Field data were collected from 36 restocks in 8 commercial forest plantations in Sutherland between May and September 2009 (see Chapter 2 for study area information and map). Restocks previously contained mature crops of un-thinned Sitka spruce *Picea sitchensis* and/or lodgepole pine *Pinus contorta*, all of which had been clearfelled using heavy machinery (harvester and forwarder). Restocks were located on the forest/moorland edge, or connected to the edge by other open ground of potential use to black grouse, i.e. pre-thicket restocks or unplanted areas (see Chapter 3, section 3.2.2).

A range of restocks was selected, from newly replanted (year 0) through to closing-canopy (9 years since restock). Each restock had been subject to either to a ‘Control’ fallow period of up to 2 years, an ‘Extended’ period of 3 to 5 years, or a ‘Super-extended’ period of 6 to 7 years. Fallow period length of each restock was assigned randomly, as part of a previous, unrelated FCS trial (Table 5.1).

5.2.1.1 Vegetation sampling

Habitat data were collected from a total of 288, 20 m transects in 36 restocks. Eight transects were located in each restock; 4 in areas planted with trees and 4 in areas left unplanted, using stratified random sampling for transect placement. All transects were more than 100 m apart and no less than 50 m from the restock edge. Methods for collection of habitat data in restocks are described in Chapter 3 (section 3.2.2).

5.2.1.2 Invertebrate sampling

Invertebrate data were collected from 72 of the 288 transects described in 5.2.1.1. Two of the eight transects in each restock were randomly selected for use; one in a planted area and one in an area left unplanted. Invertebrates were sampled by pitfall trapping, suction sampling and sweep netting, as described in Chapter 4 (section 4.2.1).

Sampling was conducted between 8 June and 15 July 2009 to coincide with the brood-rearing period when chicks are largely dependent upon invertebrate food (Robel 1969a; Starling-Westerberg 2001; Picozzi 1986; Baines *et al.* 1996). In the Sutherland study area, brood records suggest that black grouse chicks hatch from approximately early-June to at least mid-June (K. Kortland, pers. comm.), although dates are likely to vary.

5.2.1.2.1 Taxa selection and sampling method

Invertebrates were identified to Order following Chinery (1993), with the exception of Hymenoptera, which were further identified to Formicidae (ants), Symphyta (sawfly larvae) and Ichneumonidae (parasitic wasps). Spiders (Araneae) and harvestmen (Opiliones) were not distinguished, but combined and termed 'arachnids' for analyses. Invertebrates measuring ≤2 mm in length (predominantly Collembola) were considered too small to make an important contribution to the black grouse chick diet (Niewold 1990) so were discarded and not included in overall counts.

Six invertebrate taxa of potential importance to black grouse chicks were selected for statistical analyses based upon data from previous dietary studies (Chapter 4, Table 4.1). For the 2009 invertebrate studies, adult Tipulids were separated from other true flies (Diptera) and considered as a seventh group, because they represent one of the most important dipteran families within upland bird diets (Buchanan *et al*. 2006).

Taxa considered for statistical analyses were caught in restocks using three invertebrate sampling methods, as described in Chapter 4 (section 4.2.1). To avoid producing multiple, and potentially contrasting, abundance measures for the same taxon, the trapping method considered to be most appropriate for each taxon was selected for use in statistical analyses, as described in Chapter 4 (section 4.2.2; based upon recommendations in Sutherland 1996, and Standen 2000). Therefore, as in Chapter 4, pitfall data were used for beetles, arachnids, and ants (as predominantly surface-living taxa, which are active on bare ground or low vegetation), whilst suction sampling data were used for true flies and bugs due to their stronger association with field-layer vegetation. Sweep netting data were used for Lepidoptera larvae and Tipulids, as these groups (also commonly associated with the field-layer) were considered to be ineffectively sampled using the other trapping methods.

5.2.1.3 Predator abundance

Potential avian predators and scats of mammalian predators of black grouse, and their broods and nests, were recorded along 1 km transects in a randomly selected sub-sample of 24 of the 36 study restocks. One transect was established through each restock using linear habitat features such as quad-bike tracks (used for deer management), or forest vehicle tracks that passed directly alongside or through the restock. Each transect was first walked in mid-April to clear it of mammalian (red fox *Vulpes vulpes* and pine marten *Martes martes*) scats, and mammalian and avian data were then collected once per month from mid-May to mid-August 2009, which encompassed the period when hens were on eggs through to when juveniles are likely to have fledged. When walking transects, potential avian predators were counted if taking off or landing within 250 m of the transect line, or if in flight over the restock. Upon completion of avian observations along a transect, faecal scats were collected on the return journey. As scats of fox and pine marten are difficult to distinguish between reliably (Davison *et al.* 2002), all scats were classed in one ‘mammalian predator’ group. In order to avoid repeated measures of predator abundance from the same transect and to reduce the frequency of zero counts in the data, counts of avian observations and mammalian scats collected each month were pooled for each transect.

Table 5.1: Description of fallow period prescriptions, location of restocks used and number of transects per age group in the 2009 Sutherland study.

Fallow group	Description	Plantations	No. of restocks	Total transects	Age group	No. of transects
Control (2 years)	'Standard' fallow period - recommended for most restocks up until mid-2010	1, 2, 3, 6, 7, 8	13*	104	Young	32
					Intermediate	32
					Closing canopy	40
Extended (3-5 years)	Now current recommendation for all restocks in Scotland, except sites particularly prone to weed growth	1, 4, 5, 8	14	112	Young	40
					Intermediate	32
					Closing canopy	40
Super-extended (6-7 years)	Part of FC trial in late 1990's to assess pine weevil population dynamics	1, 4, 5, 8	9	72	Young	32
					Intermediate	40
					Closing canopy	0^

Plantations: 1. Dalchork, 2. Shinness, 3. Lairg, 4. Inveroykel, 5. Raemore, 6. Balblair, 7. Rogart, 8. Morangie. Refer to Chapter 2 for study area and plantations information.
*Data also used in Chapter 3. ^Restocks of this fallow period/age group not available for study.

5.2.2 Statistical analyses

5.2.2.1 Model building

5.2.2.1.1 Field-layer vegetation

Explanatory restock variables (Model 1; Table 5.2) inter-correlated at $r \geq 0.60$ were identified (Appendix Table 4a), and those inter-correlated with the effects of main interest in this study, i.e. Fallow group, Restock age and Planting Type (which represent fundamental aspects of restock management) were removed. Variables included in analyses were: Restock age, Fallow group, Planting Type, Restock size, Open space, Distance to edge, Previous crop, Altitude and Slope (see Model 1; Table 5.2 for variable descriptions). Quadratic terms of each continuous explanatory variable were tested, with a significance level of $P<0.05$. First-order interactions between Fallow group and Planting Type, and Fallow group and Restock age were included in analyses, as vegetation response is expected to differ with the length of fallow period, and results from the Chapter 3 suggest that Planting Type and Restock age are likely to be two of the main variables affecting vegetation response (section 3.3).

GLMM models were fitted specifying restock identity as the random effect. Minimal adequate models were produced by fitting all of the relevant main effects and interactions, and then removing terms according to their level of significance, until only those significant at $P<0.05$ remained. Interaction terms were tested for removal before main effects. Posthoc, pairwise tests using the 'relevel' function in R were used to compare three-level factors (i.e. the three fallow period groups), and the 'anova' function was used to generate an overall minimum adequate model.

Calluna vulgaris cover data contained a high proportion of zeros (absent from 50 of 288 transects) and could not be transformed to a normal distribution. Therefore, data were modelled using the penalized-quasi likelihood (PQL) method (Venables & Ripley 2002) to account for an unknown distribution (cover values not being based upon a set of trials), using the glmmPQL function in the 'MASS' library of R, version 2.8.1 (R Development Core Team 2008). Both *V. myrtillus* and *Eriophorum* spp. (*E. vaginatum* and *E. angustifolium*) occurred with very low frequency across transects and were therefore treated as presence or absence data, using the glmer function in the 'lme4' library (Bates *et al*. 2008), based on the binomial logistic regression model. Height of heather (*Calluna vulgaris, Erica tetralix, E. cinerea*), graminoids (grasses, *Juncus* and *Carex* spp.), and field-layer density (0 to 40 cm height, including brash) were analysed with a normal error distribution using linear mixed effects models, hence the lme function in the 'nlme' library of R (Pinheiro *et al*. 2007).

5.2.2.1.2 Invertebrates

Explanatory variables in the invertebrate Model 1 (Table 5.2) were removed if inter-correlated at $r \geq 0.60$ with the effects of main interest in this study, i.e. Fallow group, Restock age or Planting Type (which represent fundamental aspects of restock management). This resulted in removal of the variables: number of trees, mean tree height, and tree cover (Appendix Table 4a). None of the vegetation variables in Model 2 (Table 5.2) were inter-correlated at $r \geq 0.60$ (Appendix Table 4b). Quadratic terms of each continuous explanatory variable were tested, with a significance level of $P<0.05$.

Table 5.2: Explanatory variables considered in statistical models. Model 1 contains time (T), management (M), and site (S) variables in restocks. Model 2 contains field-layer vegetation variables.

Variable	Data type¶	Description	Level of data collection
Model 1. Time (T), management (M), and site (S) variables			
Restock age	T	Years since restock	Restock
Fallow group	M	Number of years spent fallow prior to restock, categorised into: Control (0-2 years), Extended (3-5 years) or Super-extended (6-7 years)	Restock
Planting Type (PT)	M	Planted with trees (PL) or left unplanted (UNP)	Transect
Restock size	S	Total restock area (ha), includes planted and unplanted	Restock
Open space	S	Total restock area (ha), unplanted only	Restock
Distance to edge	S	Restock edge to nearest plantation edge (m)	Restock
Previous crop	S*	First rotation crop: spruce or pine	Transect
No. of trees#	S	Number of planted trees in a 10x10 m square	Transect
MTH#	S	Mean tree height (m) in 10x10 m square described above	Transect
Tree cover#	S	Cover (%) by planted trees	Transect
Altitude	S	Average of 5 equidistant points	Transect
Slope	S	Average of 5 equidistant points	Transect
Model 2. Vegetation variables			
Moisture score	C	Mean cover-weighted Ellenberg moisture values	Transect
Vegetation height	C	Maximum height of all vegetation (cm)	Transect
Field-layer density	C	Index (0 to 3) of field-layer density from ground level to 40cm tall, includes vegetation and brash	Transect
Dwarf shrub cover	C	Combined cover (%) of *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, *Vaccinium myrtillus*	Transect
Graminoid cover	C	Combined cover (%) of *Carex, Eriophorum, Juncus, Luzula, Deschampsia, Agrostis, Molinia, Nardus, Festuca* and *Anthoxanthum* spp.)	Transect
Brash cover	C	Cover (%) by brash	Transect

‘Moisture score’ refers to the mean cover-weighted Ellenberg moisture score (Hill *et al.* 1999) of species recorded along a transect: wetter habitats have a higher score. # not included in analyses due to inter-correlation within the Model (see Appendix, Table 4). ¶ indicates how data were represented in statistical models: T - continuous age covariate; M - 2-level management factor; S - continuous site-dependent variable; S* - 2-level site factor; C - continuous vegetation variables.

First-order interactions tested are as described for vegetation analyses above (section 5.2.2.1.1). Interaction terms were tested for removal before main effects. Minimal adequate models were produced in the same way as for vegetation models above.

Analyses for each invertebrate taxon were undertaken using generalised linear mixed models (GLMMs), specifying restock identity as the random effect. Data for all invertebrate taxa were over-dispersed, hence the ‘glmmPQL’ function in the ‘MASS’ library (Venables & Ripley 2002) of R was used specifying ‘quasipoisson’ errors., which automatically estimates over-dispersion using a Penalised Quasi-Likelihood method (Zuur *et al*. 2009).

5.2.2.1.3 Predator abundance

As only one transect per restock was used for the assessment of predator abundance, data were analysed using a standard GLM. Data were from a non-normal distribution and were over-dispersed, hence the ‘quasipoisson’ error term was used. Only main variables of interest were tested, i.e. length of fallow period (i.e. ‘Fallow group’), restock age, and their interaction.

5.2.2.2 Calculation of R^2 values

The R^2 value produced for each model explains how much of the variation in the data is explained by the model, with a higher R^2 value meaning more variation has been explained. For glmer, R^2 values are calculated by (null deviance - residual deviance / null deviance). For glmmPQL, R^2 is calculated by the square of the correlation between the model's predicted values and the observed values.

5.3 Results

5.3.1 Field-layer vegetation

Thirty-three vascular plant species, two graminoid groups identified to genus only (*Agrostis* and *Luzula* spp.) and four moss genus groups (*Polytrichum*, *Sphagnum*, *Pleurozium* and *Racomitrium* spp.) were recorded in restocks.

5.3.1.1 Ground-, field-layer and canopy-cover development

From replanting to 2 years old, restocks with a standard 2 year fallow period ('Control') are predominantly composed of graminoids (*Juncus*, *Carex*, *Eriophorum* spp. and grasses), and non-vegetative ground cover (mainly brash), with sparse dwarf shrub cover (predominantly *Calluna vulgaris,* but also *Erica tetralix, E. cinerea* and *Vaccinium myrtillus*; Figure 5.1 and Figure 5.2a). Up to 2 years after restock, 'Extended' fallow restocks have more than double the dwarf shrub cover of restocks subject to a 'Control' fallow period, and 'Super-extended' fallow restocks have three times the dwarf shrub cover of Controls (Figure 5.1). Graminoid cover is similar between the fallow period groups, however Controls have a greater non-vegetative cover (which is predominantly composed of brash).

At 3 to 5 years old, cover in restocks subject to a 'Control' fallow period is still dominated by graminoids (Figure 5.1 and Figure 5.2b). 'Extended' and 'Super-extended' fallow restocks have nearly double the cover of dwarf shrubs and a reduced graminoid cover.

Dwarf shrub cover in Controls only reaches levels in 'Extended' fallow restocks at the onset of canopy closure, 6 to 9 years after replanting (Figure 5.1 and Figure 5.2c). *C.*

vulgaris dominates over other dwarf shrubs at every stage, on average representing more than 93% of dwarf shrub cover on transects.

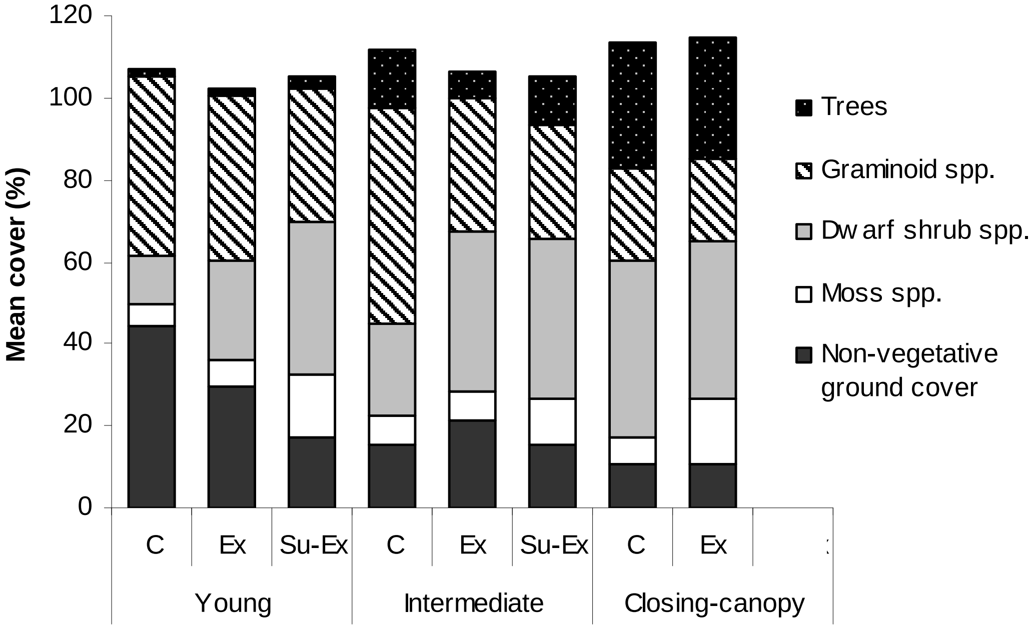
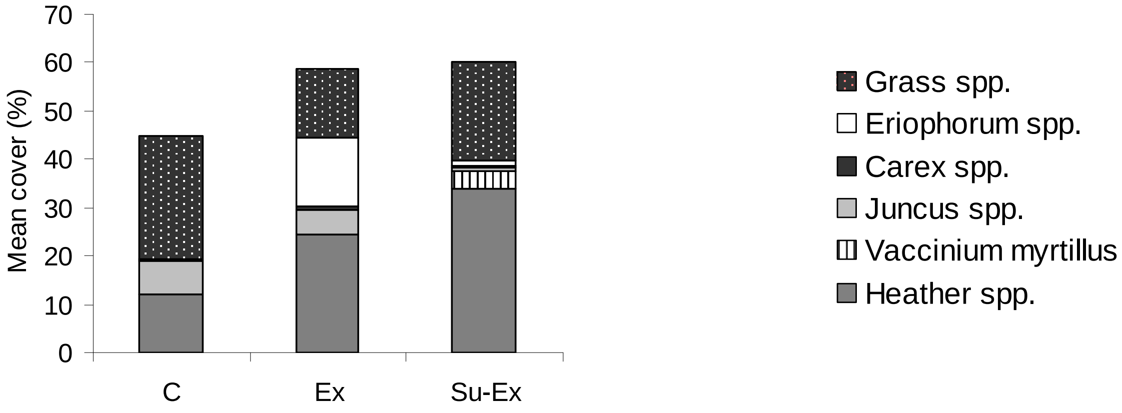
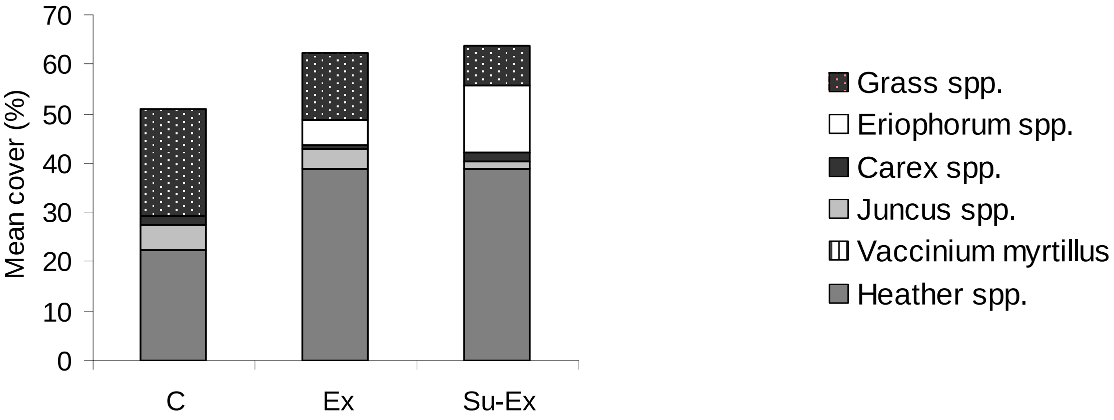


Figure 5.1: Vegetative and non-vegetative cover on 288 transects in 36 restocks subject to differing lengths of fallow period. Restocks grouped by developmental stage: Young, 0-2 years since replanting; Intermediate, 3-5 years since replanting; and Closing-canopy, 6-9 years since replanting. Length of fallow period: C – Control, 2 years fallow; Ex – Extended, 3-5 years fallow; Su-Ex – Super-extended, 6-7 years fallow. No restocks were available for study in the Closing-canopy/Su-Ex fallow group.

a) Young restocks (0-2 years since replanting), n=13



b) Intermediate restocks (3-5 years since replanting), n=14



c) Closing-canopy restocks (6-9 years since replanting), n=9

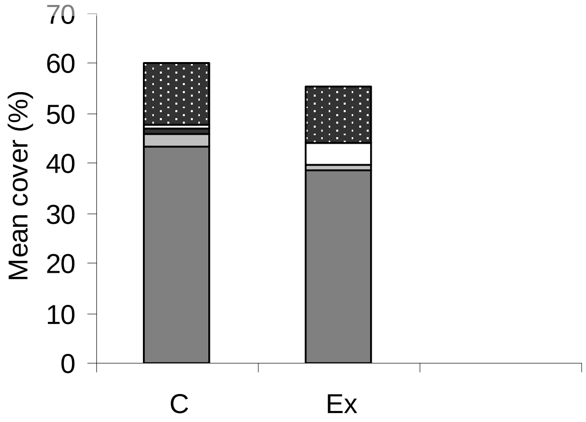


Figure 5.2: a-c) Community composition of vascular component of field-layer vegetation on 288 transects in 36 restocks subject to varying fallow periods in the Sutherland study area. Fallow period groups: C - Control, 2 years fallow; Ex - Extended, 3-5 years fallow; Su-Ex – Super-extended, 6-7 years fallow. No restocks in the closing-canopy/Su-Ex fallow group were available for study.

