Aspects of the ecology of black grouse (*Tetrao tetrix*) in plantation forests in Scotland

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Declaration

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

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

Susan Haysom

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Abstract

Aspects of the ecology of black grouse (*Tetrao tetrix*), a species of international conservation concern, in commercial plantation forests were investigated between 1996 – 1998 at three study areas in Scotland. The aim was to identify the species' habitat and area requirements in first and second rotation forestry. The distribution of males was assessed using lek surveys and studied at two spatial scales in the mixed rotation forest landscape of Cowal, Argyll and at two spatial and temporal scales in highland Perthshire – a less afforested region. In addition, a radio-tracking study was undertaken to examine the habitat selection of broods in two first rotation plantations in north Perthshire.

Pre-thicket forestry formed a preferred habitat but, in terms of lek distribution, black grouse did not differentiate between first and second rotation pre-thicket habitat patches. Patch size, the total amount of forestry in the area, the proportion that was pre-thicket stock and its level of fragmentation, however, were all correlated with the probability of a location holding a lek and the number of males attending it. Lek isolation reduced the number of males in attendance and increased the likelihood of the lek declining over time.

Brood habitat preferences differed from those of adult birds. Broods selected habitats that were 'open' enough to support a rich ground flora and presumably an adequate invertebrate fauna but also 'closed' enough to provide cover, representing a compromise between foraging potential and predation risk. Brood roost sites differed by having shorter trees but a higher degree of cover 1 – 1.5 metres above the ground.

Results from the different study areas and age classes are compared and contrasted and the implications of the research findings for 'black grouse friendly' forestry management are discussed. Finally, suggestions for further work are made.

Acknowledgements

First and foremost, I would like to thank my supervisors for their supervision and support during this research project; David Baines particularly in the field years and Peter Hudson in the writing up period. Ken Wilson revealed some of the mysteries of S-PLUS and Dan Tompkins, one of Peter's post-doctoral assistants, provided exceptionally useful advice on statistical analysis and was a valued sounding board. Thank you all.

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I am very grateful to all the landowners, agents and managers who allowed me access to their land.

The Perthshire Black Grouse Study Group generously allowed me to use their lek survey data they have collected since 1990. I would like to thank all the members of the group and the chairman, Martin Robinson, in particular.

Whilst not formally connected to this project, the co-operation and assistance provided by the Forestry Commission and Forest Enterprise were invaluable, not least for providing accommodation in the 1996 field season. In particular, Dave Anderson, Alistair Clark and Hugh Gibb, the Forest Enterprise rangers in Cowal were extraordinarily tolerant of my dawn activities and provided a great deal of information about leks in the area. On one notable occasion Dave rescued the car from a quad-bike track – thanks! Kenny Hay, Geoff Shaw, Ian Adams and John Spittal were also very helpful. Steve and Linda Petty's interest, empathy and hospitality helped to keep me this side of sanity.

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Finally, Alistair and my family have been exceptionally supportive. Thank you so much for your bemused forbearance, enthusiasm and understanding. Alistair has sorted out numerous electronic glitches and helped me to keep calm in stressful situations ... in return I have *almost* forgiven him for being more excited about a submarine than one of my best leks! Thank you. And last, but not least, all the big black chickens out there.... may you live long and prosper.

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Chapter 1 General Introduction

1.1 Introduction

The aim of this chapter is to set the thesis in context. In the following chapters the output from a research project initiated by David Baines (Game Conservancy Trust) and Peter Hudson (University of Stirling), funded by the Martin Wills Fund, is presented. The broad aim of the research was to identify the habitat and area requirements of black grouse (*Tetrao tetrix*), a species of international conservation concern, in first and second rotation forestry plantations. Management recommendations for the restructuring of commercial forests to the benefit of black grouse will be produced once the findings have been thoroughly tested by future studies.

1.2 The Black Grouse and Its Decline

The black grouse is a large, sexually dimorphic, sedentary woodland grouse whose range covers nearly all the Palearctic forest belt (Schmitz 1997; Cayford 1993). They are regarded as birds of the early stages of successional forest and forest edge habitats especially in boreal zones (Baines 1993a). Other favourable habitats include moorland and heathland dominated by heather (*Calluna vulgaris*), peat-bogs, rough grassland, open pine (*Pinus* spp.) forest and young conifer plantations (Cramp & Simmons 1980; Picozzi 1986a & b; Schmitz 1997; Sharrock 1976; Baines 1990 & 1993a; Catt *et al.* 1994; Kolstad *et al.* 1985; Robel 1969a; Parr & Watson 1988; Wegge 1983).

Fennoscandia, Russia, Belarus and the Baltic States form the stronghold of the European population, Britain supports a meagre 2 % (Mead 2000), whilst Denmark, Belgium and Germany hold relatively insignificant numbers (Schmitz 1997). The European population, currently estimated to be 700,000 individuals (Mead 2000), is steadily declining both in terms of numbers and range. The range contraction is particularly severe at the southern and western edges (Schmitz 1997; Cayford 1990a). In Holland, Denmark, Belgium and much of Central Europe populations have gone extinct or declined to extremely low levels (Hudson & Baines 1993; Picozzi 1986a; Bauer & Kalchreuter 1984; Niewold 1990). In Southern Europe only the Alps support a relatively significant population and it too is declining (Hudson & Baines 1993). Worryingly, there is little genetic variation present within the Italian Alps population (Bagliacca *et al.* 1997).

Some authors have claimed that populations in Scandinavia and Russia are 'relatively healthy and increasing' (Hudson & Baines 1993) or 'thriving' (Picozzi 1986a) yet the Finnish population is thought to have halved in 35 – 50 years (Helle *et al.* 1987) and black grouse in Norway have declined markedly since the late 1960s (Wegge 1983).

Black grouse are undoubtedly of special conservation concern. They are in SPEC Category 3[1] and their threat status has been described as 'vulnerable'[2] (Schmitz 1997). In Britain,

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[1] Species whose global populations are not concentrated in Europe, but which have an Unfavourable Conservation Status in Europe.

[2] Any of the following: i) **population in large decline and of > 10,000 breeding pairs or 40,000 wintering individuals**; ii) population in moderate decline *and* population < 10,000 breeding pairs and not marginal to a larger non-European population or European wintering and entire flyway population <40,000 birds; iii) population neither in moderate nor in large decline but <2,500 breeding pairs and not marginal to a larger non-European population, or European wintering and entire flyway population <10,000 birds and therefore at risk due to the susceptibility of small populations. Text in bold font indicates the category in which black grouse is placed

they have been placed on the 'red list'[3], i.e. of high conservation concern, of the revised 'Red Data List' on the basis that there was a ≥ 50 % decline in the United Kingdom breeding population over the previous 25 years and also a historic population decline (Gibbons *et al.* 1996a). They are protected throughout Europe under Annex II/2 of the EC Birds Directive and Appendix III of the Berne Convention.

The dramatic decline in Britain is well documented and fairly typical of that elsewhere. One of the earliest references to the species, known then as *mure cok* or *hene*, was in the 15th century when they were thought to be present, although not well known, in the eastern counties of England (Yapp 1983). They were recorded regularly throughout England, including Kent, Surrey and Sussex, in the 16th and 17th centuries, but less regularly during the 18th century with some authors attributing this reduction to over-hunting (Holloway 1996b).

Black grouse were "commonly found in virtually every English county at the end of the 19th century" (Gladstone 1924 cited in Baines 1991). Nevertheless, the 19th century witnessed a general decline throughout south and south-west England, although Welsh populations were more stable and even with game preservation measures and re-introduction attempts many populations became extinct in the first three decades of the 20th century (Holloway 1996b). Despite this pattern, local increases occurred in parts of Wales and Scotland where large-scale upland afforestation in the 1940s and '50s provided new habitat (Gibbons *et al.* 1996b; Holloway 1996b; Mead 2000). Unfortunately, the positive effects of forestry could be short-lived as the black grouse often remained only until canopy closure (Hudson &

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[3] Red listed species are either globally threatened or in rapid decline in the United Kingdom currently or historically.

Baines 1993). Grove and co-workers (1988) estimated the Welsh population of males to be less than 300 in 1986 and speculated that the population had been in decline since the mid-1970s. Ten years later, a full census found only 153 spring displaying males (Hancock *et al.* 1999).

The British distribution as a whole shrank dramatically throughout the 20th century. The range as plotted in 'The New Atlas of Breeding Birds in Britain and Ireland 1988 – 1991' (Hudson & Baines 1993) had decreased by some 28 % from that plotted in 'The Atlas of Breeding Birds in Britain and Ireland 1968 – 1972' (Sharrock 1976). In the period between the production of these two atlases the populations of Exmoor, Dartmoor and the Quantocks went extinct (Hudson & Baines 1993) and it seems likely that the dwindling Peak District population has also followed suit, as reported by Mead (2000).

It was not until the most recent survey of British black grouse that the full seriousness of the decline was recognised. The 1995/6 survey estimated the entire population of spring-displaying males to number a mere 6,510 (95 % confidence limits: 5000 – 8100) with 70 % of these located in Scotland (Hancock *et al.* 1999). Prior to this, numbers had been thought to be stable at a national level over a period of 40 years, despite a 75 % decline in the Scottish bag since 1935 (Baines 1990; Baines 1993). Only two years after the latter publication, analysis of shooting bags suggested a 90 – 93 % decline in the number of black grouse shot in Scotland and the north east of England (Baines & Hudson 1995). However, the authors did suggest that shooting bags might not have given an accurate index of the population. They believed that the analysis of shooting records might have exaggerated the decline and estimated the population of spring-displaying males to be 25,000 (95 % confidence limits: 13,800 – 36,700). The previous population estimate, for the period 1988 – 1991, had been in the region of 10,000 – 15,000 individuals (Hudson & Baines 1993) and shortly prior to this another author had also placed his estimate at "the lower end of the 10,000 – 100,000 category" (Picozzi 1986a).