5.3.1.2 Development of Calluna vulgaris

Calluna vulgaris cover significantly increased with restock age (Table 5.3; Figure 5.3) to a maximum of c.40% between 5 and 6 years. Cover decreased thereafter, as planted tree cover increased. *C. vulgaris* cover was positively related to slope, with greatest cover at a gradient of 8 to 12º (Table 5.3; Figure 5.4).

Table 5.3: GLMM models describing significant effects of an extended fallow period (Fallow group), restock age, management variables and site factors on cover of *C. vulgaris* and brash on 288 transects in 36 restocks in the Sutherland study area

Variable	Parameter	df	F	Direction of effect	Statistical test	R^2#
C. vulgaris	Intercept	1,247	48.318		glmmPQL	0.442
Cover	PT	1,247	0.113	n.s.		
	Fallow group	2,31	2.556	n.s.		
	Restock age	1,31	11.865**	+		
	Restock age^2	1,31	4.455*	∩		
	Slope	1,247	4.809*			
	Slope^2	1,247	5.009*	╮		
	PT x Fallow group	1,247	3.817**	§		
Brash	Intercept	1,251	375.287		glmmPQL	0.400
Cover	PT	1,251	38.303***	UNP>PL		
	Restock age	1,34	18.134***	-		

'Fallow group' levels consist of: Control, 2 years fallow; Extended, 3 to 5 years fallow; Super-extended, 6 to 7 years fallow. PT refers to Planting Type (UNP: Unplanted; PL: Planted). Positive effects of variables upon cover are indicated by + symbols, negative effects by – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols ∩ and ╮ represent the type of curve. See Table 5.2 for description of explanatory variables. § Relationship illustrated by Figure 5.5. # For calculation of R-sq values refer to methods. Levels of significance: ***$P<0.001$, ** $P<0.01$, * $P<0.05$, n.s. $P>0.05$.

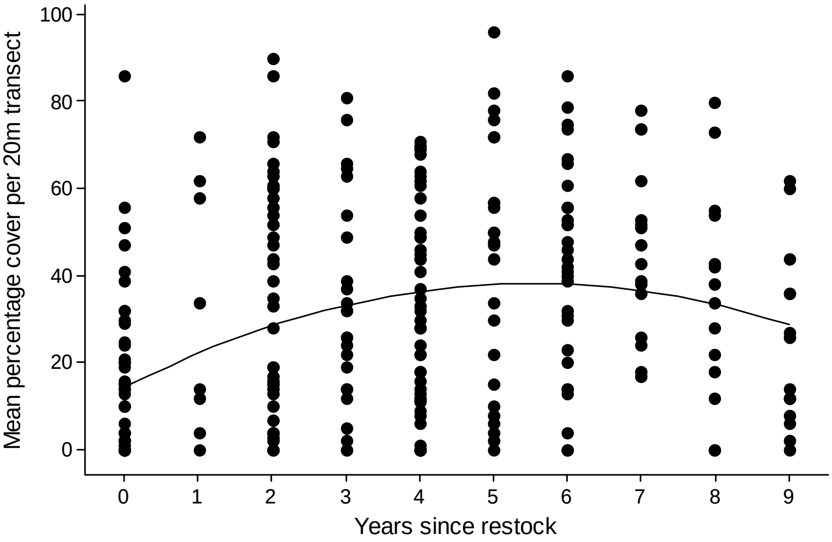


Figure 5.3: *Calluna vulgaris* cover in relation to restock age on 288 transects in 36 restocks in the Sutherland study area (*P*<0.002; Regression equation: *C. vulgaris* cover = (8.647×Restock age)+(-0.782×Restock age^2)+14.35).

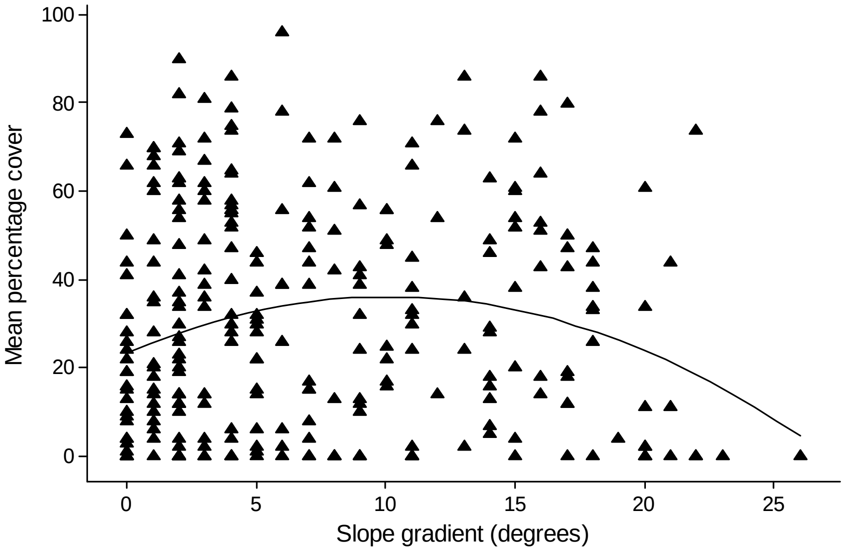
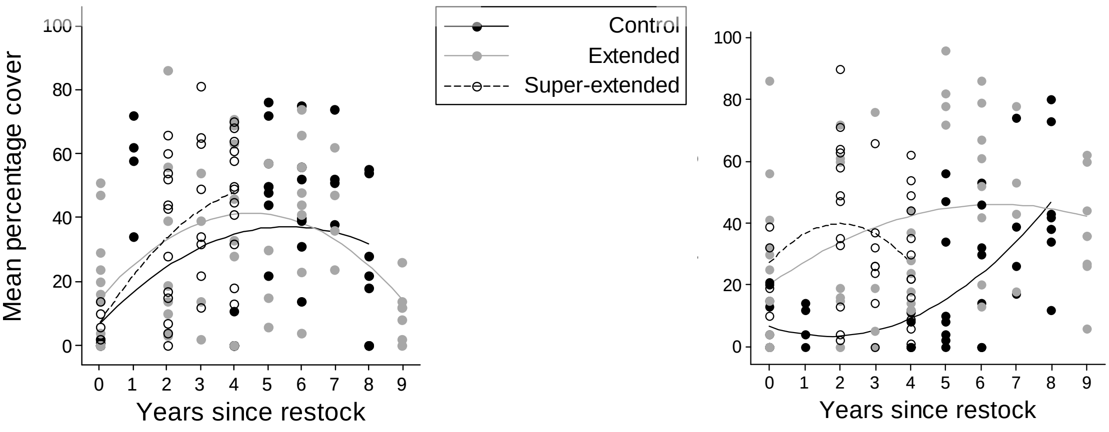


Figure 5.4: *Calluna vulgaris* cover in relation to slope on 288 transects in 36 restocks in the Sutherland study area (*P*<0.026; Regression equation: *C. vulgaris* cover = (2.53×Restock age)+(-0.125×Restock age^2)+23.42.

A significant interaction between Planting Type (planted vs. unplanted) and Fallow group (i.e. fallow period duration) was detected (t_{247}=-2.747, *P*=0.007; Table 5.3; Figure 5.5). In areas left unplanted, ‘Extended’ fallow period restocks had double the *C. vulgaris* percentage cover than Controls at year zero, and cover was greater in all years up to year 8. In planted areas, extended fallow periods also resulted in an increased cover of *C. vulgaris*, however, cover was only greater than in Controls up to year 5 and the difference wasn't as marked. No data were available for 'Super-extended' more than 4 years after restock, however up to this point, *C. vulgaris* cover was greater in the 'Super-extended' than in the 'Extended' or 'Super-extended' fallow groups. The model was a relatively good fit to the data (R^2=0.442).


a) Planted areas of restocks

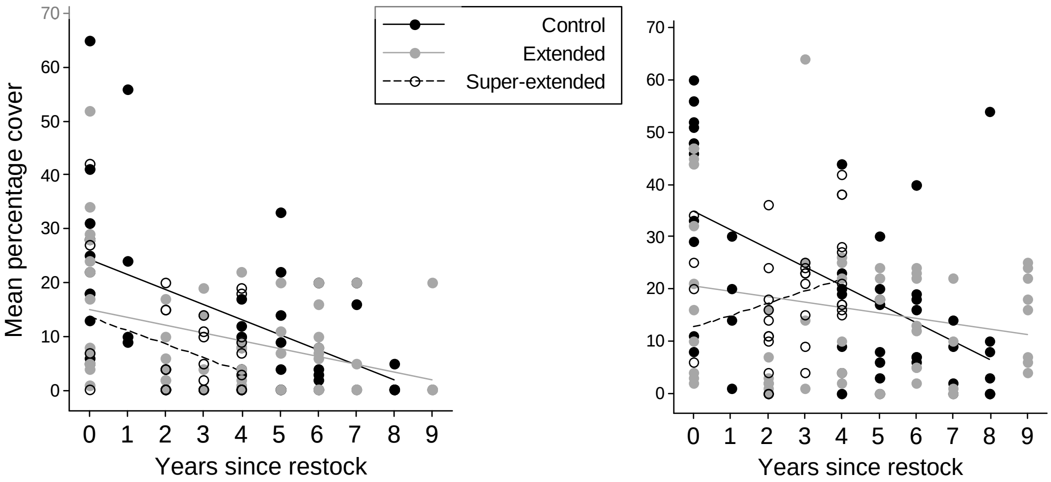
b) Unplanted areas of restocks

Figure 5.5: *Calluna vulgaris* cover in relation to planting type a) Planted and b) Unplanted, and fallow period length (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow) on 288 transects in 36 restocks in the Sutherland study area (Regression equations - a) Planted: *C. vulgaris* cover; Control = (10.770×Restock age)+(-0.959×Restock age^2)+7.030); Extended = (11.900×Restock age)+(-1.325×Restock age^2)+14.68; Super-extended = (16.140×Restock age)+(-1.497×Restock age^2)+7.40. b) Unplanted: *C. vulgaris* cover; Control = (-3.720×Restock age)+(1.091×Restock age^2)+6.541); Extended = (7.995×Restock age)+(-0.617×Restock age^2)+20.23; Super-extended = (12.730×Restock age)+(-3.187×Restock age^2)+27.13).

5.3.1.3 Influence of brash cover on C. vulgaris *development*

Similarly, in the Sutherland study area, brash cover was significantly greater in unplanted areas and decreased as restocks age (Table 5.3; Figure 5.6). Apparent increases in brash cover in unplanted areas are probably an artefact of a relatively small sample of restocks in the 0 and 1 year old 'Super-extended' fallow group.

No statistically significant effect of fallow period was detected ($F_{2,31}$=0.980, P=0.387), however restocks subject to 'Extended' fallow periods had c.17% less brash cover in unplanted areas than Controls in the first year following restock (Figure 5.6b). By year 6 to 7, brash cover levels were the same irrespective of the fallow period length. The R^2 value indicated that the model was a relatively good fit to the data (R^2=0.400).


a) Planted areas of restocks

b) Unplanted areas of restocks

Figure 5.6: Brash cover in relation to planting type a) Planted and b) Unplanted, and fallow period length (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow) on 288 transects in 36 restocks in the Sutherland study area (Regression equations - a) Planted: brash cover; Control = (-2.818×Restock age)+24.34); Extended = (-1.465×Restock age)+14.980; Super-extended = (-2.536×Restock age)+13.600. b) Unplanted: brash cover; Control = (-3.550×Restock age)+34.900); Extended = (-1.022×Restock age)+20.53; Super-extended = (2.310×Restock age)+12.620).

5.3.1.4 Other taxa examined

Eriophorum spp. (*E. vaginatum* and *E. angustifolium*) were recorded on 61 of 288 transects. Variability between restocks was high, mainly due to the majority of transects (60%) with *Eriophorum* present being located in one forest plantation.

There was a significant difference in the likelihood of *Eriophorum* spp. occurrence between fallow period groups (χ^2=12.307, *P*=0.002; Figure 5.7). Restocks subject to 'Extended' and 'Super-extended' fallow periods had a significantly greater likelihood of *Eriophorum* spp. occurrence than Controls (z=-2.158, *P*=0.031 and z=-2.596, *P*=0.009, respectively). There were no differences between 'Extended' and 'Super-extended' fallow period restocks (z=0.867, *P*=0.386).

Eriophorum spp. were also more likely to occur in unplanted than planted areas (χ^2=5.052, *P*=0.025), and in restocks at higher altitude (χ^2=5.438, *P*=0.020). The model fit to the data was relatively good (R^2=0.698).

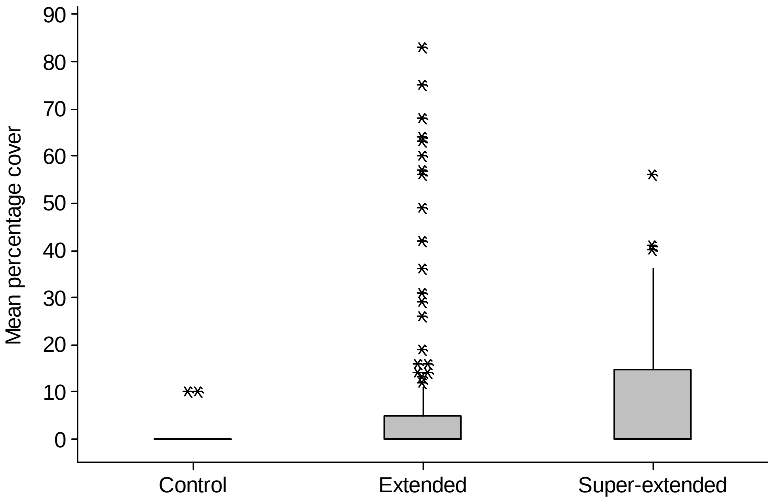


Figure 5.7: Cover of *Eriophorum* species (*E. vaginatum* and *E. angustifolium*) in relation to fallow period length prior to restock (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow) on 288 transects in 36 restocks in the Sutherland study area. Box plots show median (central line at 0), quartiles (box), 5% and 95% centiles (whiskers) and outliers (stars).

Vaccinium myrtillus presence was infrequent, occurring on 13 of 288 transects at 11% (SE± 2.5%) mean cover where present. Although presence was most likely in restocks subject to a 'Super-extended' fallow period compared with those subject to a 'Control' or an ‘Extended’ fallow period, the relationship could not be tested statistically due to infrequent occurrence of the species, which meant there were insufficient data to allow model convergence.

5.3.1.5 Vegetation height

In young restocks, height of heather species (*C. vulgaris, Erica tetralix,* and *E. cinerea*) was greater in restocks subject to an ‘Extended’ fallow period than to a ‘Control’ fallow period ($t_{27}=2.473$, $P=0.020$), but in older restocks, the reverse was recorded (Table 5.4; Figure 5.8). Heather was taller in restocks where the previous crop was pine (Table 5.5), but did not exceed 40 cm in height until 6 to 9 years after restock, irrespective of the fallow period duration or effects of management or site factors (Figure 5.8).

Graminoids (*Juncus*, *Carex*, *Eriophorum* spp. and grasses) were c.20 cm taller in restocks subject to a ‘Control’ than a ‘Super-extended’ fallow period, but only in unplanted areas ($t_{208}=-2.335$, $P=0.021$; Table 5.4) and generally remained between 55 cm and 80 cm from restocking to the onset of canopy closure.

5.3.1.6 Field-layer density

There was no effect of fallow period length on field-layer density ($F_{2,31}=1.88$, $P=0.169$). Density increased with restock age ($F_{1,34}=32.604$, $P<0.001$) and was greater in planted than unplanted areas ($F_{1,251}=18.751$, $P<0.001$). The model provided a reasonable fit to the data ($R^2=0.492$).

Table 5.4: GLMM models describing significant effects of an extended fallow period (Fallow group), restock age, management variables and site factors on height of heather and graminoids on 288 transects in 36 restocks in the Sutherland study area

Variable	Parameter	df	F	Direction of effect	Statistical test	R^2#
Heather Height	Intercept	1,195	870.802		lme	0.569
	Restock age	1,27	29.279***	+		
	Fallow group	2,27	0.648	n.s.		
	Previous crop	1,27	4.600*	Pine> Spruce		
	Restock age x Fallow group	2,27	3.475*	§		
Graminoid Height	Intercept	1,208	521.550		lme	0.381
	PT	1,208	2.562	n.s.		
	Fallow group	2,33	0.799	n.s.		
	PT x Fallow group	2,208	2.957(*)	§^{1}		

'Fallow group' levels consist of: Control, 2 years fallow; Extended, 3 to 5 years fallow; Super-extended, 6 to 7 years fallow. PT refers to Planting Type (UNP: Unplanted; PL: Planted). Positive effects of variables upon cover are indicated by + symbol. Heather comprises *C. vulgaris, Erica tetralix,* and *E. cinerea*. Graminoids comprise grasses, *Eriophorum, Juncus* and *Carex* spp. See Table 5.2 for description of explanatory variables. § Relationship illustrated by Fig. 5.8. §^{1} see text. # For calculation of R^2 values refer to methods. Levels of significance: ***$P<0.001$, ** $P<0.01$, * $P<0.05$ (*)$P=0.05$, n.s. $P>0.05$.

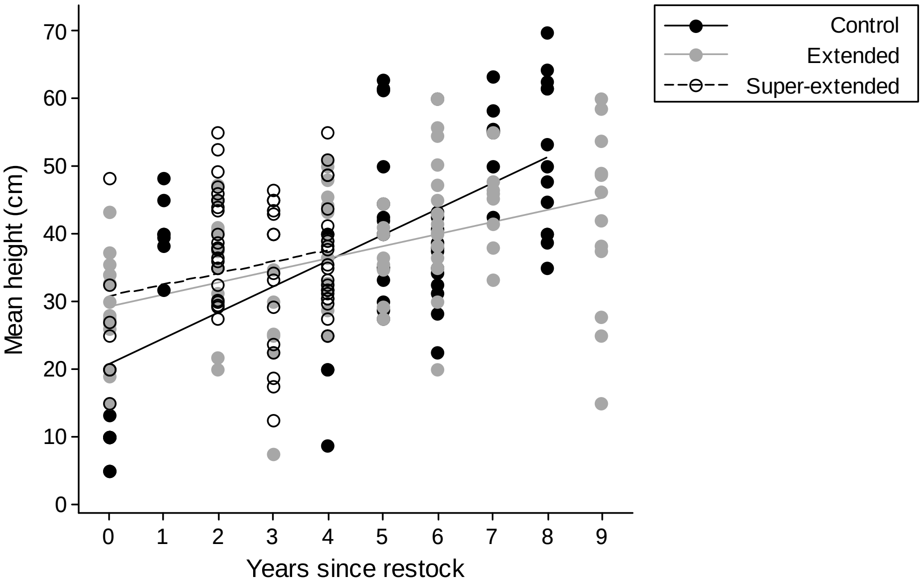


Figure 5.8: Height of heather (*C. vulgaris, Erica tetralix,* and *E. cinerea*) according to fallow period length (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow) on 288 transects in 36 restocks in the Sutherland study area (Regression equations - heather height: Control = (3.82×Restock age)+20.8); Extended = (1.78×Restock age)+29.37; Super-extended = (1.71×Restock age)+30.78).

5.3.2 Invertebrate abundance

A total of 17 714 invertebrates of >2 mm body length were captured during the trapping period in 2009. Of the 7 taxa identified as important in the diet of black grouse chicks (see methods) and used in statistical analyses, 7875 were recorded in pitfall traps (3192 beetles, 1716 arachnids, 1568 ants, 920 true flies, 406 true bugs, 55 Lepidoptera larvae and 18 Tipulids), and 1830 in suction traps (1146 true bugs, 397 true flies, 195 arachnids, 58 beetles, 27 ants, 4 Tipulids and 3 Lepidoptera larvae. The additional sweep netting method captured a total of 6779 invertebrates comprising 2844 true bugs, 1862 true flies, 848 beetles, 575 arachnids, 278 ants, 221 Lepidoptera larvae and 151 Tipulids.

The remaining 1230 invertebrates comprised Acari, Isopoda, Myriapoda, adult Lepidoptera, Trichoptera and terrestrial larvae species. Orthoptera comprised only three individuals and were not considered in statistical analysis. Symphyta larvae were not recorded at the study site.

5.3.2.1 Performance of statistical models to assess taxa response

Restock age, management and site variables explained between 21 and 68% of the variation in taxa abundance (Model 1; Table 5.5). For six of the seven taxa studied, vegetation variables explained 55 to 68% of the variation in taxa abundance (Model 2; Table 5.6). No vegetation variables were retained in the model for true flies, as also found in The Trossachs study area (Chapter 4, Table 4.4). When significant site and management variables from Model 1 were added into Model 2 to create Model 3 (Table 5.7), explained variation in abundance decreased for most taxa, for reasons described in Chapter 4 (section 4.3.2).

Table 5.5: Taxon response to restock age, management variables and site factors (Model 1). Significant relationships listed in order ($P<0.05$; most highly significant first).

Taxon	Model 1 parameter	R^2
Beetles^{P}	Distance from edge╰, Altitude^{-}, PT (UNP>PL)	0.594
Arachnids^{P}	Distance from edge ╰, Altitude$^{\cap}$	0.207
Ants^{P}	Restock age^{+}, Previous crop (Pine>Spruce)	0.488
Lepidoptera larvae^{SW}	Restock age$^{\cap}$, Open space^{+}, Altitude^{-}	0.338
True bugs^{S}	PT (PL>UNP)	0.677
True flies^{S}	PT (PL>UNP)	0.344
Tipulids^{SW}	Restock age^{+}	0.518

Arachnids group comprises spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap, ^{SW} by sweep net. Positive effects of variables upon taxa abundance are indicated by superscript + symbols, negative effects by – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols ∩ and ╰ represent the type of curve. For calculation of R^2 values see methods. PT refers to Planting Type (UNP: Unplanted; PL: Planted). See Table 5.2 for description of explanatory variables.

Table 5.6: Taxon response to restock vegetation (Model 2). Significant relationships listed in order ($P<0.05$; most highly significant first).

Taxon	Model 2 parameter	R^2
Beetles^{P}	Moisture score╰, Dwarf shrub cover$^{\cup}$	0.675
Arachnids^{P}	Dwarf shrub cover^{-}	0.594
Ants^{P}	Dwarf shrub cover$^{\cap}$	0.551
Lepidoptera larvae^{SW}	Dwarf shrub cover^{+}, Vegetation height^{+}	0.663
True bugs^{S}	Graminoid cover╭, Moisture score^{-}	0.671
True flies^{S}	NA	NA
Tipulids^{SW}	Dwarf shrub cover^{-}, Vegetation height^{+}	0.558

Arachnids group comprises spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap, ^{SW} by sweep net. 'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999): wetter habitats have a higher score. Positive effects of variables upon taxa abundance are indicated by superscript + symbols, negative effects by – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols ∪ ∩ ╰ and ╭ represent the type of curve. For calculation of R^2 values see methods. See Table 5.2 for description of explanatory variables. NA denotes no significant variables in model.

5.3.2.2 Invertebrate response to vegetation variables and restock management

Fallow period length (categorised by the 'Fallow group' variable) did not significantly affect the abundance of any invertebrate taxon considered. However, abundance of most taxa was influenced by the proportion of dwarf shrub cover, although the effect size was relatively small (Model 3; Table 5.7). *C. vulgaris*, which comprised the majority of dwarf shrub cover in Sutherland restocks, increased with extended fallow periods (in unplanted areas; section 5.3.1.2). This suggests that although the 'Fallow group' variable was adequate for assessing changes in vegetative field-layer cover, it may not have detected more subtle and localised changes in invertebrate abundance.

The relationship between dwarf shrub cover and ground-active invertebrates caught in pitfall traps varied among taxa; arachnid catches decreased, ant captures were highest at c.40% cover, and beetle catches were greatest at either relatively low or relatively high dwarf shrub cover (Table 5.7; Figure 5.9). For taxa more associated with field-layer vegetation, increased dwarf shrub cover was negatively associated with the abundance of Tipulids but positively associated with the abundance of Lepidoptera larvae (Table 5.7; Figure 5.10). Larval abundance was twice as high in areas with 70% dwarf shrub cover when compared with areas with only 10% cover, although capture numbers were relatively low at c.4 per transect. Larval abundance was also greater in areas with more structural open space (i.e. less trees) and in restocks at lower altitude (Table 5.7).

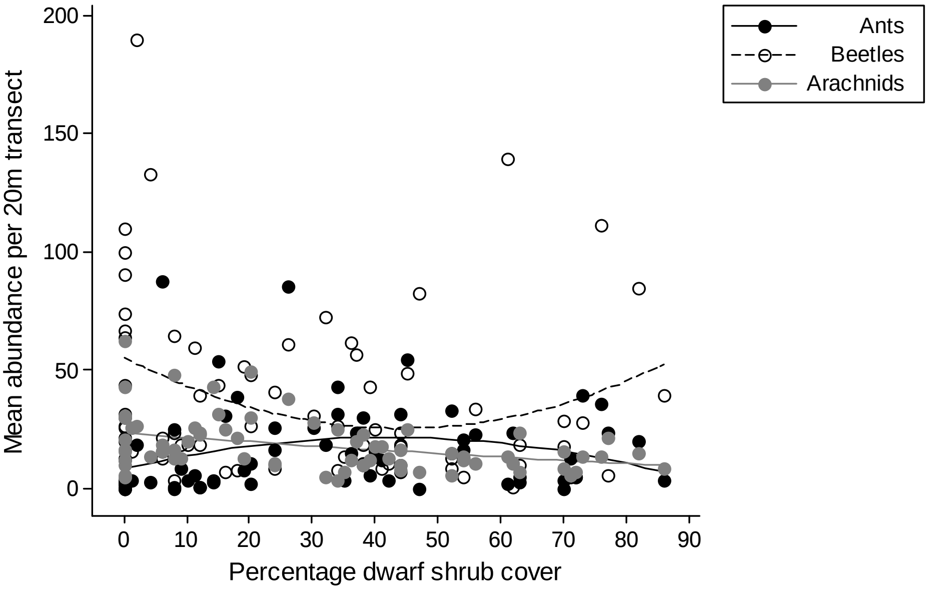


Figure 5.9: Abundance of ground-active taxa in relation to dwarf shrub cover (predominantly *Calluna vulgaris*, but also *E. tetralix*, *E. cinerea*, and *V. myrtillus*) on 72 transects in 36 restocks in the Sutherland study area. (Regression equations – Ant abundance = (0.630×Restock age)+(-0.007×Restock age^2)+8.583); Beetle abundance = (-1.358×Restock age)+(-0.015×Restock age^2)+55.520; Arachnid abundance = (-0.189×Restock age)+(0.0003×Restock age^2)+23.560). Mean abundance calculated by summing 2 pitfall traps per transect, with 4 weeks of trapping data pooled.

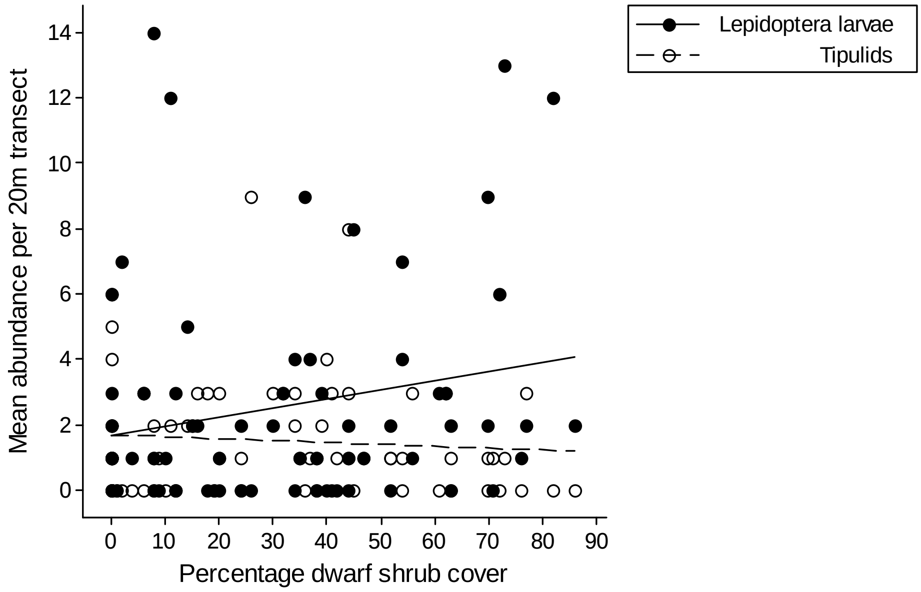


Figure 5.10: Abundance of Lepidoptera larvae and Tipulids in relation to dwarf shrub cover (predominantly *Calluna vulgaris*, but also *E. tetralix*, *E. cinerea*, and *V. myrtillus*) on 72 transects in 36 restocks in the Sutherland study area. Mean abundance calculated by pooling 5 sweep net samples, collected weekly. (Regression equations – Lepidoptera larvae abundance = (0.028×Restock age)+1.688); Tipulid abundance = (-0.006×Restock age)+1.692).

As reported in the Trossachs, restock age was also relatively strongly related to Tipulid and ant abundance, which increased from restocking, whereas Lepidoptera larvae abundance peaked after c.5 years, then decreased (Table 5.7).

The abundance of true bugs was related to graminoid cover rather than dwarf shrub cover (Table 5.7); abundance increased up to about 50% cover, levelling off thereafter. More true bugs and beetles were captured in areas with a low Ellenberg moisture score, indicating a preference for drier habitat conditions, although a small proportion of beetles was also found in relatively wet habitats (Table 5.7). The Ellenberg moisture score (which reflects habitat moisture) was relatively strongly related to the abundance of both taxa.

The previous first-rotation crop had a relatively large effect upon the abundance of ants, which were significantly more abundant where the previous crop was pine (Table 5.7). Planted areas contained significantly more true flies than unplanted areas (Table 5.7), but true fly abundance was not related to any of the restock vegetation variables measured.

Table 5.7: Minimum adequate GLMM models describing the abundance of invertebrate taxa preferred by black grouse in relation to significant time, management, site and vegetation variables on 72 transects in 36 restocks in the Sutherland study area. The table reports the overall minimum adequate model (Model 3) constructed by stepwise addition of significant variables from a restock age/management/site variables model (Model 1; Table 5.5) to a vegetation model (Model 2; Table 5.6).

Taxon	Model 3 Parameters	Estimate	SE	df	t value	Direction of effect	Statistical test	Model 2 R^2#	Model 3 R^2#
Beetles	Intercept	27.271	6.727	35	4.054		glmmPQL	0.675	0.675
	Moisture score	-6.985	2.053	32	-3.403**				
	Moisture score^2	0.512	0.155	32	3.300**	◟			
	Dwarf shrub cover	-0.029	0.011	32	-2.716*				
	Dwarf shrub cover^2	<0.001	<0.001	32	2.373*	∪			
Arachnids	Intercept	1.852	0.602	33	3.078		glmmPQL	0.594	0.466
	Dwarf shrub cover	-0.009	0.002	33	-3.921***	-			
	Distance from edge	<-0.001	<0.001	33	-1.506$^{\text{n.s.}}$				
	Distance from edge^2	<0.001	<0.001	33	2.309*	◞			
	Altitude	0.021	0.008	33	2.537*				
	Altitude^2	<0.001	<0.001	33	-2.763**	∩			
Ants	Intercept	1.901	0.317	34	5.992		glmmPQL	0.551	0.487
	Dwarf shrub cover	0.036	0.015	34	2.371*				
	Dwarf shrub cover^2	<-0.001	<0.001	34	-2.373*	∩			
	Restock age	0.207	0.055	33	3.786***	+			
	Previous crop	-0.824	0.285	33	3.786***	Pine>Spruce			

Table 5.7: *Continued.*

Taxon	Model 3 Parameters	Estimate	SE	df	t value	Direction of effect	Statistical test	Model 2 R^2#	Model 3 R^2#
Lep. Larvae	Intercept	-1.601	0.720	34	-2.223		glmmPQL	0.633	0.435
	Dwarf shrub cover	0.009	0.004	34	2.154*	+			
	Open space	0.055	0.011	32	4.991***	+			
	Restock age	0.616	0.181	32	3.410**				
	Restock age^2	-0.062	0.021	32	-3.026**	∩			
	Altitude‡	-0.009	0.003	34	-3.017**	-			
Tipulids	Intercept	-0.602	0.420	34	-1.434		glmmPQL	0.558	0.522
	Dwarf shrub cover	-0.014	0.005	34	-2.923**	-			
	Vegetation height	0.009	0.003	34	2.642*	+			
	Restock age	0.175	0.063	34	2.752**	+			
True bugs	Intercept	5.602	1.725	35	3.247		glmmPQL	0.671	0.671
	Moisture score	-0.706	0.288	33	-2.452*	-			
	Graminoid cover	0.062	0.017	33	3.686***				
	Graminoid cover^2	<-0.001	<-0.001	33	-2.345*	(			
True flies	Intercept	1.776	0.118	35	14.991		glmmPQL	NA	NA
	PT	-0.542	0.178	35	-3.054**	PL>UNP			

Arachnids group comprises spiders and harvestmen. 'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999): wetter habitats have a higher score. Restock age/management/site variables italicised. PT refers to Planting Type (UNP: Unplanted; PL: Planted). See Table 5.2 for further variable descriptions. Positive effects are indicated by + symbols, negative effects by – symbols. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, symbols ∩ ∪) (represent the type of curve. NA indicates no significant Model 2 vegetation variables (Table 5.6) to formulate Model 3. ‡ Altitude replaced the 'vegetation height' variable. # For calculation of R-sq values refer to methods. Levels of significance: ****P*<0.001; ** *P*<0.01; * *P*<0.05.

5.3.3 Abundance of potential black grouse predators in restocks

A total of 31 observations of potential avian predators to black grouse, their chicks or eggs were recorded, predominantly corvids (18 observations of carrion crow *Corvus corone*, 7 of raven *C. corax*), and 6 of common buzzard *Buteo buteo*. Fallow period length (categorised by the 'Fallow group' variable) had no influence on the number of avian predators sighted (χ^2= 6.378, *P*=0.351; Figure 5.11).

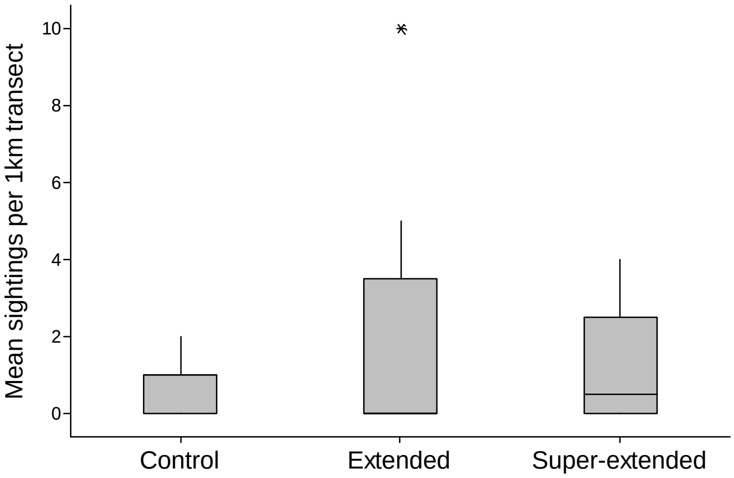


Figure 5.11: Number of sightings of potential avian predators of black grouse recorded in restocks subject to differing lengths of fallow period (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow), assessed monthly between May and August 2009 along a fixed 1 km transect in 24 restocks in the Sutherland study area, with monthly data pooled for each transect. Box plots show median (central line), quartiles (box), 5% and 95% centiles (whiskers) and outliers (starts).

A total of 109 mammalian (red fox *Vulpes vulpes* and pine marten *Martes martes*) scats were recorded. Fallow period length had a significant effect upon the numbers of mammalian scats recorded in restocks (χ^2= 10.760, *P*=0.024; Figure 5.12), with five times as many scats recorded in restocks subject to an 'Extended' and 2.5 times as many scats in 'Super-extended' fallow restocks, when compared with controls. Numbers of mammalian scats also differed according to restock age (z=22.256, *P*<0.001), most commonly recorded in restocks between four and five years old.