Population declines have been linked, often through the frequently used procedure of comparing areas or time periods with different trends (Green 1994), with various factors and combinations of factors including: fragmentation and degradation of upland habitats through agricultural improvement; blanket afforestation; increased number of predators; over-shooting; unfavourable weather conditions; increased disturbance of breeding grounds; and overgrazing by sheep and deer (Baines 1992, 1993b & 1996; Cayford 1993; Hudson & Baines 1993; Marchant *et al.* 1990; Picozzi 1986a; Schmitz 1997; Tapper 1992; Cayford & Walker 1991; Baines *et al.* 1994 & 1996; Baines & Hudson 1995; Bauer & Kalchreuter 1984; Cayford & Hope Jones 1989; Garson & Starling 1990; Helle *et al.* 1987; Niewold 1990; Parr & Watson 1988; Fuller & Gough 1999; Hudson 1990).

1.3 Forestry and Wildlife in Upland Britain

Coniferous afforestation has been cited as having both positive and negative effects on black grouse. This seemingly contradictory position is the case for many upland and woodland species, e.g. voles (*Microtus* spp.) (Staines 1983), hen harrier (*Circus cyaneus*) (Watson 1977d), red kite (*Milvus milvus*) (Newton *et al.* 1996), red squirrel (*Sciurus vulgaris*) (Lurz *et al.* 1995), and willow warbler (*Phylloscopus trochilus*) (Moss 1979).

This apparent paradox can be explained by the occurrence and density of many vertebrate species varying with the successional stage, species composition and scale of the forest (Staines *et al.* 1987; Petty & Avery 1990a). For example, the densities of spruce grouse

(*Dendragapus dendragapus*) have been shown to be related to the successional stage of lodgepole pine (*Pinus contorta*) forest (Schroeder & Boag 1991; Whitcomb *et al.* 1996).

Afforestation has been described as "the greatest modern threat" to upland habitats (Holloway 1996a; Ratcliffe 1990). The massive expansion of large-scale planting of non-native conifers gave rise to a huge outcry from conservationists and the general public in the latter half of the 20th century (see, for example, Tompkins 1989 and Lowe *et al.* 1986). Objections were made on the incalculable grounds of aesthetics and access. More quantifiable concerns were expressed over: the loss of fragile and uncommon habitats such as heathlands, moorlands, and peat bogs or flows; acidification and increased sediment load of watercourses; and increased use of biocides and fertilisers (Tompkins 1989). Whilst many of these represented real issues, beyond the remit of this thesis, the scale of the problem was thought by some to have been overstated. Much of the 'newly' afforested land was that which previously had had its native woodland destroyed in the period leading up to the 17th century (Holloway 1996a). The vast single-species single-age monoculture conifer crops of early British industrial forestry, however, bore little resemblance to the natural climax vegetation that covered about a quarter of Scotland in prehistoric times (Summers *et al.* 1999).

The structure and composition of industrial forest mosaics differ from native forests by having a rectangular age and patch size distribution rather than the negative binomial one of forests patterned by fires, insect outbreaks, storm felling and other natural processes (Drapeau *et al.* 2000; Hansson 1992). Thus, modern forestry can have low structural complexity and lack over-mature and dead trees which results in the absence of several key guilds from the avifauna it supports (French *et al.* 1986; Newton 1983).

Commercial forests in upland Britain are managed on rotations of 40 – 60 years (Busby 1974) with the crop progressing through a sequence of four stages within that period as shown below (Table 1.1).

Table 1.1. Four stages within one commercial conifer rotation (after Ratcliffe 1987).

Stage	Description	Features
Establishment	From planting till tree height 1 m	Increasing ground vegetation quality and abundance. Low levels of cover.
Pre-thicket	Tree height 1 – 3 m	High ground vegetation quality and abundance with increasing levels of cover.
Thicket	Tree height 3 – 10 m	Canopy closes. Ground vegetation declines & disappears. Variable tree growth creates glades.
Pre-felling	Tree height > 10 m	Limited ground flora returns.

Prior to afforestation of open hill ground, which was commonly heavily over-grazed (Anderson & Yalden 1981; Cadbury 1993; Ratcliffe 1990; Welch 1998), many plantation sites were fenced to exclude sheep and deer. The reduced grazing pressure and the shelter of young trees allowed the ground vegetation to flourish (Welch & Scott 1997) triggering a rapid and large increase in the abundance of invertebrates, meadow pipits (*Anthus pratensis*) (Moss 1979) and small mammals, e.g. field voles (*Microtus agrestis*). These in turn attract raptors, e.g. short-eared owl (*Asio flammeus*), kestrel (*Falco tinnunculus*) and hen harrier (Garthwaite 1971; Watson 1977a & b; Shaw 1995; Staines 1983; Petty & Avery 1990b). This temporary phenomenon only occurs during the establishment and pre-thicket stages, however, and seldom exceeds a 20 year period depending on the tree species (Welch & Scott 1997) and the density of planting (Sakura *et al.* 1985).

There is generally an increase in the diversity and density of songbirds when upland habitats are afforested (Bibby *et al.* 1985; Newton 1983), especially in edge habitats (Hansson 1992; Hawrot & Niemi 1996; Newton 1983; Patterson *et al.* 1995; Petty &

Avery 1990a). However, open country species, many of which are of conservation concern, e.g. raven (*Corvus corax*) and golden eagle (*Aquila chrysaetos*), can be displaced by plantations (Moss 1979; Newton 1983; Ratcliffe 1990). Ornithologists also feared that upland conifer forests might affect the numbers of birds on adjacent unplanted moorlands, but so far there is little evidence to support this (Avery 1989) except indirectly via elevated predation pressure (see below).

Fewer vertebrates, chiefly deer and generalist predators (Staines 1983), use the thicket and pre-felling forest stages. Indeed, many studies have shown that modern forestry supports higher densities of generalist predators than native forests or agricultural land (e.g. Andrén & Angelstam 1988; Andrén 1992; Andrén *et al.* 1985; Hansson 1992; Storaas & Wegge 1987). Predator control is practised in forestry plantations but at much lower levels than in areas where agricultural and game-rearing interests predominate (Tapper 1992). The increase in the numbers of generalist predators when forests are fragmented and a subsequent impact on woodland grouse breeding success via nest predation is well documented (e.g. Kurki *et al.* 1997; Kurki & Lindén 1995; Storaas & Wegge 1987) and has been implicated in population declines recorded in Fennoscandia in recent decades (Kurki *et al.* 2000). One study of capercaillie (*Tetrao urogallus*) in Norway also suggested that forest fragmentation by logging "caused the clumped lek system to split into a dispersed pattern of smaller leks and single displaying males" (Rolstad *et al.* 1997). In Britain, the afforestation of bare ground has produced similar fragmented forestry patterns by the reverse process.

Once the trees reach felling age they are harvested generally in a swathe as 'clearfell'. This marks the end of the first rotation. Clear-cutting is controversial (Martinsson 1995) and public opposition to it is widespread (Allan 2000; Bliss 2000). However, it is at this stage that the greatest opportunity to restructure the forest becomes available (Petty & Avery 1990d) and, if desired, it is possible to create a mixed forest of irregular structure (Blyth 1993). The second and subsequent rotations begin with the re-planting of the harvest site.

In 1980, the operative year of the most recent British woodland census, 2 % of the total woodland cover had been clearcut and most of this was due to be replanted within two to four years of harvesting (Locke 1984). Locke predicted that this proportion would increase as the major post-war plantings approached rotation age, at the turn of the century, but emphasised that this would merely be a stage in the life of successive tree crops and not an absolute loss of forest cover. In Scotland the area of forest planted increased in every decade up to 1980 (Petty & Avery 1990c), hence the proportion of cleared, and eventually restocked, land will remain high at least until 2040. A flush of vegetation and increase in small mammals is repeated during the clearcutting and replanting phases (Wegge & Storaas 1990) and species recorded in 1st rotation establishment phase stock also use 2nd rotation stock, e.g. hen harrier (Petty & Anderson 1986) and short-eared owl (Shaw 1995). However, retained trees and debris from the earlier planting increase the structural complexity and consequently restocks have been shown to support a higher diversity and density of songbirds than first generation plantings (Currie 1983; Currie & Bamford 1981). In the past, site preparation that included the clearance of harvest sites was recommended, but increasingly scarification and mounding techniques are used instead (Hibberd 1991).

1.4 Black Grouse and Forestry in Britain

In Wales and Scotland black grouse are known to be increasingly dependent on the pre-thicket stages of plantation forests (Cayford & Hope Jones 1989). The habitat requirements of black grouse in non-forest habitats are relatively well known (see e.g. Baines 1993a & Garson & Starling 1990) and some research has been undertaken in commercial plantations in Wales (Cayford & Hope Jones 1989; Cayford 1990b). However, their habitat requirements in 2nd rotation plantation forestry have not yet been examined fully and as a consequence this research project was initiated.

1.5 Thesis Structure

Data were collected in the field from areas in Cowal, Argyll and Perthshire; further details of the sites used are given in Chapter 2.

Chapters 3 and 4 address, at two spatial scales, the distribution of lekking black grouse in plantation forests. This work was carried out in Cowal chiefly by the author but with invaluable contributions from Forest Enterprise (FE) and private forestry company staff (named in the acknowledgements) and Sue Raven, who assisted me for three weeks in 1998.