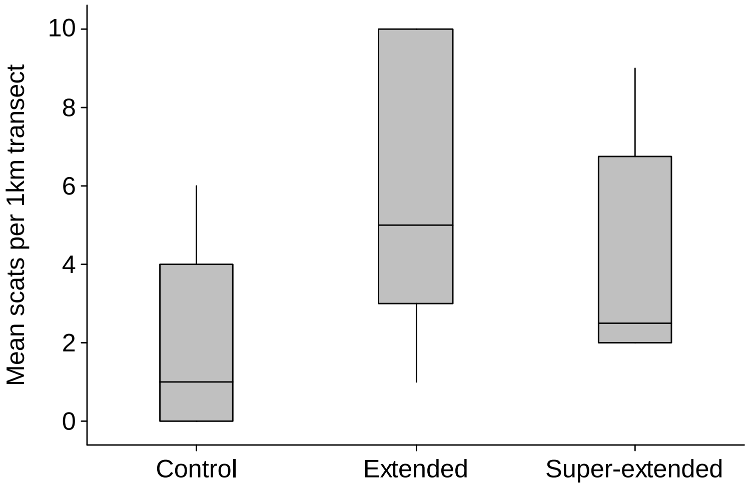


Figure 5.12: Number of scats of mammalian predators of black grouse recorded in restocks subject to differing lengths of fallow period (Control, 2 years fallow; Extended, 3-5 year fallow; Super-extended, 6-7 years fallow), assessed monthly between May and August 2009 along a fixed 1 km transect in 24 restocks in the Sutherland study area, with monthly data pooled for each transect. Box plots show median (central line), quartiles (box), 5% and 95% centiles (whiskers).

5.5 Discussion

Findings suggest that extending the fallow period in restocks from the standard two years, to between three and five years, resulted in significant increases in the cover of *C. vulgaris* (particularly in unplanted areas), and increased the occurrence of *Eriophorum* spp.. Extending the fallow period further to between six and seven years did not result in significant further cover of *C. vulgaris* or occurrence of *Eriophorum* spp., however the period during which suitable restock habitat was available to black grouse prior to canopy closure was increased. No direct effect of fallow period length upon invertebrate abundance was detected, however, abundance of most taxa was associated with the proportion of dwarf shrub cover (which was predominantly composed of *C. vulgaris*). Although an extended fallow period appears to improve field-layer habitat for black grouse in restocks, results suggest that a more attractive habitat may also inadvertently be created for mammalian predators.

5.4.1 Extended fallow periods, dwarf shrubs and Lepidoptera larvae

Unplanted areas of restocks are likely to provide the most suitable black grouse habitat in restocks in both the short- and long-term. As *C. vulgaris* cover in planted areas starts to decrease with the onset of canopy closure, cover in unplanted areas of restocks subject to an extended fallow period is double that in restocks subject to a standard fallow period, which represents an increased cover of heather to black grouse for an extended amount of time. Furthermore, this cover will remain available after canopy closure of the planted crop.

Presence of the dwarf shrub *Vaccinium myrtillus* was scarce in all restocks surveyed in Sutherland, as also reported in restocks in The Trossachs (see Chapter 3). There may be a number of reasons for its infrequency, which are described in detail in Chapter 3 (section 3.4). In restocks with an extended fallow period of six to seven years, there was an indication that occurrence of *V. myrtillus* may be increased, but records were so infrequent that statistical analysis was not possible.

Dwarf shrubs are an important component of black grouse habitat, providing roosting and nest cover (Parr & Watson 1988) and representing a significant part of the adult diet (Picozzi & Hepburn 1984; Cayford 1990b), particularly in late-autumn and winter (Starling-Westerberg 2001; Baines 1994). Black grouse utilise habitat containing dwarf shrubs adjacent to or within commercial forests (Cayford *et al.* 1989; Haysom 2001), particularly where timber crops have failed and tree canopy cover is reduced to between 15 and 40% (Cayford 1990b). Lepidoptera larvae, a key food item for black grouse chicks (see Chapter 4, Table 4.1) were found to be positively associated with dwarf shrub cover and taller vegetation in restocks in this study, as also reported by other studies conducted on upland moorlands in Britain (Webb 1989; Fielding 1992; Coulson 1988). Haysom & Coulson (1998) reported an increase in Lepidoptera larvae abundance in older 'building' and 'mature' phases of *Calluna* growth, and increased species diversity in taller stands, which may also contain larger larvae (Niewold 1990). In this study, restocks subject to extended fallow periods contained taller heather than standard fallow restocks (by c.7 cm), but only for the first four years after restock, and, irrespective of the fallow period, heather did not exceed 40 cm in height until six years after restock. Previous studies suggest a height of 40 to 55 cm to be suitable for black grouse nest cover (Grant & Dawson 2005), thus it is unlikely that restocks provide suitable nest sites in heather stands until at least year seven after restock, although graminoids are likely to be of a suitable height and cover much earlier than this.

5.4.2 Response of other invertebrate taxa to changes in field-layer vegetation

Tipulids are commonly recorded in the diet of upland moorland birds (Buchanan *et al.* 2006; Pearce-Higgins *et al.* 2005), so a negative relationship with dwarf shrub cover was unexpected and difficult to interpret. As described in Chapter 4 (section 4.4), changes in abundance of other taxa are most likely to reflect species turnover as dwarf shrub and other field-layer species cover increases with restock age - from open-habitat specialists to forest-edge specialists (Heliölä *et al.* 2001).

Extended fallow periods resulted in a greater occurrence of *Eriophorum* species, particularly in unplanted areas, which are left un-drained, providing suitable wet flushes and acid-bog conditions (Phillips 1954). Previous studies have indicated the importance of flushes or damp/tall grassy habitat within brood habitat (see Grant and Dawson 2005 for a review) possibly due to an increased abundance of invertebrates in these areas.

However, in this study there was no evidence that invertebrate abundance was increased in wetter habitats. The drainage of planted areas of restocks means that naturally occurring wet flushes are unlikely to occur, and steep-sided man-made drains are likely to be a cause of mortality for chicks in these areas. Findings from a Welsh radio-tagging study investigating the mortality of black grouse chicks demonstrated that a small proportion of tagged chicks had died from starvation and/or hypothermia after falling in to deep-sided forest drains (RSPB, unpubl.). Subsequent habitat management included the collapse of drains using a mechanical digger or the cutting back of overhanging vegetation 2 m either side of the length of the drain.

5.4.3 The importance of open space in restocks

Extended fallow periods allowed additional time for brash to degrade and for *C. vulgaris* cover to develop prior to canopy closure of the planted crop, after which areas of suitable habitat for black grouse remain in unplanted areas. This differs from first rotation crops, where trees were planted up to the edges of watercourses, and little open space was left unplanted (Avery & Leslie 1990). In these plantations, the closure of the tree canopy left only small areas of suitable habitat for black grouse, which possibly contributed to population decreases and range contraction in Scotland (Pearce-Higgins *et al.* 2007). In the present study, on average, 40% of ground was left as unplanted open space in restocks, which had a greater cover of *C. vulgaris* (particularly in restocks subject to an extended fallow period) but also an increased abundance of Lepidoptera larvae. Restocks in The Trossachs had similar proportions of open space (c.38%; Chapter 3), which were associated with an increased abundance of ants. Well-established stands of *C. vulgaris* in these areas provide seed to third-rotation restocks, which may rely upon seed rain for heather re-establishment (Eycott *et al.* 2006), as the

C. vulgaris seed bank is unlikely to persist under more than one timber crop rotation (Hill & Stevens 1981; Hill 1986; Owen, pers. obs.) unless it is sufficiently well-replenished by seed production during the second rotation establishment stage. Whether the suitability of habitat for black grouse created in areas left unplanted can be attributed to forest management, or alternatively, due to the 'type' of areas that are initially selected to be left unplanted, mean that the specific cause for suitability is difficult to establish. Leaving an area of a restock unplanted will not necessarily result in greater *C. vulgaris* recovery as environmental factors such as soil type and moisture content, fundamental environmental factors for vegetation growth, will underpin plant community re-establishment in restocks, as discussed previously (see 3.4.5).

5.4.4 Performance of statistical models

Changes in field-layer vegetation resulting from extended fallow periods are likely to induce knock-on effects in the invertebrate community. All taxa were significantly affected by an increase in dwarf shrub cover as restocks aged (with the exception of the true bugs and true flies), however no significant differences were detected when comparing the abundance of each invertebrate taxon between restocks with differing lengths of fallow period. This suggests that changes in abundance of invertebrate taxa may have been detected at different spatial scales, i.e. detected by the more 'sensitive' and localised dwarf shrub cover variable collected at the transect level, but not detected by the 'fallow period length' management variable at the restock level. This variable may also have been less effective in detecting change in invertebrate abundance due to the small sample size of restocks from which data were collected. Additionally, 'restock age' and 'fallow group length' variables may have been confounded in statistical analyses; as extended fallow periods were introduced in Sutherland in the late

1990's, young restocks with standard fallow periods are fairly uncommon, and restocks subject to a six to seven year fallow period are mostly still under four years old. As a result, sample sizes of both groups were insufficient in analyses, and significant effects of fallow period length may have been missed.

5.4.5 Restock habitat modification and predator abundance

In commercial conifer forests in Britain, small mammals are a principal component in the diet of pine marten (Caryl 2009) and red fox (O'Mahony *et al.* 1999). An increase in the abundance of small mammals such as field voles *Microtus agrestis* (Petty 1999) may occur in restocks with extended fallow periods as a result of changes to field-layer vegetation, which in turn may attract more predators into these restocks. Abundance of small mammals was not directly assessed in this study, however there was no clear explanation why restocks with extended fallow periods should attract more small mammals and subsequently, more mammalian predators. Abundance of small mammals is positively influenced by increased structural heterogeneity and taller vegetation in managed forests (Ecke *et al.* 2002), however neither of these effects were recorded in restocks with an extended fallow period.

Increased mammalian abundance may be linked with factors not assessed by this study, such as geographical location of restocks or physical aspects of transect location, including track width, presence of linear habitat features, level of human disturbance, etc., which require further investigation. Nonetheless, the period when habitat in restocks may be most attractive to black grouse - around years five to six - during which cover of *C. vulgaris* is optimum and abundance of Lepidoptera larvae is greatest, is also when mammalian scats were recorded most frequently in restocks.

Habitat in restocks created by extended fallow periods was not related to an increase in the observation of avian predators of black grouse. The most frequently recorded predator was the carrion crow *Corvus corone* which will consume eggs and chicks, and may influence breeding productivity of black grouse (Summers *et al.* 2004). Crows are unlikely to be attracted by changes in ground vegetation to the same extent as terrestrial mammalian predators, although changes may influence nest detection.

5.4.6 Management conclusions

Generally, results suggest that further extending the fallow period from three to five years (extended), to six to seven years (super-extended), had no further significant effect upon field-layer vegetation commonly used by black grouse. However, the 'super-extended' fallow period represents an increase in the amount of time that suitable open-ground habitat is available to black grouse prior to canopy closure of planted trees. As this further extension does not seem to influence predator abundance, it is likely to be the most beneficial for black grouse. Further research is necessary however, as the 'super-extended' group comprised a relatively limited dataset, as older (>4 years old) super-extended fallow restocks were not yet available for study.

Management methods applied to increase the cover of dwarf shrubs and prolong their availability as a mature stand are likely to result in the increased abundance of Lepidoptera larvae and ants in restocks, which are key food items and make up a large proportion of the diet of black grouse in other British studies (Picozzi, 1986; Cayford *et al.* 1989). Although larval abundance appeared to be low on transects in this study, food items in shorter supply can often be highly selected for by grouse chicks, and food abundance does not necessarily indicate chick preference. For example, in commercial forestry plantations in Wales, fewer Lepidoptera larvae were recorded per pitfall trap from a brood's home range than in this study, yet they were highly selected by chicks, and comprised 33% of the diet (Cayford *et al.* 1989).

Forest restock management must take into account many factors, including the economical production of timber, reduction of chemical usage, and habitat requirements of protected wildlife species. Delayed planting involves a number of direct cost implications, such as higher site preparation costs for planting due to increased vegetation growth, but also indirect costs, including increased incidences of heather check on planted trees (particularly Sitka spruce) and the slower growth of planted trees that may result from asynchrony between brash nutrient release and critical tree growth stages (Proe *et al.* 1999).

Benefits to black grouse populations will mainly be gained by long-term maintenance of unplanted areas, including un-drained locations that are likely to develop cover of *Eriophorum* species. Extended fallow periods will contribute in the short-term by generally increasing heather cover in restocks, with subsequent increases in the abundance of some invertebrate food items preferred by black grouse. For black grouse populations that rely on patches of commercial forestry, these management options may be critical.

Chapter 6: Differences in habitat and invertebrate availability to black grouse between leks and restocks

6.1 Introduction

Habitat quality can be critical in influencing the survival of black grouse and their broods (Cayford 1993). Black grouse require a diverse mosaic of habitats depending on seasonal requirements, including *Calluna* moorland for feeding, nesting, roosting and cover from predators, forests with an understory of dwarf shrubs such as bilberry *Vaccinium myrtillus*, and wet moors with cotton-grass *Eriophorum* spp. and mature deciduous trees, particularly birch *Betula* spp., from which catkins and twigs are eaten in winter when snow covers the ground (see Baines 1995 for a review). Prior to breeding, hens utilise habitats with vegetation that provides a protein- and energy-rich food source, such as cotton grass *Eriophorum* species (Baines 1994; Starling-Westerberg 2001), which are likely to improve body condition and subsequent breeding success (Watson & Moss 2008). Nesting habitats are selected that provide adequate vertical cover by species such as heather *Calluna vulgaris*, at a density that also allows easy movement for hens with broods (Erikstad 1985), with tall vegetation in wet flushes, which often contain an invertebrate-rich food source for chicks (Picozzi & Hepburn 1984; Cayford 1990b). Adult birds also utilise tall field-layer vegetation for cover from predators, particularly when moulting (Parr & Watson 1988).

The ‘lek’ mating system exhibited by black grouse, whereby males display and fight to mate with females on small territories at lek sites, takes place at traditional sites where males return each spring (Watson & Moss 2008). Both males and females are relatively sedentary (Toms 2002; Cramp & Simmons 1980) and generally remain within a few kilometres of the lek throughout the year (Cayford 1993), with hens often nesting within 1 km of the lek (Robel 1969a; Picozzi, 1986). The home range of broods after leaving the nest is often relatively small (30 to 60 ha: Wegge *et al.* 1982; under 50 ha: Starling 1990), although some broods travel large distances in a day within the range (Cayford *et al.* 1989; Haysom 2001). Movements of some broods have been recorded as up to 5.6 km in a 7-day period (Wegge *et al.* 1982), which may be related to poorer habitat quality and the need to travel further to locate suitable invertebrate densities (Erikstad 1985). The home range of adults is larger and likely to contain both moorland and forest (Robel 1969b). In north-east of Scotland, the home range of individual radio-tracked males varied between c.3 and 6.9 km^2 (Robel 1969b), however much smaller home ranges for groups of lekking males, as little as 1 to 2 km^2, are often recorded (Watson & Moss 2008). Females are more mobile, but generally have a home range of c.5 km^2 (Watson and Moss 2008). As black grouse appear to be selective in their habitat use (Haysom 2001; Picozzi 1986; Cayford *et al*. 1989) and remain relatively close to the lek, it is likely that this habitat contains field-layer vegetation and invertebrates suitable for all life stages. Consequently, management for black grouse is often focussed at the lek scale; habitat within 1.5 km^2 of known leks is often targeted by management (Calladine 2002).

Research from this study has suggested that second rotation restocks located on the edge of commercial plantations, or connected to the edge by open habitat, often contain field-layer vegetation suitable for black grouse adults and broods (Chapter 3), and that invertebrates preferred by chicks are commonly recorded in these restocks (Chapters 4 and 5). However, measurements of vegetation and invertebrate abundance in restocks are difficult to interpret and place into context without comparable data from habitat in the vicinity of leks. Therefore, this chapter aims to quantify the cover, height and density of field-layer vegetation and to assess the abundance of invertebrates preferred by black grouse chicks in two habitats: i) areas within 1 km of leks, and ii) second rotation restocks. By quantification of field-layer vegetation and invertebrate provision to black grouse around leks (which are likely to represent suitable habitat), the comparative quality of second rotation restocks can be gauged.

6.2 Methods

6.2.1 Field data collection

6.2.1.1 Field-layer vegetation sampling

Sampling took place in 72 restocks and in habitat surrounding 8 black grouse leks in The Trossachs and Sutherland study areas, (see Chapter 2 for study area information and map) along a total of 701, 20 m transects (Appendix Table 2). Thirty-six restocks and 3 leks were sampled in The Trossachs study area and 36 restocks and 5 leks in Sutherland (Table 6.1). Restocks were aged between 0 and 9 years since re-planting. Vegetation sampling was conducted between May and September, 2009.

Table 6.1: Sample size and site characteristics of restocks and leks in The Trossachs and Sutherland study areas.

Study area	No. of restocks	No. of leks	Mean altitude m a.s.l. (range)	Mean slope (degrees (range)
Trossachs	36	3	265 (150-262)	16 (0-27)
Sutherland	36	5	168 (160-298)	7 (0-20)

See Chapter 2 for further description of study areas and Appendix Table 2 for transect information.

In restocks, stratified random sampling was used for transect placement, with 288 transects located in Sutherland and 337 transects in The Trossachs. Transects were located more than 100 m apart and no less than 50 m from the restock edge. Methods for collection of vegetation data from transects are described in full in Chapter 3 (section 3.2.2). Details of datasets used are summarised in Appendix Table 2.

Leks were selected for sampling if:

(i) Situated on open ground within commercial plantations containing study restocks or within 2 km of the edge of a plantation containing study restocks, and

(ii) Black grouse males had been counted at each lek for the previous 3 years, and ≥2 males had been present each year, with the number of males counted being either stable or increasing over the 3 years (i.e. numbers did not decrease in any year), indicating that habitat around leks may either be suitable or improving. The exception to this is two Trossachs leks (lek T2 and T3; Table 6.2) where the general population has recently rapidly expanded to a size where birds have dispersed from the main leks to form additional surrounding 'satellite leks' nearby (Dave Anderson, pers. comm.), indicating good quality surrounding habitat despite a decline in the main lek count. Lek counts were conducted by Forestry Commission and RSPB staff.

Table 6.2: Number of black grouse counted at study leks and general habitat description within 1 km radius of lek.

Study area	Lek code	Habitat within 1 km radius of lek centre	2006	2007	2008	2009
Trossachs	T1	40% loch, 35% ericaceous heather moorland, 20% bog myrtle *Myrica gale*, 5% birch *Betula* spp. scrub/woodland	6	12	16	18
	T2	40% boggy areas (bog myrtle *Myrica gale*, bog asphodel *Narthecium ossifragum,*, *Juncus*, *Carex* and *Eriophorum* spp.), 30% ericaceous heather moorland, 20% birch *Betula* spp. and willow *Salix* spp. scrub/woodland, 10% improved grassland	9	11	14	5†
	T3	40% loch, 40% bog myrtle, 10% boggy areas (*Juncus*, *Carex* and *Eriophorum* spp.), 10% improved grassland	1	5	5	2†
Sutherland	S1	60% commercial conifer 2nd rotation restock, 20% ericaceous heather moorland, 20% *Eriophorum* spp.	^	1	2	2
	S2	30% loch, 20% commercial conifer 2nd rotation restock, 20% mature, thinned commercial conifer forest with bilberry *Vaccinium myrtillus* understory, 20% boggy areas (predominantly *Eriophorum* spp.), 10% mature Scot's pine *Pinus sylvestris* woodland regeneration	^	2	2	4
	S3	40% ericaceous heather moorland, 30% boggy areas (predominantly *Eriophorum* spp.), 20% Scot's pine *Pinus sylvestris* woodland regeneration, 10% mature commercial conifer forest	^	2	2	2
	S4	45% ericaceous heather moorland, 45% boggy areas (predominantly *Eriophorum* spp.), 10% mature commercial conifer forest	^	1	2*	5
	S5	40% loch, 20% ericaceous heather moorland, 20% boggy areas (predominantly *Eriophorum* spp.), 10% Molinia grass, 10% bog myrtle	^	0	0	2*

^2006 information not available. †Additional satellite leks formed nearby. *Birds heard lekking rather than seen.

Vegetation data were collected from 36, 20 m transects around leks in The Trossachs, and 40 transects in Sutherland. Sampling was conducted within a 1 km radius from the centre of each lek - the area most likely to contain nests of black grouse hens (Robel 1969a; Picozzi 1986), and therefore likely to be utilised by broods, particularly during the early invertebrate-feeding stage. Using OS maps, an equal number of transects were randomly assigned to each quarter of the circular radius, and grid references generated for later location in the field using GPS. Methods for vegetation sampling on transects were identical for restocks and for leks.

6.2.1.2 Invertebrate sampling

Invertebrate data were collected from 45 restocks and 8 leks, utilising a sub-sample of 130 of the 701 transects described in 6.2.1.1. Invertebrate sampling was conducted between 5 June and 15 July 2009 in both study areas to coincide with the brood-rearing period when chicks are largely dependent upon invertebrate food (Robel 1969a; Starling-Westerberg 2001; Picozzi 1986; Baines *et al.* 1996).

Of the 36 restocks in Sutherland, two transects in each restock used for vegetation data collection (described above in 6.2.1.1) were randomly selected and used for invertebrate sampling. In The Trossachs, only 9 of the 36 restocks containing vegetation transects were sampled for invertebrates. Up to four vegetation transects within each restock were sampled for invertebrates. At leks in each study area, four vegetation transects were selected at random, such that one transect was used for invertebrate data collection in each quarter of the 1 km radius around the lek centre.

6.2.1.2.1 Taxa selection and sampling method

Taxa selection and sampling were as described in Chapter 4 (section 4.2.2), although, suction sampling was not used to capture invertebrate taxa in 2009 due to time restrictions. Therefore, beetles, ants, and arachnids were sampled using pitfall trapping, and Lepidoptera larvae, tipulids, true bugs and true flies were sampled using sweep netting. Further details relating to invertebrate sampling methods are provided in Chapter 4 (sections 4.2.1.1 and 4.2.1.3).

In The Trossachs, invertebrate sampling at restocks and leks was conducted over a one-week period. Two sweep net samples were collected from each transect in restocks and in leks (the first on 9 June and the second a week later). In order to reduce the frequency of zero counts and to avoid repeated measures of invertebrate abundance from the same transect, sweep net data for both weeks were pooled for each transect. Additionally, two pitfall traps were set along each transect for a 7-day period, which were also collected on 16 June. Catches from pitfall traps located along a transect were pooled and stored in 70% ethanol. In Sutherland, sampling took place over a longer period (5 weeks). Sweep netting and pitfall trapping were conducted on transects every 7 days over the 5-week period, thus five sweep net samples and four pitfall trap samples per transect were collected. As with the Trossachs data, weekly data were pooled for each transect.

It is accepted that comparisons of invertebrate abundance between study areas are likely to be biased (i.e. higher in Sutherland), as captured invertebrates were pooled on each transect for the study duration, yet duration differed between study areas (5 weeks in Sutherland and only 1 week in The Trossachs). Differences in abundance between habitat type, however, are directly comparable, as sampling at leks and restocks was conducted over the same period within each study area, e.g. transect data from Sutherland restocks are comprised of 5 weekly samples, as are lek data.

6.2.2 Statistical analyses

6.2.2.1 Model building

Restock management factors considered in previous chapters, i.e. Planting Type, Extraction Type, and Extended fallow period were not considered in this chapter. Instead, a two-level 'Habitat Type' factor was used for comparison of restock habitat and lek habitat in statistical models, in addition to two continuous site variables - 'altitude' and 'slope' (see Model 1; Table 6.3 for further variable information) and a two-level 'Study area' factor, which compared Sutherland and Trossachs data, although differences in abundance between study areas will partly reflect differences in sampling effort. Whilst it is acknowledged that restock habitat will vary according to management (reported in Chapters 3 to 5), the 'Habitat Type' factor allows comparisons between restocks and leks to be made in analyses based upon current habitat and invertebrate availability to black grouse, irrespective of management.

6.2.2.1.1 Vegetation

None of the explanatory variables were correlated at $r \geq 0.60$ (Appendix Table 5a). Quadratic terms of each continuous explanatory variable were also tested, with a significance level of $P<0.05$. Interactions between explanatory variables were not tested as none were relevant to the aims of the study. GLMM models were fitted specifying restock/lek identity as the random effect. Minimal adequate models were produced by fitting all of the relevant main effects, and then removing terms according to their level of significance, until only those significant at $P<0.05$ remained.

Calluna vulgaris cover data contained a high proportion of zeros (absent from 158 of 702 transects) and could not be transformed to a normal distribution. Therefore, data were modelled using the penalized-quasi likelihood (PQL) method (Venables & Ripley 2002) to account for an unknown distribution (cover values not being based upon a set of trials), using the glmmPQL function in the 'MASS' library of R, version 2.8.1 (R Development Core Team 2008). Both *V. myrtillus* and *Eriophorum* spp. (*E. vaginatum* and *E. angustifolium*) occurred with very low frequency across transects and were therefore treated as presence or absence data*,* using the glmer function in the 'lme4' library (Bates *et al*. 2008), based on the binomial logistic regression model. Height of heather (*Calluna vulgaris, Erica tetralix, E. cinerea*), graminoids (grasses, *Juncus* and *Carex* spp.), and field-layer density (0 to 40 cm height, including brash) were analysed with a normal error distribution using linear mixed effects models, hence the lme function in the 'nlme' library of R (Pinheiro *et al*. 2007).

6.2.2.1.2 Invertebrates

Explanatory variables considered in invertebrate models are listed in Model 1 (Table 6.3). None of the explanatory variables were inter-correlated at $r \geq 0.60$ (Appendix Table 5a & 5b). Quadratic terms and interactions were tested as described in 6.2.2.1.1, and minimal adequate models were produced in the same way as described for vegetation models (see 6.2.2.1.1).

Analyses for each invertebrate taxon were undertaken using Generalised Linear Mixed-effects Models (GLMMs; Zuur *et al.* 2009), specifying restock/lek identity as the random effect. Data for all invertebrate taxa were over-dispersed, hence the ‘glmmPQL’ function in the ‘MASS’ library (Venables & Ripley 2002) of R was used specifying ‘quasipoisson’ errors, which automatically estimates over-dispersion using a Penalised Quasi-Likelihood method (Zuur *et al*. 2009).

Invertebrate abundance is likely to be affected directly by cover and structure of field-layer vegetation, which in themselves reflect factors specific to study sites. As demonstrated in Chapter 3, field-layer vegetation is itself a product of site factors. Therefore, a three-step model building procedure was used to construct invertebrate models, as described previously in Chapters 4 and 5. Abundance of each invertebrate taxon was first examined in relation to site factors (Model 1; Table 6.3). Secondly, abundance of each invertebrate taxon was examined in relation to vegetation variables (Model 2), which were simplified into the two broad plant functional types (PFTs; Wookey *et al*. 2009) that dominated the field-layer (i.e. percentage cover of dwarf shrubs and graminoids), field-layer vegetation height, field-layer density, and Ellenberg moisture score values (Hill *et al.* 1999), which represent a position on a moisture gradient (Model 2; Table 6.3).

Having produced these two models, significant effects from Model 1 were tested for entry to Model 2, to produce a third minimum adequate model (Model 3), which considered both field-layer vegetation and site factors. Vegetation variables were removed if the inclusion of significant site factors caused them to become non-significant (at $P<0.05$).

6.2.2.2 Calculation of R^2 values

The R^2 value produced for each model explains how much of the variation in the data is explained by the model, with a higher R^2 value meaning more variation has been explained. R^2 is calculated by the square of the correlation between the model's predicted (fitted) values and the observed values (Fuentes-Montemayor *et al*. 2011).

Table 6.3: Explanatory variables considered in statistical models. Model 1 contains site variables, Model 2 contains field-layer vegetation variables.

Variable	Data type¶	Description	Level of data collection
Model 1. Site variables			
Habitat Type	S*	Within restocks or within a 1 km radius of a black grouse lek	Restock
Study area	S*	Sutherland or The Trossachs	Restock
Altitude	S	Average of 5 equidistant points	Transect
Slope	S	Average of 5 equidistant points	Transect
Model 2. Vegetation variables			
Moisture score	C	Mean cover-weighted Ellenberg moisture values	Transect
Vegetation height	C	Maximum height of all vegetation (cm)	Transect
Field-layer density	C	Index (0 to 3) of field-layer density from ground level to 40 cm tall, includes vegetation and brash	Transect
Dwarf shrub cover	C	Combined cover (%) of *Calluna vulgaris*, *Erica tetralix*, *E. cinerea*, *Vaccinium myrtillus* and *Myrica gale*	Transect
Graminoid cover	C	Combined cover (%) of *Carex, Eriophorum, Juncus, Luzula, Deschampsia, Agrostis, Molinia, Nardus, Festuca* and *Anthoxanthum* spp.)	Transect

¶ indicates how data were represented in statistical models: S* - 2-level site factor, S - continuous site-dependent variable, C - continuous vegetation variable. 'Moisture score' refers to the mean cover-weighted Ellenberg moisture score (Hill *et al.* 1999) of species recorded along a transect: wetter habitats have a higher score.

6.3 Results

6.3.1 Field-layer vegetation

Nineteen vascular plant species were recorded in lek habitat in Sutherland. Similar species were present around leks in The Trossachs, with the addition of the dwarf shrub bog myrtle *Myrica gale*. Additionally, in both study areas, two graminoid groups identified to genus only (*Agrostis* and *Luzula* spp.) and 3 moss genus groups (*Polytrichum*, *Sphagnum* and *Pleurozium* spp.) were recorded.

In restocks, 32 vascular plant species were recorded in Sutherland and 39 species in The Trossachs. Three graminoid groups were identified to genus only (*Agrostis*, *Luzula* and *Festuca* spp.) plus 3 moss genus groups (*Polytrichum*, *Sphagnum*, *Pleurozium* spp.). Additionally, in Trossachs restocks, the moss genus *Racomitrium* was recorded.

Generally, restocks had an increased non-vegetative ground cover (consisting mainly of timber harvest residue), in addition to a greater cover of trees, moss and *Juncus* spp. (Figure 6.1). Leks had a greater cover of dwarf shrubs (*Calluna vulgaris*, other heather spp. consisting of *Erica tetralix* and *E. cinerea*, and *Vaccinium myrtillus*), *Eriophorum* spp., bog myrtle *Myrica gale*, and bog asphodel *Narthecium ossifragum*.

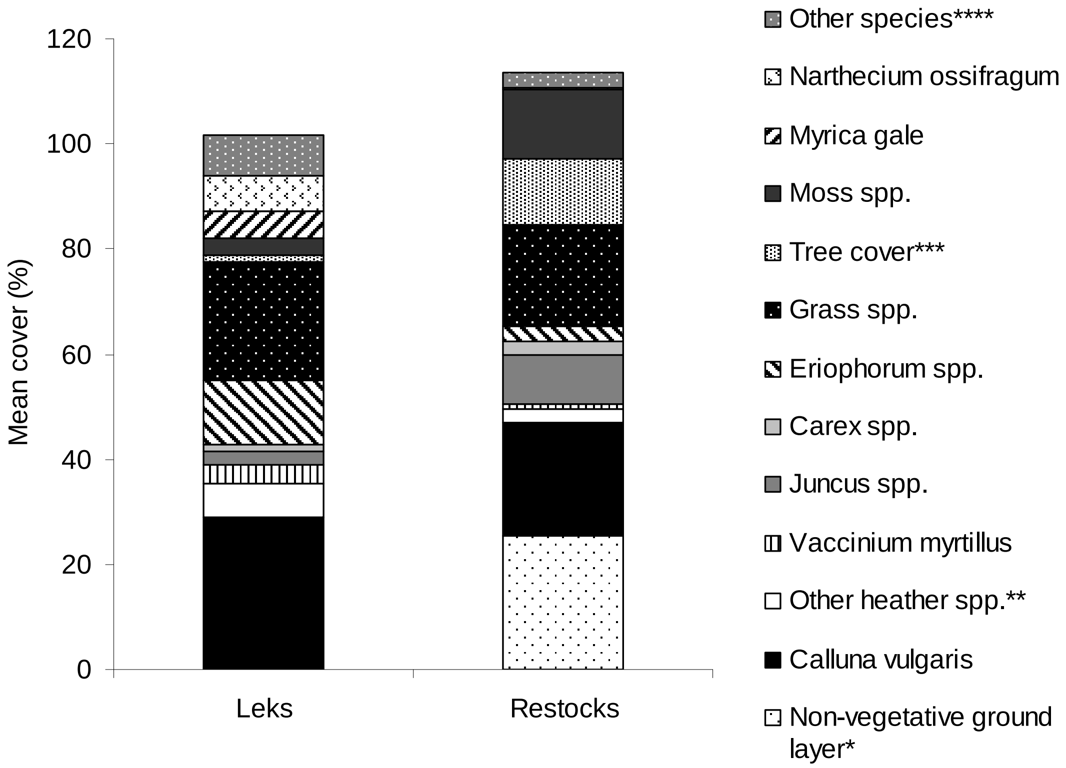


Figure 6.1: Proportion of vegetative and non-vegetative cover on 76 transects within 1 km of 8 leks and 625 transects in 72 restocks in the Sutherland and Trossachs study areas. *comprises 67% brash, 15% needles and 12.2% mounds and 6.3% bare ground, **comprises *Erica tetralix* and *E. cinerea*, ***comprises planted and naturally regenerated trees, **** Cumulative total of species with <5% cover. See Appendix, Table 5 for species information.

6.3.1.1 Cover of Calluna vulgaris

Mean *Calluna vulgaris* cover was greater in lek habitat than in restocks, however, the difference was not statistically significant (t=-1.184, *P*=0.240; Figure 6.2). Cover, however, changed significantly with slope and was greater in Sutherland than in the Trossachs study area (Table 6.3; Figure 6.3). A quadratic relationship between *C. vulgaris* cover and altitude indicated greatest cover between c.50 and 200 m, decreasing thereafter (Table 6.3; Figure 6.4). The model was a relatively good fit to the data (R^2=0.451).

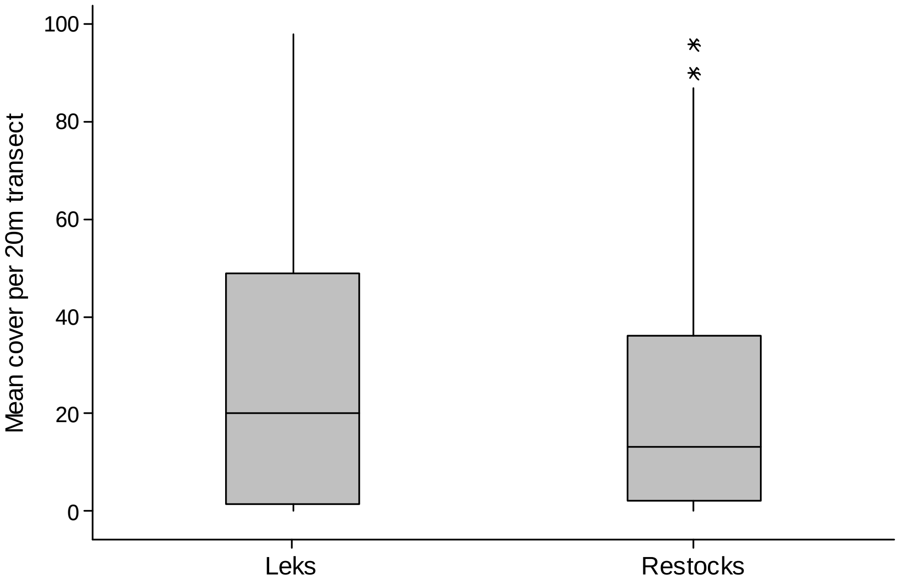


Figure 6.2: Percentage cover of *Calluna vulgaris* on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas. Box plots show median (central line at 0), quartiles (box), 5% and 95% centiles (whiskers) and outliers (stars).

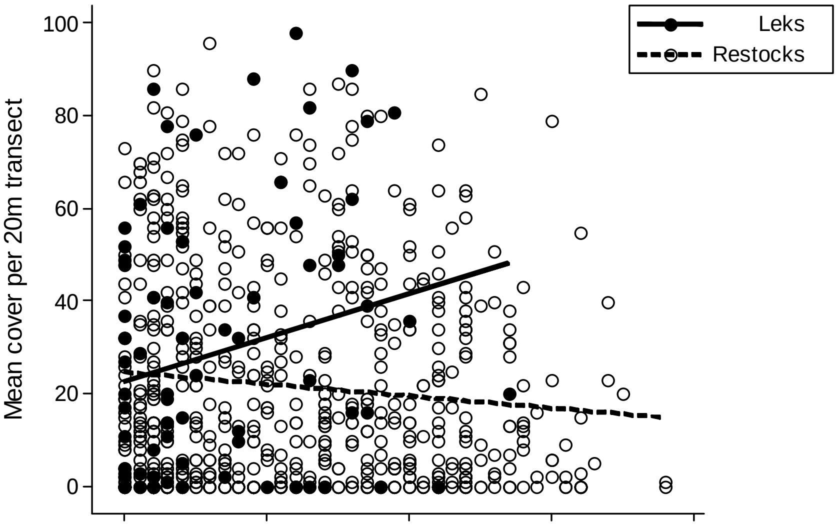


Figure 6.3: Percentage cover of *Calluna vulgaris* in relation to gradient of slope on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas. (Regression equations – Leks: *C. vulgaris* cover = (0.945×Altitude)+22.7; Restocks – *C. vulgaris* cover = (-0.257×Altitude) +24.7.

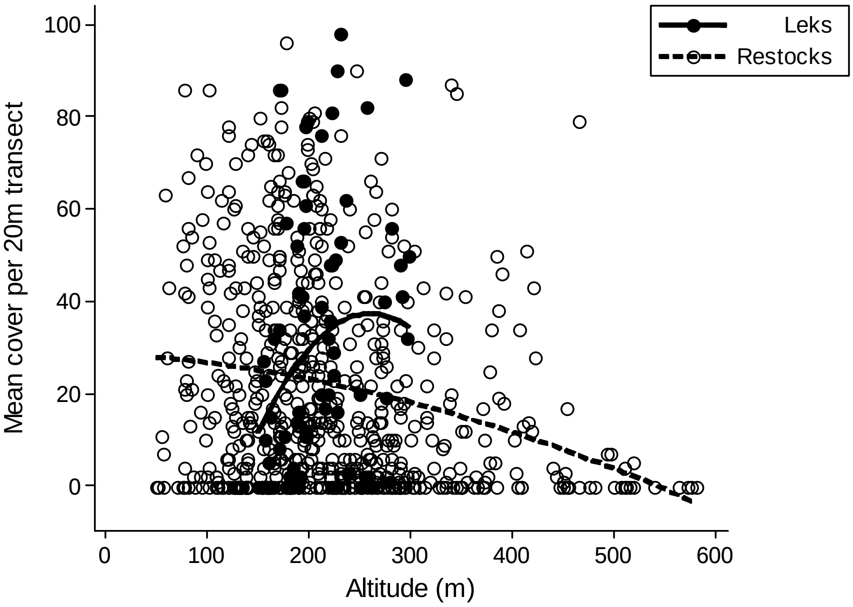


Figure 6.4: Percentage cover of *Calluna vulgaris* in relation to altitude on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas. Regression equations: Leks – *C. vulgaris* cover = $(1.104\times\text{Altitude})+(-0.002\text{x}\text{Altitude}^2)-106.300$; Restocks – *C. vulgaris* cover = $(-0.014\times\text{Altitude})+(<-0.001\text{x}\text{Altitude}^2)+28.92$.