Chapter 5 investigates, at two spatial and temporal scales, the distribution of lekking black grouse in highland Perthshire 1990 – 1998. Members of the Perthshire Black Grouse Study Group (PBGSG) and Game Conservancy Trust (GCT) staff generously provided the lek survey data they collected during that period. In addition, David Baines made GCT questionnaire results available to me.

Chapter 6 addresses brood habitat selection and the fieldwork was performed in plantations near Trinafour, Perthshire. The landowner kindly allowed access to the site. GCT staff and students performed the essential tasks of counting and catching chicks. Stirling University and GCT funds were used to purchase radio-telemetry transmitters and equipment.

The final chapter draws together the main results from the preceding chapters and integrates them into the existing body of knowledge. Management recommendations and suggestions for future research are presented.

Chapter 2 Study areas

2.1 Introduction

Several different sites in Scotland were used to collect field-data for the different aspects of the study discussed in each chapter. Figure 2.1 shows the locations of all the study areas described in the text below.

In Chapters 3 and 4 the distribution of lekking black grouse in plantation forests is investigated at two spatial scales. This work was carried out in Cowal, Argyll.

In Chapter 5 the distribution of lekking black grouse in highland Perthshire 1990 – 1998 is investigated at two spatial and temporal scales.

In Chapter 6 brood habitat selection is investigated. The fieldwork was performed in plantations near Trinafour, Perthshire.

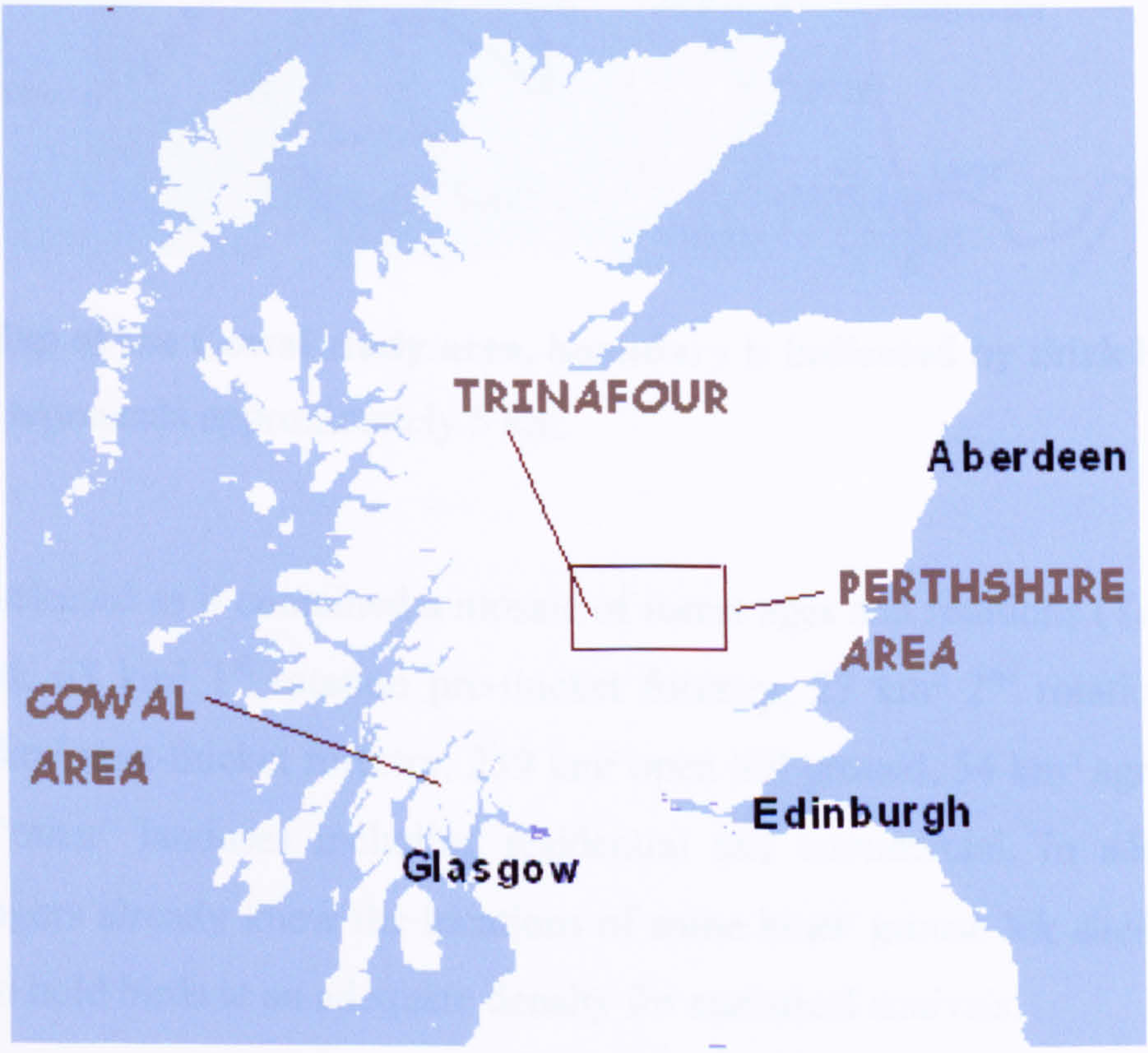

Figure 2.1. Map of Scotland, showing the locations of the three study areas.

2.2 Cowal, Argyll

In 1996 fieldwork was undertaken in the main study site (Figure 2.2), the Cowal peninsula in Argyll. The Cowal study area took its landward boundary as the National Forest boundary extending south-east from Strachur (O.S. grid reference: NN 095015, O.S. Landranger Sheets 55, 56, 62 and 63) to the coast and then followed the coastline. This encompassed an area of approximately 630 km^2.

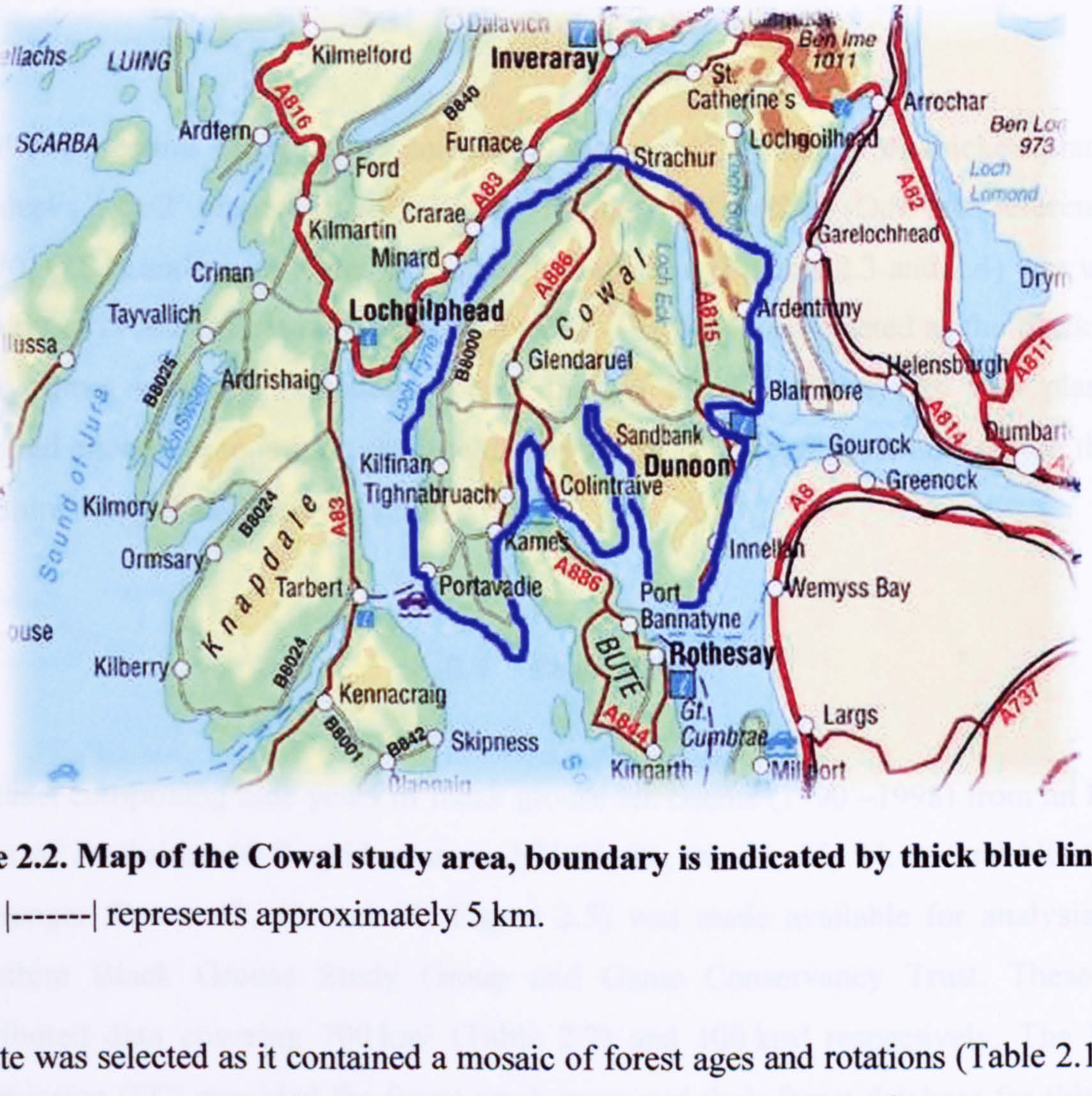

Figure 2.2. Map of the Cowal study area, boundary is indicated by thick blue line. Scale: |-------| represents approximately 5 km.

The site was selected as it contained a mosaic of forest ages and rotations (Table 2.1). The site comprised: 63 km² 1st rotation pre-thicket forestry, 27 km² 2nd rotation pre-thicket forestry, 234 km² post-thicket forestry, 239 km² open hill ground, 54 km² agricultural land and 15 km² 'other' landuses including residential and commercial. In addition, Forest Enterprise rangers already knew the locations of some black grouse lek sites and the area was thought to hold birds at an adequate density for statistical analysis.

Table 2.1. Estimate of the area and percentage of the Cowal study site covered by the main habitats.

Habitat	Area Covered (km²)	Percentage of study site
1st rotation pre-thicket forestry	63	10
2nd rotation pre-thicket forestry	27	4
Post-thicket forestry	234	37
Open hill ground	239	38
Agricultural land	54	9
'Other' landuses	15	2

2.3 Trinafour, Perthshire

In 1997 a second study area, consisting of two 1st rotation pre-thicket plantations 'Auchleeks 1 & 2' (approximately 3.5 km² in total) at Trinafour (O.S. grid reference: NN 730670, O.S. Landranger Sheet 42) in north Perthshire (Figures 2.3 and 2.4) was used for the study of brood habitat selection (Chapter 6). This site was selected as the black grouse density there was approximately double that in the Cowal and the two plantations supported enough broods for a radio-telemetry study to be feasible. It falls within the main Perthshire study area described below.

2.4 Perthshire

A dataset comprising nine years of black grouse lek counts (1990 –1998) from an 800 km² region of Perthshire (O.S. grid squares: NN 76, 86, 96, 75, 85, 94, 95 and NO 05, O.S. Landranger Sheets 42, 43 and 52; Figure 2.5) was made available for analysis by the Perthshire Black Grouse Study Group and Game Conservancy Trust. These bodies contributed data covering 700 km² (Table 2.2) and 100 km² respectively. The Forestry Commission (FC) provided the forest stock maps and their forest database for this region. Additional habitat data were extracted from the Land Cover Map of Great Britain using the Countryside Information System version 5.23. These data were used in Chapter 5 to investigate the rate and direction of changes in the number of lekking males in different habitats and identify any associations with forest or moorland elements. The dataset was selected as it allowed a temporal as well as a spatial analysis to be made, in contrast to the other sites. Also, the gross habitat mosaic ('islands' of forestry within a 'sea' of moorland) contrasted with that found in the Cowal study area.

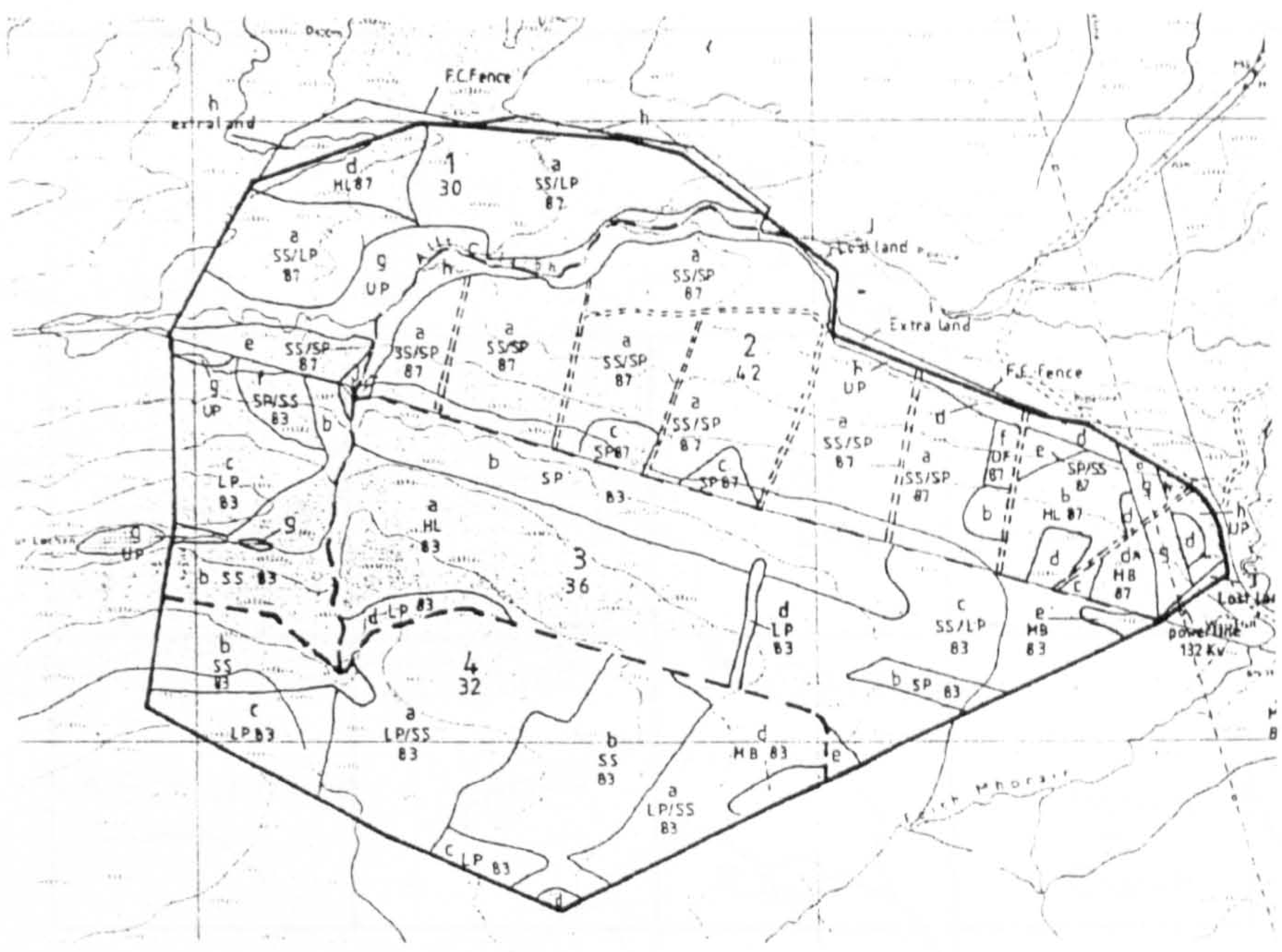

Figure 2.3. Forest stock map* of Auchleeks 1, Trinafour, Perthshire.

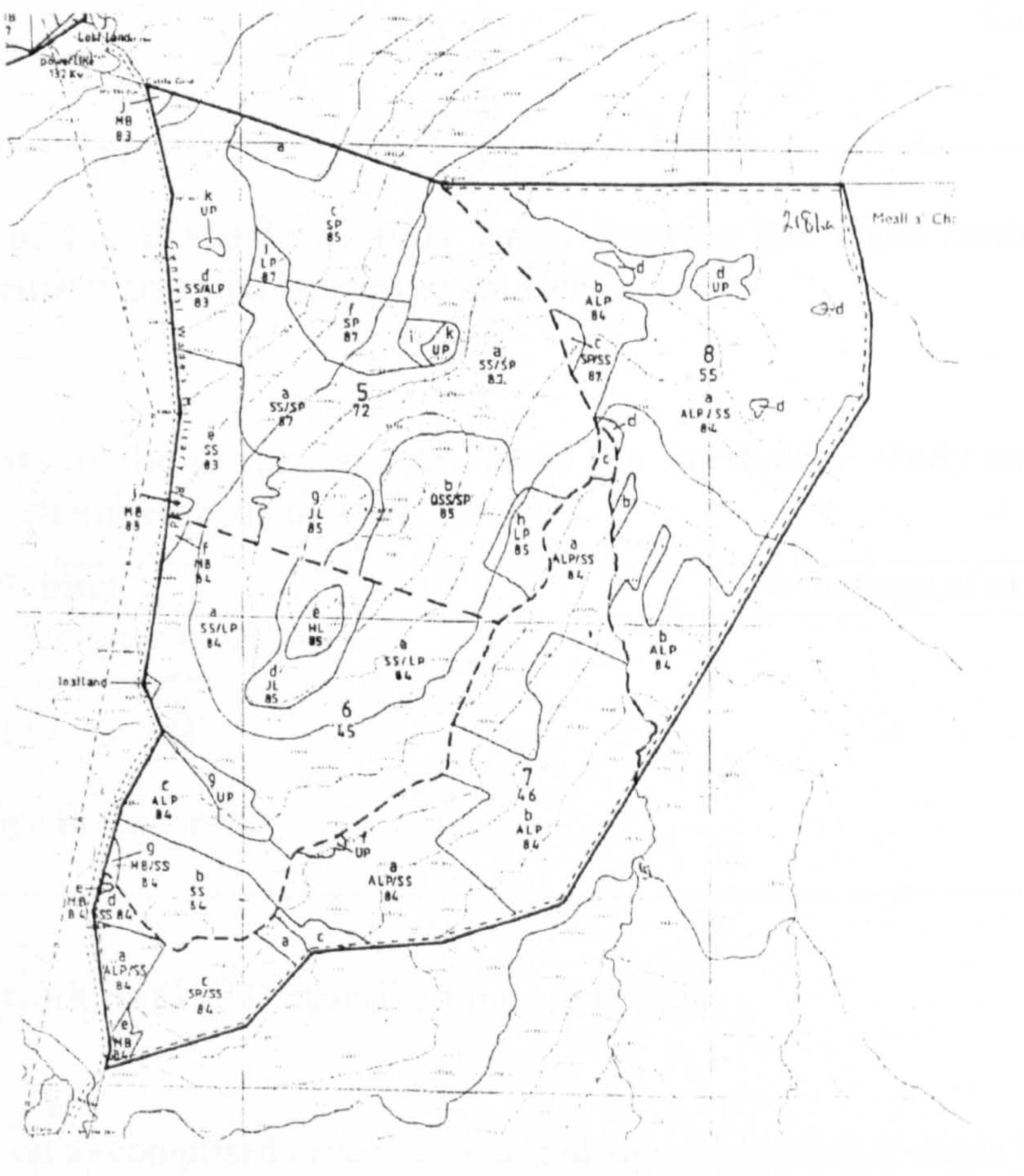

Figure 2.4. Forest stock map* of Auchleeks 2, Trinafour, Perthshire.