Table 6.4: GLMM models describing effects of study area, Habitat Type, altitude and slope upon cover of *C. vulgaris* on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas.

Variable	Parameter	df	t	Direction of effect	Statistical test	R^2#
C. vulgaris	Intercept	618	-4.277		glmmPQL	0.451
Cover	Study area	78	-4.068	S>T		
	Altitude	618	2.304			
	Altitude^2	618	-2.812	⌒		
	Slope	618	4.946	+		

Study area: S: Sutherland; T: The Trossachs. Positive effects of variables upon cover are indicated by + symbols. Where a curvilinear fit was more appropriate than a linear fit, ⌒ represents the type of curve. See Table 6.3 for description of explanatory variables. # For calculation of R-sq values refer to methods. Levels of significance: ****P*<0.001, ** *P*<0.01, * *P*<0.05.

6.3.1.2 Other taxa examined

Both *Eriophorum* spp and *Vaccinium myrtillus* occurred relatively infrequently; they were present on 133 and 113 of 701 transects, respectively. The likelihood of *Eriophorum* spp. occurrence was significantly greater around leks than in restocks (z=-

3.413, $P<0.001$) and occurrence increased in flatter areas (z=5.112, $P<0.001$) and with increased altitude (z=2.693, $P=0.007$). This model explained 50% of variation in the dataset ($R^2=0.499$).

The likelihood of *V. myrtillus* occurrence was also greater around leks than restocks (z=-2.010, $P=0.045$), although differences were marginal. Likelihood of occurrence was significantly greater in the Trossachs than the Sutherland study area (z=5.446, $P<0.001$), however, the model fit was poor ($R^2=0.183$), possibly due to low occurrence of the species.

6.3.1.3 Vegetation height

Heather (*Calluna vulgaris, Erica tetralix* and *E. cinerea*) was c.5 cm taller in lek habitat than in restocks, however, the difference was not statistically significant (t=1.332, $P=0.187$). Mean heather height was 34.3 cm (SE ± 1.4 cm), which increased on steeper ground (t=3.26, $P=0.001$) and at lower altitude (t=4.09, $P<0.001$); at 100 m height was c.40 cm, but at 500 m, height was c.20 cm. This model explained 64% of variation in the dataset ($R^2=0.640$).

Graminoid height (*Juncus*, *Carex*, *Eriophorum* spp. and grasses) did not differ between leks and restocks (t=1.08, $P=0.284$). Mean height was 67.5 cm (SE ± 3.3 cm) and graminoids were c.5 cm taller in the Trossachs than the Sutherland study area (t=3.05, $P=0.003$) and taller at lower altitude (t=2.72, $P=0.007$). This model explained 38% of variation in the dataset ($R^2=0.381$).

6.3.1.4 Field-layer density

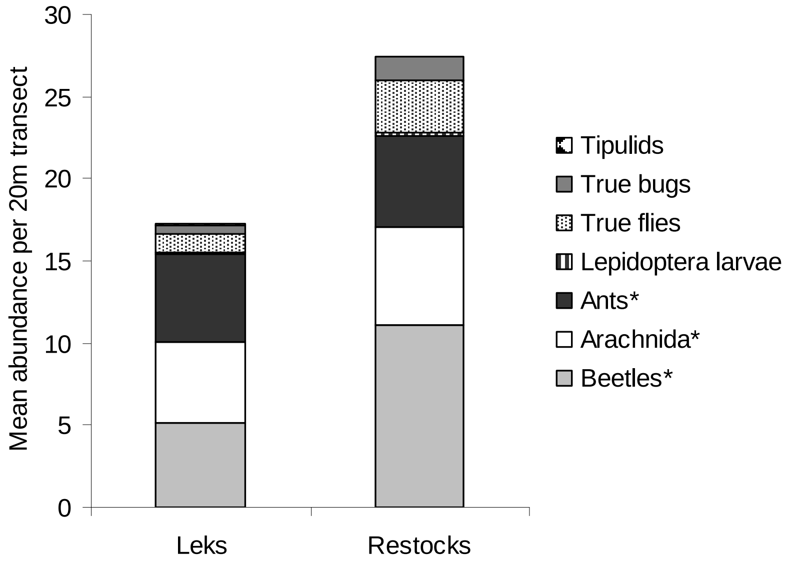
Field-layer density was greater around leks (mean density 68% ± 7%) than in restocks (55% ± 2%), although this difference was marginally non-significant (t=1.922, $P=0.057$). Density decreased with altitude (t=3.70, $P<0.001$). This model explained 53% of variation in the dataset ($R^2=0.528$).

6.3.2 Invertebrate abundance

A total of 20 447 invertebrates of >2 mm body length were captured during the trapping period in 2009. Of the seven taxa identified as important in the diet of black grouse chicks and used in statistical analyses, 10 453 were recorded in pitfall traps (4029 beetles, 2446 arachnids, 2281 ants, 1107 true flies, 463 true bugs, 89 Lepidoptera larvae and 38 Tipulids; Figure 6.5), and 9477 in sweep nets (3394 true bugs, 2385 true flies, 1176 beetles, 971 Lepidoptera larvae, 814 arachnids, 362 ants and 375 Tipulids (Figure 6.6).

The remaining 517 invertebrates were taxa not identified by previous studies as important food items in the black grouse chick diet, thus were not included in statistical analyses, including Isopoda, Myriapoda, adult Lepidoptera, Ichneumonidae, Trichoptera and terrestrial larvae spp. (all <1%). Symphyta larvae were not recorded at either study site in 2009.

a) Sutherland pitfall trap data



b) Trossachs pitfall trap data

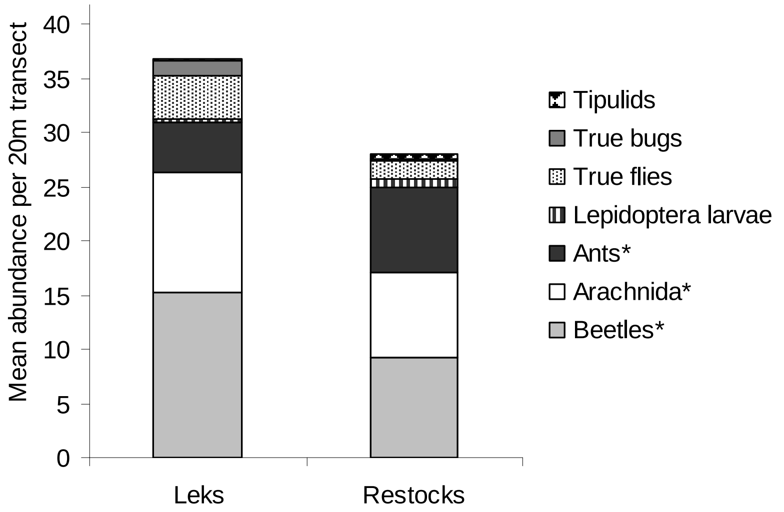
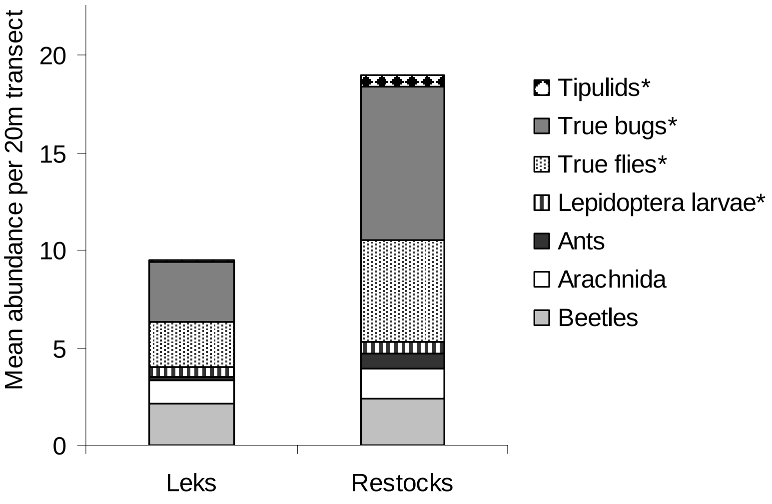


Figure 6.5: Abundance of invertebrate taxa considered to be important in black grouse chick diet in a) the Sutherland study area (72 transects in restocks and 20 transects within 1 km of leks), and b) The Trossachs study area (26 transects in restocks and 12 transects within 1 km of leks). Invertebrates captured by pitfall trapping (means consist of 4 weeks of pooled data for Sutherland and 1 week for The Trossachs). Note scale differences between graphs. *Dataset used in statistical analyses. Arachnida group comprise spiders and harvestmen.

a) Sutherland sweep net data



b) Trossachs sweep net data

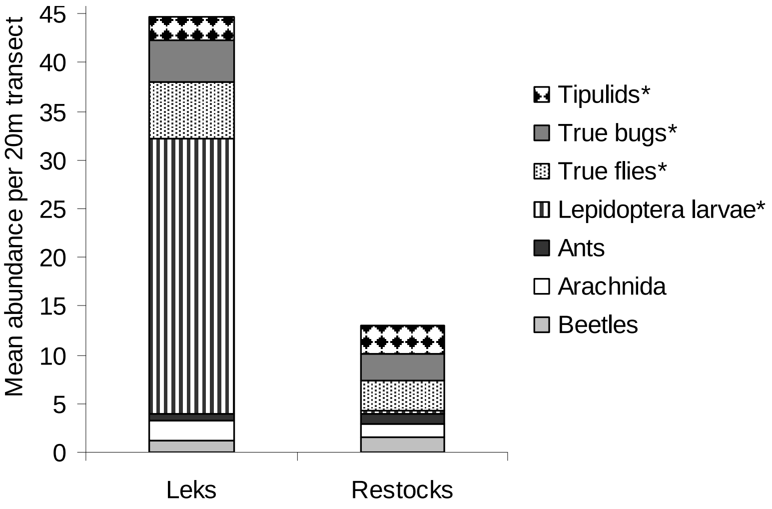


Figure 6.6: Abundance of invertebrate taxa considered to be important in black grouse chick diet in a) the Sutherland study area (72 transects in restocks and 20 transects within 1 km of leks), and b) The Trossachs study area (26 transects in restocks and 12 transects within 1 km of leks). Invertebrates captured by sweep netting (means comprise 5 sampling occasions pooled for Sutherland and 2 sampling occasions pooled for The Trossachs). Note scale differences between graphs. Arachnida group comprise spiders and harvestmen. * Dataset used in statistical analyses.

6.3.2.1 Performance of statistical models to assess taxa response

Habitat type (lek or restock) and other site variables explained between 19 and 60% of the variation in taxa abundance (Model 1; Table 6.5). Vegetation variables explained between 32 and 66% of the variance in taxa abundance (Model 2; Table 6.6).

Table 6.5: Taxon response to Habitat Type (Restock or Lek) and other site variables (Model 1). Significant (at $P<0.05$) relationships listed in order (most highly significant first).

Taxon	Model 1 parameter	R^2
Beetles^{P}	Study area (S>T), Slope^{+}	0.602
Arachnids^{P}	Study area (S>T)	0.194
Ants^{P}	Study area (S>T), Altitude$^{\cap}$	0.495
Lepidoptera larvae^{SW}	Altitude^{-}, Habitat type (Lek>Restock), Slope^{-}	0.350
True bugs^{S}	Study area (S>T), Slope$^{\cap}$	0.526
True flies^{S}	Study area (S>T), Slope⎞	0.581
Tipulids^{SW}	Study area (T>S), Slope^{-}, Habitat type (Restock>Lek)	0.509

Arachnids group comprise spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap, ^{SW} by sweep net. Positive effects of variables upon taxa abundance are indicated by superscript +, negative effects by –. Where a curvilinear fit was more appropriate than a linear fit, symbols ∩ and ⎞ represent the type of curve. Study area: S – Sutherland, T – Trossachs. R^2 calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. See Table 6.3 for further description of explanatory variables.

Table 6.6: Taxon response to restock vegetation variables (Model 2). Significant (at $P<0.05$) relationships listed in order (most highly significant first).

Taxon	Model 2 parameter	R^2
Beetles^{P}	Moisture score⎝	0.662
Arachnids^{P}	Dwarf shrub cover^{-}, Field-layer density$^{\cap}$	0.500
Ants^{P}	Graminoid cover$^{\cap}$	0.447
Lepidoptera larvae^{SW}	Dwarf shrub cover^{+}, Moisture score^{+}, Field-layer density⎛	0.340
True bugs^{S}	Moisture score^{-}	0.655
True flies^{S}	Moisture score^{-}, Field-layer density⎛	0.643
Tipulids^{SW}	Vegetation height^{+}, Dwarf shrub cover^{-}	0.517

Arachnids group comprise spiders and harvestmen. Superscript in first column refers to trapping method: ^{P} indicates capture by pitfall trap, ^{S} by suction trap, ^{SW} by sweep net. The 'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999): wetter habitats have a higher score. Positive effects of variables upon taxa abundance are indicated by superscript + symbols, negative effects by – symbols. Where a curvilinear fit was more appropriate than a linear fit, symbols ∩ ⎝ and ⎛ represent the type of curve. R^2 calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. See Table 6.3 for further description of explanatory variables.

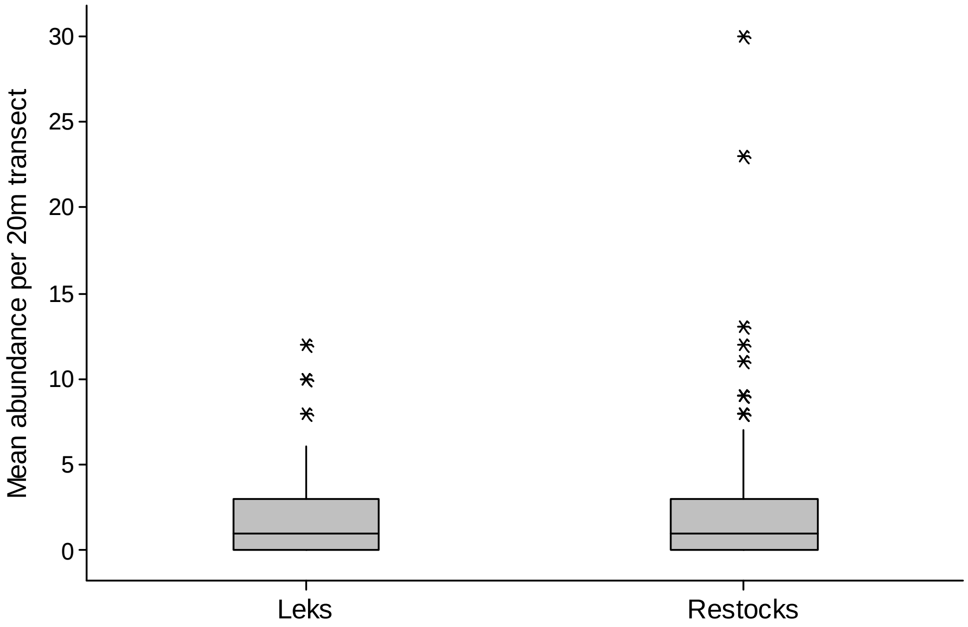
When significant Habitat Type and site variables from Model 1 were added into Model 2 to create Model 3 (Table 6.7), explained variation in abundance decreased for most taxa, for reasons described in Chapter 4 (section 4.3.2).

6.3.2.2 Invertebrate response to vegetation, habitat type and other site characteristics

Although abundance of Tipulids was generally low, more Tipulids were recorded in restocks than around leks (Model 1; Table 6.5), partly due to outbreaks in abundance not recorded as often around leks (Figure 6.7a). Conversely, in habitat around leks, double the number of Lepidoptera larvae were recorded compared with restocks (Model 1; Table 6.5). Again, abundance on transects was generally very low in both habitat types, with the exception of outbreaks of northern winter moth *Operophtera fagata* larvae recorded on six transects in habitat containing *M. gale* surrounding leks (Figure 6.7b). Lepidoptera larvae were most abundant in areas where dwarf shrub cover was increased, in areas with wetter habitat conditions, and where field-layer density was moderate to high (Table 6.7).

The abundance of arachnids and true flies was also positively related to field-layer density (Table 6.7); arachnids were more abundant at moderate field-layer density and true flies more abundant between moderate and high density. Tipulids were the only taxon related to vegetation height, and were most abundant on vegetation c.80 to 90 cm tall.

a.



b.

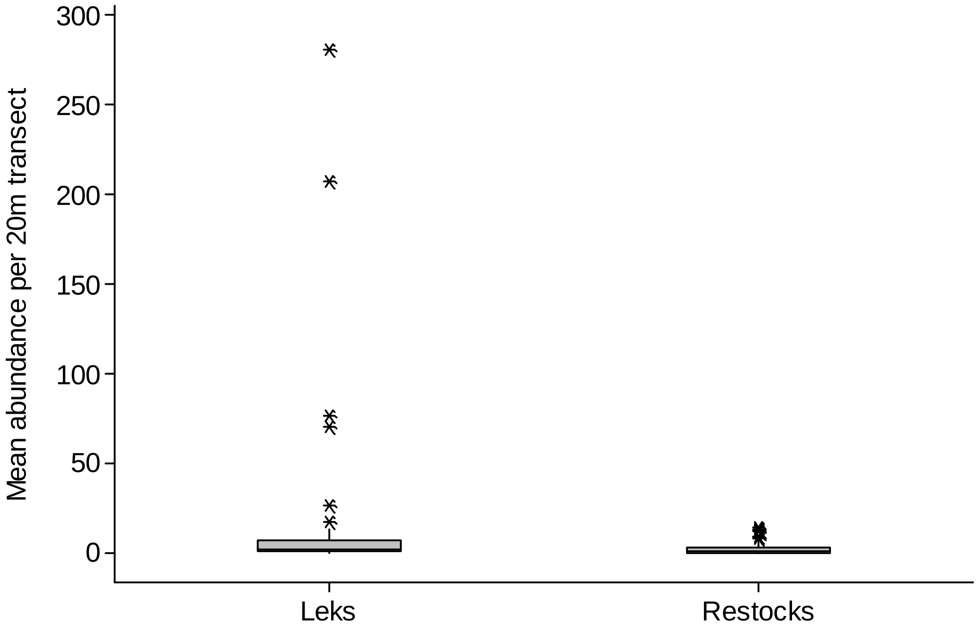


Figure 6.7: Abundance of a) Tipulids and b) Lepidoptera larvae on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas. Mean abundance calculated by pooling sweep net samples from each transect (5 samples per transect in Sutherland and 2 samples in The Trossachs). Box plots show median (central line at 0), quartiles (box), 5% and 95% centiles (whiskers) and outliers (stars).

Table 6.7: Minimum adequate GLMM models describing the abundance of invertebrate taxa preferred by black grouse in relation to significant site and vegetation variables on 625 transects in 72 restocks, and on 76 transects within 1 km of 8 leks, in the Sutherland and Trossachs study areas. The table reports the overall minimum adequate model (Model 3) constructed by stepwise addition of significant variables from a site variables model (Model 1; Table 6.4) to a vegetation model (Model 2; Table 6.5).