Scale: Grid square = 1 km²

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* Key to forest stock maps shown: Large font number = Compartment code; Medium font number = Area of compartment (ha); Small font number after initials = Planting year; Small font letter = Sub-compartment code; HL = hybrid larch; SS = Sitka spruce; LP = lodgepole pine; SP = Scots pine; UP = unplanted; DF = Douglas fir; MB = mixed broadleaves; JL = Japanese larch.

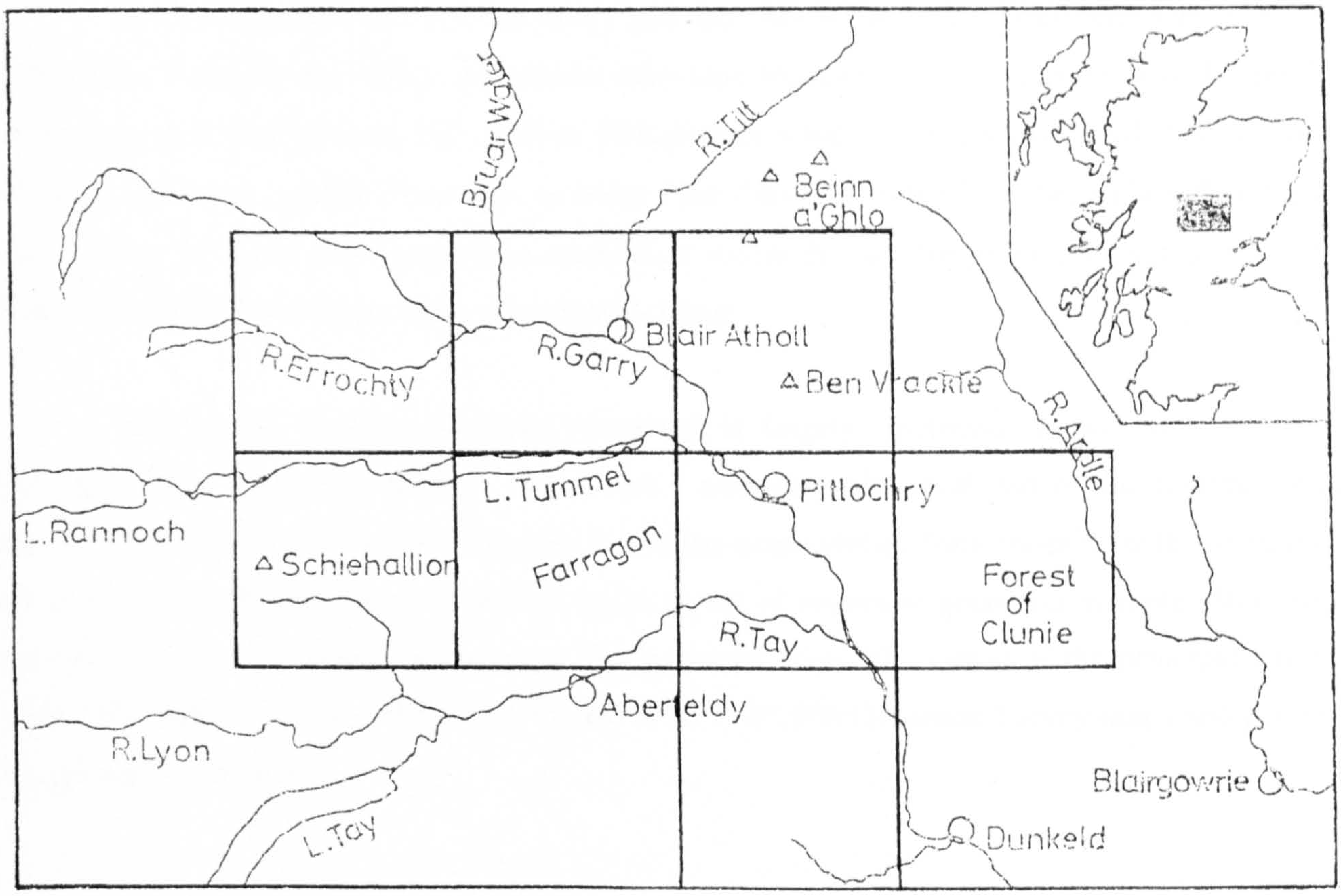

Figure 2.5. Map of the Perthshire study area, showing the eight component 10 km grid squares (amended from Robinson *et al.* 1993).

Table 2.2. Estimate of the percentage of 7/8 of the Perthshire study area covered by the main habitats (from Robinson *et al.* 1993).

Habitat	Percentage of area covered
Unenclosed heather dominant moorland	50
Conifer plantation (pre-thicket)	10
Conifer plantation (post-thicket)	15
Birch woodland	5
Valley bottoms, inbye fields, towns	18
Lochs	2

Robinson and co-workers (1993) described the study area:

" (The study area) comprised seven[4] 10 km grid squares forming a single block in highland Perthshire mainly across the area where the Rivers Garry, Tummel and Tay meet. To the east, it includes the watershed between the Rivers Tummel and Ardle.

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[4] An additional 10 km grid square was used in the analysis in Chapter 5.

The interface between wooded valley and open hill is particularly well represented in most of the area. Typically the valleys and stream sides have blocks of birch *Betula spp.* wood emerging on to open moorland between 200 – 300 m. This pattern is not followed however where plantations of larch *Larix spp.*, spruce *Picea spp.* or Scots Pine *Pinus sylvestris* have been planted along the valley sides. Many of these have been established within the last ten years, although some in the Blair Atholl and Tummel areas are considerably older.

The heather *Calluna* dominant moorland is largely traditional grouse moor managed through rotational burning. Blanket bog covers a comparatively small part of the moorland area, but small flushes and mires are frequent. Grassland communities form mosaics with the heather, especially along stream sides and around lochs. Areas of improved grassland in some places form continuous belts or isolated fields below the moorland edge. The extent of the principal habitats within the study area were roughly estimated from 1: 25,000 Ordnance Survey maps and personal knowledge of the area."

Chapter 3 The distribution of lekking black grouse in plantation forests: I. Patch Analysis

3.1 Introduction

There are currently three competing hypotheses that have been applied to explain the formation of leks: 'female choice', 'black hole' or 'hotspot' and debate centres on which hypothesis best explains observed behaviour (Davies 1991). The 'female choice' hypothesis states that females are attracted to large clusters of males so they can select the fittest mate. This hypothesis makes a series of predictions one of which is that the distance between leks should be equal to the diameter of a female home range plus the distance from which a lek can be detected (Bradbury *et al.* 1986; Stillman *et al.* 1996). Similarly, the 'black hole' hypothesis predicts that clusters of male territories retain mobile females but it omits female mating preferences. The predicted inter-lek distance again approximates to the diameter of a female home range (Stillman *et al.* 1996). In contrast, the 'hotspot' hypothesis is based on the idea that females settle first and then leks form at the points of maximum overlap of female home ranges, i.e. 'hotspots' of female activity (Bradbury *et al.* 1986; Stillman *et al.* 1996). Predictions from 'hotspot' models likewise encompass an inter-lek distance of one female home range but this settlement model also allows leks to be closer (Bradbury *et al.* 1986). Thus, it is not possible to test between the three competing hypotheses using lek spacing data alone. In general, results from a number of radio-tracking studies (Bradbury *et al.* 1989; Gibson 1996) tend to support the 'hotspot' model when a coarse scale of resolution is used, with fine scale tuning coming from male habitat preferences (Bradbury *et al.* 1989).

To complicate matters still further, results from a recent study using microsatellite markers to compare the genetic structuring of groups of males within and between leks found that kin selection could also be a factor in the evolution and maintenance of the black grouse lek mating system (Höglund *et al.* 1999). The distribution of matings on leks is highly skewed such that a few males reproduce whilst the majority do not. The kin selection hypothesis has been put forward as a possible explanation for the lower ranking males (those that will seldom reproduce) attending the lek despite attaining few matings. According to this hypothesis males attend a lek where the top ranking male is a close relative thus the lower ranking male enhances his inclusive fitness by 'helping' the top male. This 'help' is mediated through increased lek size attracting more females (Alatalo *et al.* 1992). Höglund and co-workers' (1999) study supported this theory by finding that male black grouse on leks were more related than expected by chance.

Irrespective of which hypothesis or combination of hypotheses is most appropriate, all predict that leks should be evenly distributed (Stillman *et al.* 1996). Consequently, points where leks are expected but are absent presumably occur because habitat is not suitable[5]. This logic can be extended to identify the habitat requirements of a lekking species. This study applied this approach to black grouse inhabiting commercially afforested areas.

The spatial distribution of lekking black grouse in relation to habitat structure was investigated. The specific aim was to determine their habitat and area requirements and the relative importance of first and second rotation components of forest structure.

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[5] Assuming that the landscape is full; if not, then one would assume that the best areas for the species would be occupied first and/or abandoned last.

To meet this aim two complimentary approaches were used: patch analysis (this chapter) and home range analysis (Chapter 4). In this chapter, the following broad question was addressed: is the presence of a lek associated with habitat features at the 'patch' scale? In this study a 'patch' is defined as an area of homogeneously structured habitat such as a pre-thicket forest stand. Two specific questions were then asked:

1. Was the presence or absence of a lek within a patch associated with habitat features at that scale?

2. Where leks were present, were the number of leks, the total number of males and the mean lek size within the patch associated with habitat features at that scale?

Previous workers have found that the factors associated with the distribution and abundance of a species are specific to the scale of the investigation (Angelstam 1990; Angelstam & Martinsson 1990; Bland 1997), so multiple spatial scales were investigated in this study. Angelstam (1990) found that the size and position of preferred habitat patches, when examined at large geographical scales, determined the local and regional distribution of breeding male black grouse in Sweden. The density of males was related to the level of primary production of the major food plants within this broad scale. However, variation in breeding success was the main cause of population change in spring numbers on the scale of the single population. Angelstam (1990) concluded:

> "unless population studies are performed at different spatial and temporal scales, that is, in both good and poor habitats and over several years, a detailed understanding of the factors affecting distribution and abundance of a species is impossible to achieve".

May (1999) points out that "important ecological questions simply have to be addressed on the right scale – which often means an uncomfortably large scale". The appropriate ecological scale varies with species and the questions being asked. An organism with a small home range, for example, may perceive a landscape containing small patches of suitable habitat as fragments of suitable versus unsuitable habitat whereas an organism with a large home range might perceive it as a fine-grained mixture of small patches (Wiens 1994).

In this study, three years were taken to undertake a thorough spatial census; however, since only one temporal scale could be used, the years were combined to give a single 'snapshot' in time. Two spatial scales were used, 'patch' and 'home range' scales, which are both justified by the ecology of black grouse. The patch scale was defined by habitat structure in terms which are thought to be perceived by black grouse, for example, pre-thicket conifers are a preferred habitat and are presumably perceived to be different from post-thicket conifers, an avoided habitat. These habitat preferences were taken from previous studies including: Angelstam (1984a); Cayford (1990b & 1993); Kolstad *et al.* (1985); Marcström *et al.* (1982); Swenson & Angelstam (1993); Cayford *et al.* (1989).

3.2 Methods

The data used in this chapter were collected from the Cowal study area in Argyll (for further details see Chapter 2, section 2.2).

3.2.1 Lek Survey and Habitat Mapping

Lekking males were surveyed in 1996, 1997 and 1998. The surveyor contacted landowners, stalkers, farmers, forest rangers, etc. before survey work commenced in order to obtain access permission. This opportunity was also used to ask for information on known lek sites. All ground within the study area was searched; leks were located by following up sightings and/or sounds of black grouse or from local reports. The location and number of males attending each lek between late March and late May (the peak lekking season) were recorded; having recorded these data the surveyor moved to the next lek so that more than one lek could be visited in one morning. Leks were visited and the males counted from first light up to 2 hours after dawn. This time period was restricted thus to reduce the variation in numbers of males since numbers are known to vary both throughout the season and the day (Baines 1995; Cayford & Walker 1991). Ideally, each lek should have been visited twice each year during the survey period but this was not always feasible. Displaying singletons were included (after Hancock *et al.* 1999) although leks are generally considered to consist of two or more displaying males (Davies 1991; Krebs & Davies 1993; Robinson *et al.* 1993). Data quality was considered to be the same across habitat types since black grouse generally select areas of relatively flat open ground with short vegetation (< 5 cm) and good all round visibility as lek sites and displaying black grouse males are not attempting to be inconspicuous. The lek survey is now used as a standard method for assessing the number and distribution of male black grouse.

Lek locations were plotted on forest stock maps (scale 1:10,000) which also provided coarse habitat data. The habitat mosaic was stratified into six habitat types: first rotation pre-thicket (0-15 years after tree planting in the first rotation) (1[*]), second rotation pre-thicket (0-15 years after tree planting in the second rotation) (2[*]), post-thicket (greater than 15 years after tree planting to harvest) (3[*]), open-ground, agriculture and other (including

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[*] These numerals are used as symbols in graphs to identify the habitat types

lochs, broad-leaved trees and residential land-use). These habitat types were mapped which allowed the identification of discrete habitat patches.

The maximum number of males attending a lek each year was used to calculate an average figure for the years in which the lek was observed. Solo-displaying males or 'singletons' are more mobile than those that attend traditional leks (Cayford & Walker 1991, Hancock *et al.* 1999) consequently they are difficult to survey accurately and some surveyors, e.g. Robinson & co-workers (1993) exclude them from analyses. However, singletons can represent a high proportion of a population (Cayford & Walker 1991, Grove *et al.* 1988, Hancock *et al.* 1999), indeed in this study 21 – 35 % (see results section 3.3.1.) of all displaying males were singletons so excluding them would have been inappropriate. Including all singletons in all years would also be inappropriate since their mobility would lead to double counting. In this study an alternative strategy was used, singletons seen displaying at a site in one year only were excluded except in 1998 – this reduced the likelihood of double counting without excluding singletons entirely. Observations regularly revealed that a displaying singleton would often be found at the site of a larger traditional lek so these records were important in terms of lek locations as well as representing the entire population of displaying males. The average number of males calculated in this way was used in the analyses described below.

3.2.2 Patch Analysis

In total, 370 habitat patches were identified. For each patch the following attributes were measured and recorded:

i) presence or absence of a lek (1,0);

ii) number of leks, if present;

iii) total number of males, if present;

iv) mean lek size (number of males per lek);

v) distance to the nearest lek (km);

vi) number of males at the nearest lek;

vii) distance to the nearest patch of open-ground habitat (km);

viii) patch size (km²);

ix) habitat type (one of the six categories described above in section 3.2.1.);

x) tree age – mean and standard deviation (years since planting, the mean and standard deviation were calculated from a random sample of 10 points per patch).

To investigate whether the presence of a lek was significantly associated with habitat features at the patch scale the data were analysed using generalised linear modelling (GLM). The error structure of the model (normal, Poisson, binomial or negative binomial) was selected such that it matched the error structure of the dependent variable. The link function used was the default option (often referred to as the canonical link functions) for the given error structure:

Error Structure	**Link**
Normal	Identity
Poisson	Log
Binomial	Logit
Negative Binomial	Reciprocal

The maximal model comprised all the habitat variables (v – x) as explanatory variables and 'occupation' - the presence or absence of a lek in a patch (i), the number of leks in a patch (ii), the total number of males in a patch (iii), or mean lek size (iv) sequentially as the dependent variable. Step-wise elimination of insignificant terms produced the minimal model. These analyses were performed twice, first including lekking singletons, then excluding them. However, the results from the former only are presented as these generally explained a higher proportion of the variation in the dataset and can be considered real leks on the basis of repeated observations and represent a large proportion of the total population of lekking males.

Data analysis was conducted using S-PLUS 4.5 for Windows (MathSoft 1998). To ensure that appropriate models were fitted the residuals were checked for normality and constant variance. A significance level of $P \leq 0.05$ was adopted throughout.

3.2.3 Patch Analysis – Fieldwork

In 1998, elements of habitat structure were recorded from a random sub-sample of 11 occupied and 11 unoccupied 1st rotation pre-thicket patches and 10 occupied and 13 unoccupied 2nd rotation pre-thicket patches. These methods were determined to quantify variables thought to relate to the presence and abundance of black grouse.

i) presence or absence of a lek (1,0);

ii) number of leks, if present;

iii) mean lek size (number of males per lek);

iv) rotation (1, 2);

The following data (variables v to xiv) were collected from 10 points at 100 m intervals along a transect randomly placed in the patch. An average value for the patch was calculated from the 10 sample plots and this was used in subsequent analyses.

v) number of broad-leaved trees within a 5 m radius, expressed as stems per ha;

vi) number of coniferous trees within a 5 m radius, expressed as stems per ha;

vii) canopy cover (%) visually estimated to the nearest 5 % over a 2 x 2 m quadrat (this method was adopted as a 2 x 2 m quadrat straddles planting rows and canopy cover on this scale is relatively uniform within a habitat type);

viii) average crop tree height (m) within a 5 m radius (visually estimated to the nearest 0.5 m);

ix) distance (m) to the nearest tree in each of the four cardinal compass quadrants;

x) species of the nearest tree in each of the four cardinal compass quadrants;

xi) whether the canopy of the nearest tree in each of the four quadrants interlocked with that of another;

xii) the height at which the canopy of the nearest tree in each of the four quadrants interlocked with that of another;

xiii) ground cover (%) (subjectively estimated to the nearest 5 %) in a 2 x 2 m quadrat of each of the following plant groups: *Calluna vulgaris* and *Vaccinium* species[6]; bog myrtle (*Myrica gale*); grass (*Gramineae*); bracken (*Pteridium aquilinum*); rushes (*Juncus spp.*); herbs;

xiv) vegetation profile: the density of vegetation in 4 height bands (0 – 0.5, 0.5 – 1, 1 – 1.5, 1.5 – 2 m) recorded as the percentage (0 – 20, 21 – 40, 41 – 60, 61 – 80, 81 – 100 %) of a pole obscured by the vegetation when viewed from 10 m away (north, south, east and west) (after Nudds 1977).