Taxon	Model 3 Parameters	Estimate	SE	df	t value	Direction of effect	Statistical test	Model 2 R$^{2\#}$	Model 3 R$^{2\#}$
Beetles	Intercept	14.180	4.224	75	3.356		glmmPQL	0.662	0.600
	Moisture score	-3.395	1.250	75	-2.715 **				
	Moisture score^2	0.260	0.917	75	2.831 **	⎝			
	Study area	-1.448	0.279	50	-5.188 ***	S>T			
	Slope	0.031	0.011	75	2.853 **	+			
Arachnids	Intercept	2.160	0.451	75	4.797		glmmPQL	0.500	0.422
	Field-layer density	1.196	0.523	75	2.287 *				
	Field-layer density^2	-0.324	0.141	75	-2.312 *	∩			
	Dwarf shrub cover	-0.009	0.002	75	-4.038 ***	-			
	Study area	-0.554	0.154	50	-3.598 ***	S>T			
Ants	Intercept	2.449	0.211	76	11.618		glmmPQL	0.447	0.434
	Graminoid cover	0.026	0.012	76	2.084 *				
	Graminoid cover^2	<-0.001	<0.001	76	-2.291 *	∩			
	Study area	-0.698	0.310	50	-2.248 *	S>T			

Table 6.7: *Continued.*

Taxon	Model 3 Parameters	Estimate	SE	df	t value	Direction of effect	Statistical test	Model 2 R$^{2\#}$	Model 3 R$^{2\#}$
Lep. Larvae	Intercept	-2.518	1.661	73	-1.516		glmmPQL	0.340	0.340
	Moisture score	0.609	0.135	73	4.494***	+			
	Field-layer density	1.613	1.276	73	1.264$^{n.s.}$				
	Field-layer density^2	-0.760	0.329	73	-2.307*	⎛			
	Dwarf shrub cover	-0.031	0.007	73	4.703***	+			
	Altitude	-0.011	0.003	73	-3.125**	-			
Tipulids	Intercept	-0.706	0.408	76	-1.731		glmmPQL	0.517	0.509
	Vegetation height	0.009	0.003	76	2.848**	+			
	Slope‡^{1}	-0.053	0.012	76	-4.371***	-			
	Study area	1.748	0.285	49	6.130***	T>S			
	Habitat type	0.837	0.352	49	2.378*	Restock>Lek			
True bugs	Intercept	2.760	0.158	76	17.441		glmmPQL	0.655	0.526
	Study area	-1.604	0.269	50	-5.965***	S>T			
	Slope	0.116	0.032	76	3.592***				
	Slope^2‡^{2}	-0.004	0.001	76	-2.547*	∩			
True flies	Intercept	2.657	0.134	76	19.814		glmmPQL	0.643	0.582
	Study area‡^{3}	-0.934	0.222	50	-4.202***	S>T			
	Slope	0.074	0.026	76	2.784**				
	Slope^2	-0.002	0.001	76	-2.342*	⎞			

Arachnids group comprises spiders and harvestmen. 'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999): wetter habitats have a higher score. Restock site variables italicised. Study area: S – Sutherland, T – The Trossachs. See Table 6.3 for further variable descriptions. Positive effects indicated by +, negative effects by –. Where a curvilinear fit of an independent variable was more appropriate than a linear fit, symbols ∩ ∪ ⎞ ⎝ and ⎛ represent the type of curve. ‡^{1} replaced the 'Dwarf shrub cover' variable, ‡^{2} replaced the 'Moisture score' variable, and ‡^{3} replaced the 'Moisture score' and 'Density' variables. $^{\#}$R^2 calculated by the square of the correlation between the model's predicted (fitted) values and the observed values. Levels of significance: ***$P<0.001$; ** $P<0.01$; * $P<0.05$.

The abundance of beetles, true bugs and true flies were associated with habitat moisture (measured by the weighted mean Ellenberg moisture score), although relationships were negative, indicating a preference for drier habitat conditions (Table 6.7). The inclusion of the ‘slope’ variable (in the case of true bugs) and the ‘study area’ variable (in the case of true flies) caused the Ellenberg moisture score variable to become non-significant, suggesting that whilst habitat moisture may affect abundance of these taxa, this may be partly explained by site topography (i.e. wetter in flatter areas) and the study area (drier conditions in Sutherland); thus moisture co-varies with topography and with study area. Previous analyses of invertebrate data from restocks also associated beetle and true bug abundance with drier habitats (measured by the Ellenberg moisture variable; Chapter 5 only), however, a relationship with Lepidoptera larvae or true fly abundance was not recorded in previous chapters.

As expected, Sutherland had a greater abundance of most taxa, as the trapping period duration was longer than in The Trossachs (see 6.2.1.2.1). Despite differences in trap-period duration, abundance of Lepidoptera larvae was similar between study areas, and Tipulid abundance was higher in The Trossachs, suggesting that if the trapping period length had been equal between study areas, abundance of these taxa would far exceed those available further north in Sutherland.

6.4 Discussion

Results suggest that the percentage cover and height of *Calluna vulgaris* was marginally greater in habitat surrounding leks than in second rotation restocks, although differences were not statistically significant. Field-layer density was greater around leks and there was also a higher chance of occurrence of *Eriophorum* spp. and *Vaccinium myrtillus* than in restocks, but neither species was recorded frequently, and variation in the *V. myrtillus* dataset explained by statistical models was particularly low. Lepidoptera larvae were more abundant in habitat surrounding leks, but, conversely, Tipulids were more abundant in restocks. The abundance of other invertebrate taxa considered was similar between leks and restocks.

6.4.1 Comparative quality of field-layer habitat between leks and restocks

Lek habitat had a reduced non-vegetative cover, which is predominantly composed of brash and often covers a large proportion of ground in younger restocks, suppressing heather recovery and the abundance of some invertebrate taxa important to black grouse chicks (see Chapters 3 to 5). In terms of habitat provision to black grouse, field-layer vegetation around leks and restocks was not markedly different, although there was an indication that habitat surrounding leks contained significantly more *V. myrtillus* and *Eriophorum* spp. than restocks, together with cover of the dwarf shrub *M. gale* – species that are often of particular importance to black grouse (see Baines 1995 for a review; Baines *et al*. 1996). Despite their relatively infrequent occurrence in this study, it is likely that black grouse will be highly selective of habitats containing these species, and their comparative rarity in (or absence from) restocks could be of potential importance for future management of black grouse habitat in second rotation forests.

Differences between restocks and lek habitat may be attributable to previous afforestation of the latter with non-native trees species such as Sitka spruce *Picea sitchensis* and Lodgepole pine *Pinus contorta*, which are likely to have restricted light availability to *V. myrtillus* during the 40 to 60 year rotation (see Chapter 3). Furthermore, drainage of plantations to improve planted tree establishment and confer stability against windthrow created drier, less favourable habitat for *Eriophorum* spp. (Angelstam 2004; this study, Chapter 3). Both plant species are likely to be beneficial to black grouse by improving body condition at important times of the year; autumn berries of *V. myrtillus* help build reserves prior to winter, and flower-heads of *Eriophorum* spp. are likely to contribute to pre-breeding condition of hens in spring (Watson & Moss 2008). Body condition during nesting probably exerts an influence on the frequency of breaks needed for feeding and therefore reduces incubation duration, which may reduce predation risk (Storaas & Wegge 1997).

6.4.2 Invertebrate availability in field-layer vegetation surrounding leks and within restocks

Increased field-layer density recorded around leks may provide better cover from predators for nesting hens and young broods (Baines 1996), and may also result in an increased density of invertebrate food for chicks (Erikstad 1985). In this study, increased field-layer density was associated with a greater abundance of Lepidoptera larvae, a key food item for black grouse, and abundance remained high even in very dense vegetation. Larval abundance was also positively related to an increased cover of dwarf shrubs and wetter habitats; abundance was increased in areas with greater heather cover, but large outbreaks of larvae (>50 individuals per 20 m transect) predominantly occurred in habitats containing *M. gale*, with large areas up to 100 m^2 visibly defoliated by caterpillars, primarily of northern winter moth *Operophtera fagata* (J. Owen, unpubl. data). Previous studies have reported a positive relationship between Lepidoptera larvae abundance and the presence of *M. gale* on moorland in Scotland, furthermore, in these areas, hatching of black grouse chicks appeared to be timed to coincide with the peak biomass of larvae (Baines *et al.* 1996). In this study, *M. gale* was only recorded in habitat surrounding leks and not in restocks (Figure 6.1), and Lepidoptera larvae numbers around leks were approximately double that recorded in restocks. Although *M. gale* is present around the edges of some restocks within the Trossachs study area (J. Mulgrew, pers. comm.), as a light-loving plant and a wet site indicator (Hill *et al*. 1999; Skene *et al.* 2000), its presence is unlikely in the majority of restocks, where sites are drained and the early canopy closure of planted trees further restricts growth (see Chapter 3).

Drainage of restocks not only results in a habitat that is potentially less attractive to black grouse in terms of field-layer species composition, but may also pose a threat to the survival of chicks utilising restocks. Forest drains are approximately 1 m wide and up to 1 m deep with steeply sloping sides, and restocks are often crossed by a network of connected drains (J. Mulgrew, pers. comm.). Chicks can easily become trapped and drown in man-made forest drainage systems (Ludwig *et al*. 2008), particularly in the first 4 to 5 days of life before they are able to fly (Ludwig *et al*. 2006). Furthermore, in years when predator densities are high, nest predation can be higher in drained than un-drained areas (Ludwig 2007).

6.4.3 Importance of other invertebrate taxa

Other invertebrate taxa were as common in restocks as in habitat surrounding leks, which suggests that, with the exception of Lepidoptera larvae, invertebrate provision to black grouse chicks in restocks is at least comparable to lek habitat in terms of quantity. Selection of invertebrate taxa by grouse chicks may be dependent upon more than just availability of the most nutritious food items, and these other taxa are likely to be important. In Norway, willow grouse chicks selectively fed on Lepidoptera larvae during a warm summer, however, in a cold summer, their preference switched to smaller food items, such as true bugs and true flies (Erikstad & Spidso 1982). Rather than changes in taxa availability, the switch was thought to reflect changes in habitat use by chicks during wet weather; an avoidance of dense vegetation (which contained the best food supply) probably resulted in reduced nutrient intake, but prevented chicks from getting wet and risking hypothermia. The decreased field-layer density in restocks may allow easier movement of broods and the drying out of chicks in wet weather, however, decreased cover may also increase susceptibility to predation (Baines 1996). Furthermore, the generally drier habitat that appears to be present in restocks may be more suitable for beetles, true bugs and true flies, abundance of which decreased in wetter vegetation. The increased abundance and outbreaks of Tipulids in restocks and on taller vegetation of 80-90 cm may be linked to a preference of final instar larvae for *Juncus* spp. (Coulson 1962), cover of which is greater in restocks, although this link is tenuous and requires further investigation.

An obvious limitation in the comparison of habitats to determine relative 'quality' is that the quality of the lek habitats, against which restocks were compared, was itself unknown. By sampling around leks that had a stable or increasing number of males present at spring lek counts, it is presumed that habitat quality was either suitable or improving; therefore, comparisons with habitat in restocks should be meaningful.

6.4.4 Restock quality for black grouse and their broods

This is the first study to directly address differences between occupied black grouse habitat and potential habitat for black grouse in planted forest restocks. Results provide an important insight into how managed forest habitats differ from that utilised by black grouse around leks, and how differences in vegetation can affect abundance of food items (i.e. invertebrates). An obvious limitation to the study is the relatively small sample size of habitat data collected from transects around leks, and further data collection is necessary to determine the wider applicability and reliability of conclusions. Data collection limitations, however, were merely a result of simple logistical and time constraints, rather than inadequacies of study design, sampling or effort.

In terms of ‘quality’, field-layer vegetation provision to black grouse in restocks is poorer than around leks, as potentially important species such as *V. myrtillus*, *Eriophorum* spp. and *M. gale* occur less frequently or are absent. Presence of species such as *V. myrtillus* does not, however, appear to be critical for black grouse, and populations persist in areas where this species is virtually absent (Baines 1994). By contrast, the presence of *Eriophorum* spp. is likely to be important to black grouse during the egg-laying period (Angelstam 2004). As *M. gale* often supports large quantities of Lepidoptera larvae (this study; Baines *et al*. 1996), its presence is likely to indicate good quality habitat for broods. In terms of invertebrate abundance, the quality of second rotation restock habitat to black grouse broods appears to be similar to that recorded around leks, with the exception of reduced Lepidoptera larvae abundance, although this may be offset to some degree by the greater Tipulid abundance in restocks.

Although a temporal effect was not assessed in this chapter, habitat quality will be further reduced in younger restocks when compared with lek habitats, as suppression of field-layer vegetation by brash will delay development and limit invertebrate abundance. Furthermore, where preferred field-layer species are available in restocks, their presence is likely to be limited by canopy closure of planted trees, making restock habitat less attractive to black grouse. Therefore, future restock management for black grouse, which may aim to restore or encourage habitats containing preferred field-layer species, should be focussed on areas left unplanted where temporal constraints are not an issue.

Chapter 7: General Discussion

Black grouse have long been associated with commercial forestry in Britain and populations often flourish when new forests are planted (Thom 1986). As planted forests mature and are felled, second rotation restocks become available, although little is known about resources provided for black grouse and their broods in this habitat. The broad aims of this study therefore, were to investigate the determinants, composition and structure of field-layer vegetation in second rotation restocks, and to understand how contrasting forest management methods could increase suitable habitat for black grouse prior to canopy closure of planted trees. Subsequent changes to the abundance of predators resulting from habitat modification in restocks were also assessed. Furthermore, the influence of forest management upon the abundance of invertebrate food potentially available to broods in restocks was determined, and the comparison of restock and lek habitat allowed an objective assessment of restock 'quality' in terms of food and cover provision.

As a large proportion of afforested land is still to be felled and restocked in Britain (77% of conifer stands were categorised as ready to harvest within the next 20 years in 2000; Mason 2007), the current chapter will review how second rotation restocks and restocks of future rotations may influence future black grouse population trends, using findings from the present study.

7.1 Main overview of findings

Black grouse require a mosaic of habitats throughout the year (see Baines 1995 for a review) and as a relatively sedentary species throughout much of their range (including in Britain), they require these habitats to be within reasonably close proximity. This makes the species difficult to manage for, as a number of field-layer habitats are required, and field-layer height and density requirements differ according to seasonal requirements; i.e. nesting, brood cover, seasonal variation in adult dietary requirements and hence food plants, cover for moulting and from predators. Habitat requirements will also change with weather: tall, high density vegetation to provide adequate shelter, low-density vegetation for movement of chicks in wet weather, open areas for dust-bathing, etc. - no single habitat can provide for all requirements and no single management recommendation can be made that will improve all restock habitat.

In Britain, second rotation commercial plantations often form part of the home range of black grouse (Cayford *et al.* 1989; Haysom 2001), however, the relative 'value' provided by such habitats to black grouse (in terms of cover, food, and shelter) may differ between restocks and between forests. Topography strongly underpins field-layer habitat development in restocks; results from this study suggest that restocks on steeper ground are more likely to develop heather-dominated habitats likely to be more suitable for feeding, nesting and cover of black grouse adults, whereas flatter ground is more likely to be associated with wetter vegetation communities with taller graminoid vegetation and an increased field-layer density likely to be more suitable for young broods. These habitats may be further manipulated to benefit black grouse by forest management at the restocking stage. The redistribution of brash and subsequent reduction in its overall cover that occurs when preparing a site for restocking can lead to increased cover and height of heather in restocks, when compared with areas left unplanted. Thus, in planted areas, suitable field-layer vegetation is available to black grouse for a longer period between restock and canopy closure.

In the longer term, unplanted areas are likely to provide more suitable habitat for black grouse through the retention of open habitats, whilst also maintaining a viable seed source for apparently important species, such as *Calluna vulgaris*. On average, restocks in study plantations had c.40% of ground left unplanted in both study areas, which represents a large area of potentially suitable habitat that was not available during the first rotation. These open areas will need to be managed in the long-term, however, to prevent the natural regeneration of non-native tree species such as Sitka spruce, seedlings of which are present when clearfelled forest coupes are restocked.

One of the main restrictions preventing second rotation restocks from providing habitat of use to black grouse is likely to be the length of time that suitable field-layer habitat is available prior to canopy closure of planted areas, as also reported for forests of the first rotation (Pearce-Higgins *et al*. 2007). Results from this study suggest that in the south-west Highlands of Scotland (The Trossachs study area) where timber crops are mostly Sitka spruce and tree growth is rapid, the duration of availability of *C. vulgaris* to black grouse in restocks may be restricted to only six to seven years prior to the onset of canopy closure, with percentage cover being above 25% for just a few of these years. Results from the north-east Highlands (Sutherland study area) suggest that the duration of availability of preferred field-layer vegetation can be successfully increased by extending the fallow period prior to planting, however from a forestry perspective, this option may not be suitable in all areas due to increased weed growth within some restocks. Increasing the total length of time that habitats remain open from clearfell to canopy closure is likely to benefit black grouse, but increases in the abundance of some predators recorded in these modified habitats may offset these habitat benefits, and this possibility requires further investigation. An evaluation of trophic cascades must be integral to any assessment of the relative advantages and disadvantages of alternative management prescriptions for conservation of black grouse, or other species of potential conservation concern.

Prior to the current study, research into the provision of invertebrate food in second rotation restocks to black grouse chicks had not been conducted in Britain. Whilst dietary studies have highlighted the importance of several invertebrate food items to black grouse chicks, most emphasise Lepidoptera larvae as a key item, which is often recorded in relatively large quantities in the diet, and is taken frequently even when in short supply. Findings from this study suggest that increases in dwarf shrub cover (particularly heather) are likely to result in the increased abundance of Lepidoptera larvae, and that extended fallow periods are likely to prolong this increased availability to chicks. However, not all invertebrate taxa are positively associated with dwarf shrub cover, and the contrasting habitat preferences of each taxon highlight the benefits of a variety of dwarf shrub and graminoid habitats in restocks to ensure a diverse food supply, particularly in years when some taxa may not be so abundant (e.g. when the abundance of Lepidoptera larvae is reduced in wet summers; Erikstad & Spidso 1982).

7.2 Restocks in the wider landscape context

Results from the comparative study of second rotation restocks and leks, suggest that restocks are likely to provide habitat and food suitable for black grouse and their broods. Restocks lack cover of *Vaccinium myrtillus* and *Eriophorum* spp., which are likely to be an important food item for black grouse, and *Myrica gale*, which was positively related to the abundance of Lepidoptera larvae in this study. As the latter two species are associated with wetter habitats and all three species are unlikely to survive under the low-light conditions of a closed-canopy Sitka spruce plantation, it is unsurprising that their occurrence in young second rotation restocks was scarce. However, these species may colonise suitable areas of restocks left unplanted and undrained in future years, so it is vital that these areas are managed to prevent natural regeneration of non-native trees. Regeneration of native species, however, such as low-density birch scrub, is likely to be of further benefit to black grouse, however, careful consideration should be given to the loss of any suitable open habitat.