Once collected, the field data were combined in a dataset with the map data and analysed in the same way as the map habitat data alone.

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[6] With hindsight it would have been better to split the *Calluna vulgaris* and *Vaccinium* category into two as these species have different tolerances to shade and disturbance.

3.2.4 Graph Plotting

With the exception of Figures 3.1, 3.2 and Table 2.5 raw data are not shown in this chapter as a modeling approach was taken and the results of the models are shown instead. The modeling process described in 3.2.2 was used to generate models (and their R^2 values) from real data collected as described.

These models were then used to predict occupancy (or the number of leks in a patch, the total number of males in a patch or mean lek size) keeping all explanatory variables except one constant (varying more than one variable at a time was beyond the available statistical advice) at the mean value recorded in the study area. The results were plotted in graphs made up of 1000 calculations from the varied explanatory variable that ranged between the minimum and maximum values observed in the study area. The outputs from this process are fitted curves of the dependent variable.

The mean values of the other variables in the model should be borne in mind when looking at the absolute values plotted. In addition, the relative lack of data points at the extremes of the x-variables ranges (in particular at the upper limits) make the models less robust in these areas. The patterns and trends shown within the graphs are more generally relevant. Raw data were not plotted on these graphs since the data have a non-normal error structure and would not show how good a fit the fitted curves represent. The R^2 value indicates what percentage of the variation in the dataset the model explains and this is the best available measure of the 'goodness of fit'.

3.3 Results

3.3.1 Lek Survey Results

The eastern half of the Cowal study area was surveyed in 1996 and the remainder in 1997 and the results from these surveys were combined (survey 1). In 1998 the entire Cowal study area was surveyed again (survey 2) when all previously known leks were counted and several new leks were found. Nineteen leks were surveyed in all three years (1996, 1997 & 1998) and of these 6 were not used in 1998 but 4 of these 6 were singletons observed in 1996 only.

Sixty-eight leks were surveyed in 1996 and/or 1997 and 1998 and of these 30 were not used in 1998 but 18 of these were singletons observed in either 1996 or 1997 only. The frequency distributions of leks and males are shown in Figures 3.1 and 3.2.

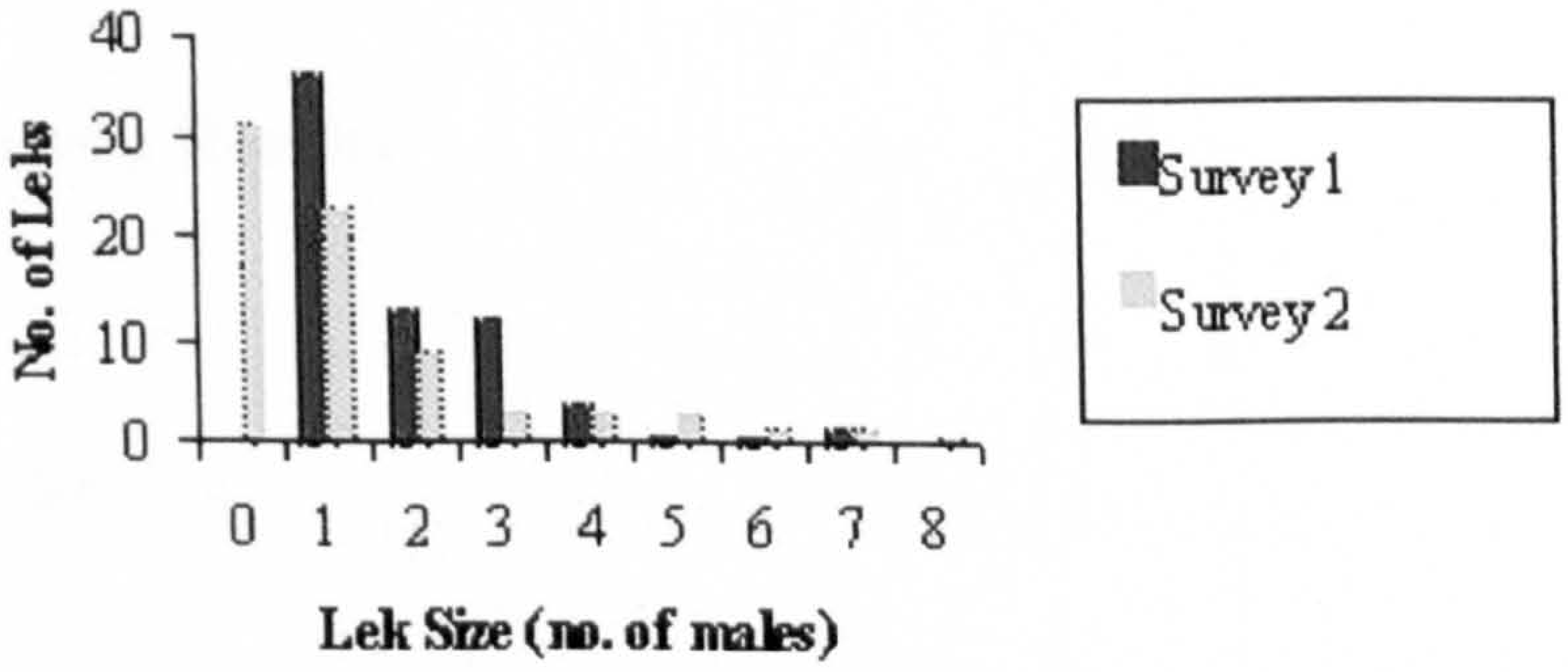

Figure 3.1. Frequency distribution of lek size observed in the Cowal study area from first and second surveys[7].

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[7] In the second survey, all leks visited in the first survey were visited again and if no males were present these were recorded as zeros hence zeros could only be recorded in the second survey.

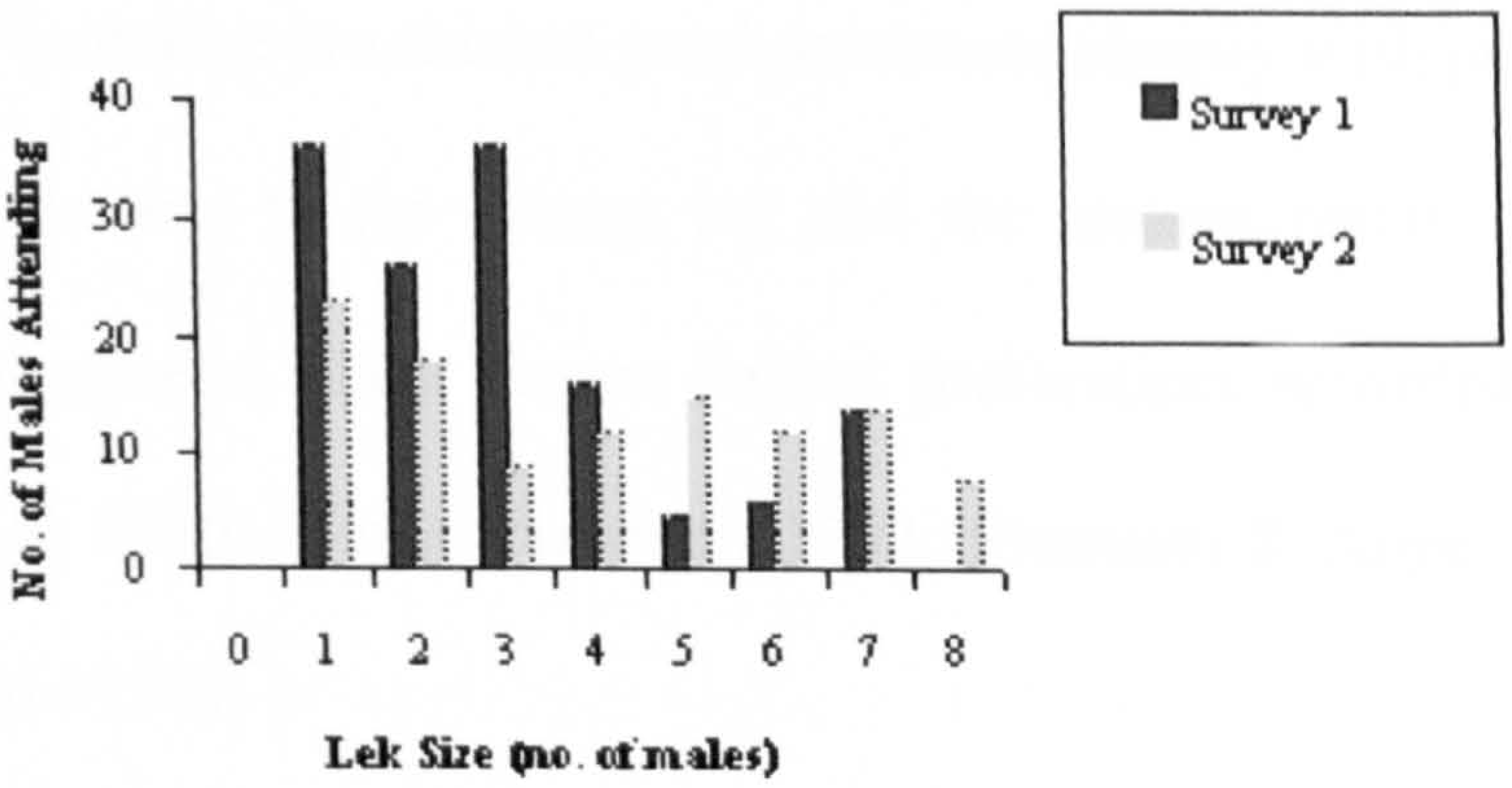


Figure 3.2. The total number of individual males attending leks of different sizes, observed in the Cowal study area.