7.3 Main limitations of the study

One inevitable limitation is that the work could only be conducted as a correlative study. Therefore, whilst statistically significant results suggest associations of potentially important variables, caution is required in drawing conclusions until relationships are tested using replicated experiments (Green 1994). For example in this study, increased *C. vulgaris* cover and an increased abundance of food items for black grouse chicks recorded in areas of restocks left unplanted may result from forest management, but may also occur in some cases as a result of the ground type selected by foresters to be left unplanted, e.g. heathery areas. In forestry, replicated experiments are often impractical (due to the large areas that are required for fully-replicated and blocked research plots, and the decadal time-scales involved). This problem is not unique to this study, however, and is a routine element of much research in the earth sciences.

Further investigation into the use of second rotation restock habitat by black grouse is currently being undertaken in Perthshire, Scotland using radio-tagged birds, and data will provide valuable complementary information to this study. Although habitat use by black grouse in restocks in this study could not be formally assessed, black grouse are known to use some of the second rotation restocks sampled in this study frequently (J. Owen, pers. obs.). Results from the Perthshire study may shed light upon which habitats in restocks are used by black grouse, particularly in relation to seasonal usage.

7.4 Future considerations for restock management

The removal of brash from restocks for biofuel energy generation is a relatively new consideration for restock management (Moffat *et al*. 2006), and may contribute towards the achievement of Government renewable energy policies (Department of Trade and Industry 1999). Indications from this study suggest that brash can suppress heather recovery, particularly in the early years following restock. However, as the whole tree (including brash) is removed by cable-winch from areas of restocks with a more varied topography, cover of heather is increased in these areas. Cable-winched areas of restocks represent one of the greatest opportunities for the supply of brash to the biofuel market (Alexander 1996; Drake-Brockman 1996), but may also benefit black grouse, not only through the provision of increased heather cover, but also through the subsequent increase in abundance of some food items preferred by chicks. Thus, there may be potential benefits for black grouse and their broods from brash removal in restocks.

7.5 Conservation management for black grouse in European managed forests

Changes to the forest structure in Scandinavia, from natural forest to managed single-species and single-cohort stands (Peltola 2006) have probably contributed to the decline of black grouse and other woodland grouse, although the mechanisms of this interaction are not yet well understood (Lakka & Kouki 2009). Changes to forest structure and management are often implicated in the decline of black grouse, along with Capercaillie *Tetrao urogallus* and hazel grouse *Bonasa bonasia* (Gregersen & Gregersen 2009; Aberg *et al.* 2003; Helle & Helle 1991). In Britain, changes to forest structure resulting from tree maturation within planted forests are likely to have contributed to declines (Pearce-Higgins *et al*. 2007).

Whilst clearfelling was the dominant forestry method in parts of Scandinavia from the 1950's (Bernes 1994), the use of felling methods that do not leave the ground completely bare have increased during the last two decades (Hannerz & Hanell 1997), and the intensive form of forest management common to Scotland, i.e. clearfelling large forest blocks then restocking with fast-growing, non-native trees, is rarely practised. Research often aims to assess the results of different timber-felling regimes in forests that provide an alternative to clearfell and allow a vegetative under-storey to develop, such as selection-felling at varying intensities (e.g. Jalonen *et al.* 2001; Bergstedt & Milberg 2001; Khanina *et al.* 2007). Many studies report clearfelling to be detrimental to forest biodiversity, particularly when compared with less-intensive forms of forest management (e.g. Atlegrim & Sjoberg 1995), although this is not necessarily the case for all species (e.g. Atlegrim *et al*. 1997).

Changes to black grouse populations as a result of forestry are difficult to separate from climate-induced changes (Ludwig 2007), which have resulted in warmer weather and the push of climatic zones northwards, imposing a demonstrable effect upon living systems (Parmesan & Yohe 2003). In some areas, black grouse have responded to warmer weather in spring by advancing egg-laying, however, early summer has not advanced, and chicks now have to face colder post-hatching conditions and an increased risk of mortality (Ludwig *et al.* 2006). Therefore, in addition to the current challenges of a changing landscape, black grouse will also need to adapt to a changing climate, with possible effects upon demography, geographic range and breeding phenology.

7.6 Management recommendations

As a direct result of this study, a number of recommendations can be made for the management of second rotation restocks for black grouse:

1. When excavators are preparing ground for re-planting, brash should be piled or redistributed to ensure maximum light availability to recovering field-layer vegetation.

2. Areas of suitable *C. vulgaris* habitat within restocks should be encouraged to grow to maturity, to an age, height and density preferred by nesting black grouse hens and to ovipositing female Lepidoptera (>40 cm).

3. Where weed growth is unlikely to be a major issue for foresters, an extended fallow period should be considered to maintain habitats suitable for black grouse for the maximum number of years possible prior to canopy closure of planted trees.

4. A greater diversity of invertebrates, of taxa known to comprise a substantial part of the black grouse chick diet, is likely to result from a more heterogeneous habitat in restocks. Whilst mature, tall stands of heather are likely to provide

suitable habitat for adults and nesting hens, a more species-diverse field-layer containing additional dwarf shrub species and graminoids is likely to benefit chicks.

5. Regenerating non-native trees naturally encroach onto areas of restocks left unplanted. These areas should be maintained to keep unplanted areas open and allow regeneration of native birch and willow scrub.

6. Trees should not be re-planted in boggy, wet areas of restocks, or around areas of *Eriophorum* spp., *V. myrtillus* or *M. gale*. Cover of these species should also be encouraged.

7. Minimum drainage in restocks should be considered to allow suitable black grouse habitat to develop. In unplanted areas, any remaining operational drains should be blocked.

8. Whilst results can be extrapolated to other afforested areas in Scotland, the re-vegetation of restocks will differ considerably according to a number of factors, including: geographical location; topography; slope; altitude; soil moisture content; timber harvesting regime and brash management. These factors should be taken into consideration before management recommendations are actioned.

7.7 Suggestions for further work

Results from the current study have prompted further questions that warrant investigation:

1. Further research into the development of field-layer vegetation in areas of restocks left unplanted is necessary, particularly to investigate the recovery of important species such as *Eriophorum,* and to ascertain how much of a problem the encroachment of non-native tree seedlings is likely to be on open, unplanted ground in the future.

2. Radio-tracking of adult black grouse should aim to determine which aspects of field-layer vegetation in restocks are important, and if there is seasonal usage of restocks.

3. Black grouse chicks should be radio-tracked and faecal analysis conducted to determine the most important invertebrate taxa taken by chicks in restocks, and to determine if food items differ from those selected in other habitats.

4. Implications of permethrin spraying in restocks (to reduce damage to planted trees by pine weevil *Hylobius* spp.) upon non-target invertebrate taxa of importance to black grouse should be assessed.

5. Forest drains pose a significant threat to chick survival (Ludwig *et al*. 2008), and the risk to chicks using second rotation restocks should be assessed. Alternatives to standard drainage systems in restocks should be discussed, and the effectiveness of current management options, including back-filling of drainage trenches with tree stumps should be assessed.

6. Trials of planting or sowing to accelerate re-colonisation of black grouse friendly species (*Myrica gale, Eriophorum* spp.*, Vaccinium myrtillus, Calluna vulgaris*) should be conducted soon after felling on areas of restocks to remain unplanted.

7. Further studies into *C. vulgaris* seed bank and seed rain availability in second rotation restocks should be conducted, to inform management of this resource in the third and future rotations. It is unknown whether areas currently left unplanted are sufficient to provide adequate seed sources to colonise the next generation of restocks.

8. Further investigation into the abundance and movement of predators in second rotation restocks should be conducted, particularly in restocks where the fallow period has been extended. Additionally, any temporal variation in predator abundance should be assessed over the period from egg-laying to chick fledging. The practice of leaving standing deadwood of native tree species in restocks should be investigated, as single trees remaining in restocks appear to provide good perching posts for avian predators such as goshawks.

9. The viability of restock management options suggested, i.e. leaving areas unplanted and extending fallow periods, should be assessed in terms of forest economics.

10. As brash is removed from restocks for biofuel, studies should be conducted to investigate potential benefits (or otherwise) to black grouse from subsequent changes to field-layer vegetation.

11. To date, a limited set of third-rotation restocks is currently available for study in Scotland. As forests are clearfelled in the future, studies should focus upon re-vegetation of the field-layer to determine changes in species composition that may be of importance to black grouse in restocks of the third rotation.

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Appendix

Appendix Table 1: Inter-correlated variables in restock field-layer vegetation sampling data (Chapter 3). Top right of table considers variables used in analyses of restocks with a more varied topography (timber extraction by harvester/forwarder or cable-winch; Trossachs dataset only), bottom left of table refers to variables used in analyses of vegetation in restocks where only harvesters/forwarders were used (Trossachs and Sutherland datasets).

	Restock age	PT	ET	Restock size	Open space	Previous crop	No. of trees	MTH	Tree cover	Study area	Altitude	Slope
Restock age		0.057	-0.087	-0.08	-0.036	0.040	-0.023	**0.602**	**0.509**^{*2}	-	-0.243	0.079
PT	0.053		0.070	-0.064	-0.136	0.059	**0.724**	[0.579]	[0.475]	-	-0.075	-0.037
ET	-	-		0.180	0.035	0.001	-0.079	0.056	0.047	-	-0.204	**-0.765**
Restock size	-0.016	-0.010	-		-0.055	0.173	-0.003	-0.132	-0.191	-	-0.041	-0.139
Open space	0.005	-0.082	-	-0.209		0.016	-0.102	-0.190	-0.147	-	-0.113	0.110
Previous crop	0.024	-0.028	-	[-0.407]	0.156		-0.045	0.083	0.054	-	-0.108	0.016
No. of trees	0.045	**0.758**	-	0.028	-0.041	-0.075		0.319	0.220	-	-0.007	0.026
MTH	**0.622**	[0.523]	-	-0.071	-0.205	-0.028	0.359		**0.860**	-	-0.304	-0.038
Tree cover	**0.510**^{*1}	[0.498]	-	-0.104	0.121	-0.033	0.336	**0.778**		-	-0.223	0.007
Study area	0.088	-0.055	-	[-0.479]	0.064	**0.851**	-0.076	0.055			-	-
Altitude	-0.186	-0.037	-	0.250	-0.017	[-0.529]	-0.022	-0.221	-0.146	[-0.524]		0.251
Slope	0.108	0.121	-	0.127	0.075	-0.078	0.157	0.046	0.059	-0.058	0.194	

PT denotes: Planting Type, ET: Extraction Type, MTH: mean tree height. ^{*1}when considering transects in planted areas only, r=0.744, ^{*2}: r=0.738. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4. Refer to Table 3.2 for further description of variables.

Appendix Table 2: Datasets used in statistical analyses to investigate the influence of forest management upon vegetation and invertebrate availability to black grouse. Light grey fill indicates datasets used, dark grey fill indicates dataset not used. Management types considered are 'Tree extraction method' (conventional harvesting HF or cable-winch WI) and 'Fallow period length' (Standard, Extended or Super-extended).

				Trossachs data (2008)		Sutherland data (2009)		
Data chapter	Dataset analysed	Number of restocks/leks	Number of transects	Tree extraction method		Fallow period Length		
3	Vegetation[1]	49	441	HF	WI	Standard	Extended	Super-extended
	Vegetation[2]	36	337	HF	WI	Standard	Extended	Super-extended
4	Vegetation	36	78	HF	WI	Standard	Extended	Super-extended
	Invertebrates	36	78	HF	WI	Standard	Extended	Super-extended
5	Vegetation	36	288	HF	WI	Standard	Extended	Super-extended
	Invertebrates	36	72	HF	WI	Standard	Extended	Super-extended
	Predator	24	24	HF	WI	Standard	Extended	Super-extended
6	Vegetation[3]	72	625 (restocks) 78 (leks)	HF	WI	Standard	Extended	Super-extended
	Invertebrates[3]	8	20 (restocks) 12 (leks)	HF	WI	Standard	Extended	Super-extended

[1] Conventionally harvested sites only. [2] Sites with more varied topography. HF refers to tree extraction by mechanical harvester and forwarder; WI refers to removal by cable-winch. Fallow period lengths are Standard (2 years), Extended (3 to 5 years) and Super-extended (6 to 7 years). See methods section of relevant chapter for further information. [3] Vegetation and invertebrates collected from all management types, but types not differentiated between in analyses.

Appendix Table 3: Inter-correlated variables in a) Model 1: time, management and site variables, and b) Model 2: vegetation variables; recorded in restocks in The Trossachs study area (Chapter 4).

a) Model 1	Restock age	PT	ET	Restock size	Open space	Dist. from edge	Previous crop	No. of trees	MTH	Tree cover	Altitude
PT	0.028										
ET	-0.084	0.083									
Restock size	-0.185	-0.109	0.162								
Open space	0.017	-0.106	0.051	-0.037							
Dist. from edge	0.139	-0.003	0.115	0.003	[-0.411]						
Previous crop	0.001	0.096	-0.002	0.168	0.043	-0.026					
No. of trees	-0.072	**0.611**	-0.192	-0.106	-0.119	-0.029	-0.084				
MTH	[0.548]	**0.604**	0.040	-0.240	-0.145	0.106	0.054	0.298			
Tree cover	***0.466**	[0.516]	-0.027	-0.288	-0.107	-0.004	0.079	0.245	**0.893**		
Altitude	-0.299	-0.040	-0.165	-0.033	-0.100	-0.348	-0.107	0.006	-0.309	-0.24	
Slope	0.083	-0.020	**-0.710**	-0.093	0.156	-0.214	-0.027	0.079	-0.046	0.015	0.155

PT denotes: Planting Type, ET: Extraction Type, Dist. to edge: Distance from restock to plantation edge, MTH: mean tree height. Refer to Chapter 4, Table 4.2 for further description of variables. *when considering transects in planted areas only, r=0.732. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4.

b) Model 2	Moisture score	Brash cover	Field-layer density	Vegetation height	Dwarf shrub cover
Brash cover	0.044				
Field-layer density	0.214	-0.242			
Vegetation height	0.111	[-0.402]	[0.412]		
Dwarf shrub cover	-0.137	[-0.420]	[0.563]	0.170	
Graminoid cover	**0.603**	-0.247	0.039	0.166	-0.300

'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999). Refer to Chapter 4, Table 4.2 for further description of variables. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4.

Appendix Table 4: Inter-correlated variables in a) Model 1: time, management and site variables, and b) Model 2: vegetation variables; recorded in restocks in the Sutherland study area (Chapter 5).

a) Model 1

	Restock age	Fallow group	PT	Restock size	Open space	Previous crop	No. of trees	MTH	Tree cover	Altitude
Fallow group	-0.200									
PT	0.000	0.000								
Restock size	-0.050	0.320	0.000							
Open space	-0.098	0.057	0.000	-0.173						
Previous crop	-0.317	0.033	0.000	-0.342	0.183					
No. of trees	-0.021	0.106	**0.798**	0.051	-0.024	0.024				
MTH	**0.627**	-0.152	[0.411]	-0.087	-0.209	-0.203	0.317			
Tree cover	***0.485**	-0.101	[0.489]	-0.053	-0.092	-0.209	0.359	**0.699**		
Altitude	0.171	0.164	-0.026	0.168	-0.015	-0.130	0.007	0.137	0.041	
Slope	-0.043	-0.216	0.030	-0.013	-0.002	0.077	0.020	-0.092	-0.083	-0.263

PT denotes: Planting Type, MTH: mean tree height. Refer to Chapter 5, Table 5.2 for further description of variables. *when considering transects in planted areas only, r=0.788. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4.

b) Model 2

	Moisture score	Brash cover	Field-layer density	Vegetation height	Dwarf shrub cover
Brash cover	0.100				
Field-layer density	-0.267	-0.235			
Vegetation height	-0.036	-0.001	0.208		
Dwarf shrub cover	-0.277	-0.328	0.452	0.109	
Graminoid cover	0.327	-0.065	-0.316	0.117	-0.504

'Moisture score' variable refers to the Ellenberg moisture score (Hill *et al.* 1999). Refer to Chapter 5, Table 5.2 for further description of variables. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4.

Appendix Table 5: Inter-correlated variables in a) Model 1: Site variables, and b) Model 2: vegetation variables; recorded in restocks and in habitat within 1 km^2 of black grouse leks in the Trossachs and Sutherland study areas (Chapter 6).

a) Model 1

	Study area	Lek vs. restock	Altitude
Lek vs. restock	-0.041		
Altitude	[-0.512]	0.031	
Slope	[-0.478]	0.190	0.374

Refer to Chapter 6, Table 6.2 for further description of variables. Bold type denotes strong correlation r>0.6. Square brackets denote 0.6>r>0.4.

b) Model 2

	Moisture score	Field-layer density	Vegetation height	Dwarf shrub cover
Field-layer density	-0.026			
Vegetation height	0.160	0.245		
Dwarf shrub cover	-0.301	0.372	-0.051	
Graminoid cover	0.387	-0.188	0.157	[-0.519]

‘Moisture score’ variable refers to the Ellenberg moisture score (Hill *et al.* 1999). Refer to Chapter 6, Table 6.2 for further description of variables. Square brackets denote 0.6>r>0.4.

Appendix Table 6: List of species recorded in restocks and in habitat surrounding leks in the Trossachs and Sutherland study areas.

Code	Scientific name	Common name
Agr_spp	*Agrostis* spp.	Bent grass spp.
Ant_odo	*Anthoxanthum odoratum*	Sweet vernal grass
Ble_spi	*Blechnum spicant*	Hard fern
Call_vul	*Calluna vulgaris*	Ling heather
Car_bin	*Carex binervis*	Green-ribbed sedge
Car_ech	*Carex echinata*	Star sedge
Car_nig	*Carex nigra*	Common sedge
Car_ova	*Carex ovalis*	Oval sedge
Car_vir	*Carex viridula*	Common yellow sedge
Cha_ang	*Chamaenerion angustifolium*	Fireweed
Cir_spp	*Cirium* spp.	Thistle spp.
Des_cae	*Deschampsia caespitosa*	Tufted-hair grass
Des_fle	*Deschampsia flexuosa*	Wavy-hair grass
Dig_pur	*Digitalis purpurea*	Foxglove
Eri_ang	*Eriophorum angustifolium*	Common cottongrass
Eri_cin	*Erica cinerea*	Bell heather
Eri_tet	*Erica tetralix*	Cross-leaved heath
Eri_vag	*Eriophorum vaginatum*	Hare’s-tail cottongrass
Fes_spp	*Festuca* spp.	Fescue grass spp.
Gal_apa	*Galium aparine*	Goosegrass
Gal_sax	*Galium saxatile*	Heath bedstraw
Hol_spp	*Holcus* spp.	Grass spp.
Jun_art	*Juncus articulatus*	Jointed rush
Jun_bul	*Juncus bulbosus*	Bulbous rush
Jun_con	*Juncus conglomeratus*	Compact rush
Jun_eff	*Juncus effusus*	Soft rush
Jun_squ	*Juncus squarrosus*	Heath rush
Luz_spe	*Luzula* spp.	Woodrush
Mol_cae	*Molinia caerulea*	Purple moor grass
Nar_str	*Nardus stricta*	Mat grass
Oxa_ace	*Oxalis acetosella*	Wood sorrel
Ple_spp	*Pleurozium* spp.	Moss spp.
Pol_spp	*Polytrichum* spp.	Moss spp.
Pot_ere	*Potentilla erecta*	Tormentil
Pte_aqu	*Pteridium aquilinum*	Bracken
Rac_spp	*Racomitrium* spp.	Moss spp.
Rub_fru	*Rubus fructicosus*	Bramble
Sph_spp	*Sphagnum* spp.	Moss spp.
Vac_myr	*Vaccinium myrtillus*	Blaeberry