Mean lek size in survey 1 was 1.5 males per lek, or 2.0 males per lek when singletons were excluded (2.4 and 3.8 respectively in survey 2). Density of males was 0.16 per km^2 (0.17 in survey 2); displaying singletons comprised approximately 35% (21% in survey 2) of the total population of lekking males.

The number of leks with 2 or more males present in the second survey was not significantly different to that found in the first ($\chi^2 = 7.05$, 6 d.f., $P > 0.05$).

3.3.2 Patch Analysis Results

3.3.2.1 All Habitats

In analyses incorporating all six habitat types pre-thicket habitats were the most likely to be occupied, whilst agriculture and 'other' were the least likely to be occupied irrespective of patch size. Post-thicket and open ground fell between these two extremes. In all habitats, probability of occupation increased as patch size increased until a threshold was reached beyond which increasing patch size had no effect and as the distance to the nearest lek increased the probability of occupation decreased. The total number of males and mean lek size in a 1st or 2nd rotation pre-thicket patch increased steeply with patch size but decreased with increasing distance to the nearest lek and the nearest patch of open ground. These results reflect the general black grouse habitat preferences recorded by previous workers (e.g. Kolstad *et al.* 1985; Marcström *et al.* 1992; Swenson & Angelstam 1993; Cayford *et al.* 1989; Cayford 1990).

As the aim of this project was to identify the habitat and area requirements of black grouse inhabiting afforested areas non-forest habitat patches were excluded from all subsequent analyses as described below.

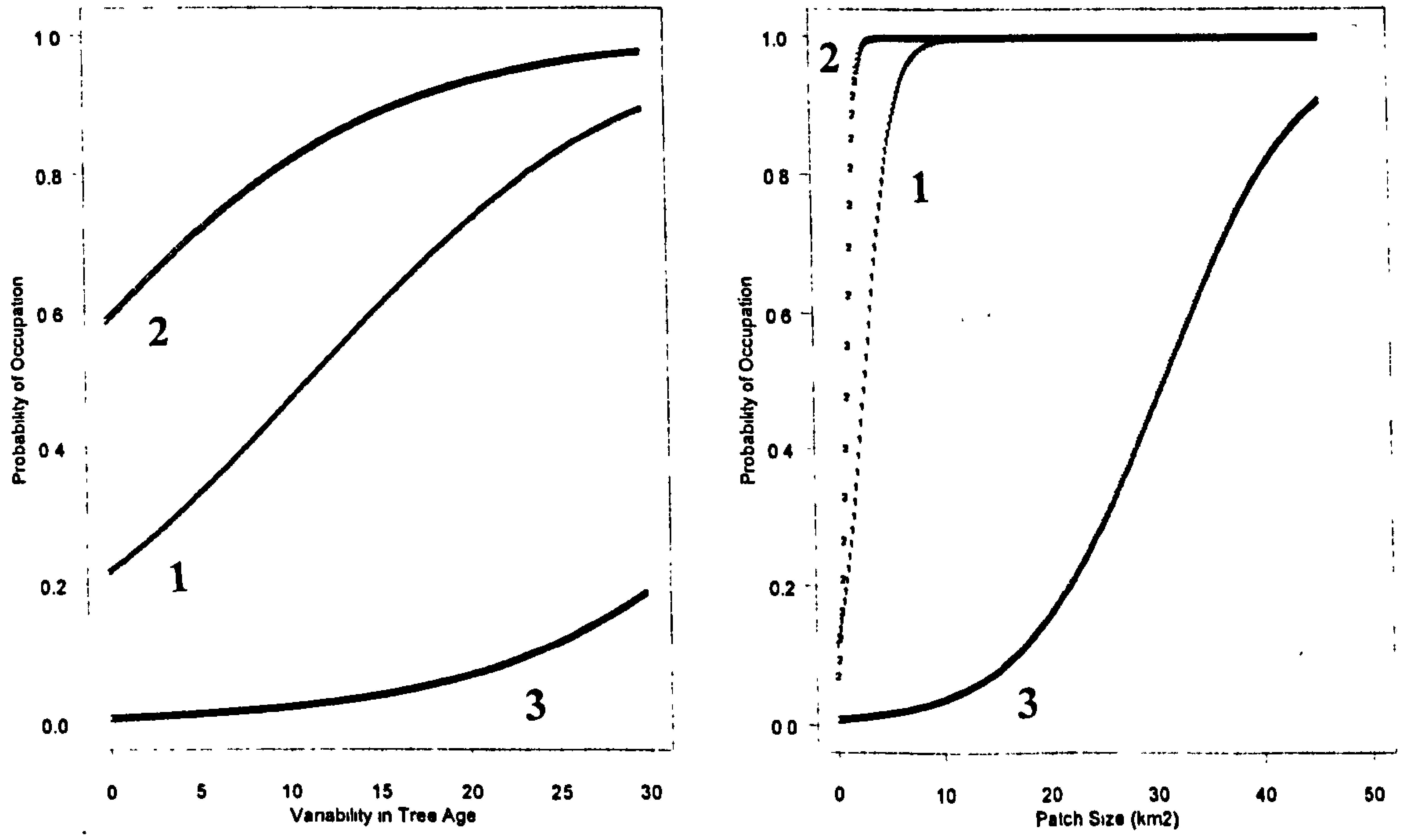
3.3.2.2 Forest Habitats

In these analyses the three forest habitat types were considered: first rotation pre-thicket (1), second rotation pre-thicket (2) and post-thicket (3). Analysis of the data was carried out twice using the variables listed in section 3.2.2. Habitat type was excluded from the second analysis as this variable was partially generated from the tree age. Performing both analyses allowed examination of which variable (habitat type or tree age) best explained the variation in the dataset. One result was therefore generated for tree age, and another for habitat type where mean tree age dropped out of this analysis (note however that the variability in tree age remained significant). Results from both approaches were very similar. Results from the analysis using tree age as the habitat descriptor are not shown here as they merely reflect the results where habitat type was used but with more explanatory variables and a lower r^2 value as a consequence of a reduced sample size. Thus, for parsimony the habitat category approach is used. The analysis including tree age did, however, show that the probability of occupation decreased (in an exponential manner) with increasing tree age so that a patch became less and less suitable as the trees aged from 0 to 20 years and eventually became totally unsuitable when the trees were 30 years old.

The probability of occupation increased as the variability of tree age in a patch increased, and this pattern was similar in all forest habitats (Figure 3.3a). Model details are shown in Table 3.1. The pattern of changing probability of occupation with patch size was similar for all forest habitats (Figure 3.3b) – it increased with patch size to an asymptote.

Key to symbols used in all Chapter 3 model graphs:

1 = 1st rotation pre-thicket   2 = 2nd rotation pre-thicket   3 = post-thicket



(a)   (b)

Figure 3.3. Fitted logit model of the probability of occupation predicted for the 3 forest habitat categories under a range of (a) tree age variability and (b) patch sizes.

The next step was to identify the habitat variables that were associated with the total number of males in a patch. The minimal models generated to explain this are shown in

Table 3.2. The number of males in a 1st or 2nd rotation pre-thicket patch increased steeply as the patch size increased (Figure 3.4a) and this pattern was repeated in post-thicket patches. However the change in gradient did not start until a post-thicket patch size of 20 km² was exceeded.

The number of males in a patch decreased with increasing distance to the nearest lek (Figure 3.4b) and the nearest patch of open ground (Figure 3.4c). More males were found in pre-thicket than post-thicket patches.

Construction of a model to predict mean lek size was not possible due to the narrow range of mean lek sizes with adequate replications observed in the field. The distribution of the data did not fit, nor could it be transformed to fit, Poisson or negative binomial distributions.

To summarise the results of the forest habitats analysis, the occupation and total number of males in a patch can be explained largely by the habitat of the patch and its size. Occupation was more likely, and the total number of males greater, in pre-thicket patches than post-thicket. Examination of pre-thicket patches alone should allow us to identify any patterns particular to this habitat. Given that pre-thicket forestry is the preferred habitat type (see section 3.1) the results of these analyses should be the most interesting with respect to understanding black grouse habitat and area requirements in commercial plantations, and eventually, for habitat management.

Table 3.1. Summary of minimal models generated to predict the probability of occupation from patch analysis.

Habitat used in Model	R^2 (%)	GLM Error Structure	Link Function	Habitat	Patch Size	Distance to nearest lek	Variability in Tree Age	Canopy Cover	Average Crop Tree Height	Grass Ground Cover	Vegetation Profile 0 – 0.5 m (VPA)	Interactions	Figures in text
Forest	40	B	Logit	0.000^{1}	0.000^{2}	-	0.011	-	-	-	-	0.003^{12}	3.3
Pre-thicket (M)	30	B	Logit	-	0.000	-	0.013	-	-	-	-	-	-
Pre-thicket (M & F)	47	B	Logit	-	-	-	-	0.025^{1}	0.001^{2}	0.015	0.001^{3}	0.028^{123}	3.5

Table 3.2. Summary of minimal models generated to predict the number of males in a patch from patch analysis.

Habitat used in Model	R^2 (%)	GLM Error Structure	Link Function	Habitat	Patch Size	Distance to open ground	Distance to nearest lek	No. males at nearest lek	Variability in Tree Age	Canopy Cover	Average Crop Tree Height	Grass Ground Cover	Vegetation Profile 0 – 0.5 m (VPA)	Vegetation Profile 0.5 – 1 m (VPB)	Vegetation Profile 1 – 1.5 m (VPC)	Interactions	Figures in text
Forest	69	P	Log	0.000^{1}	0.000^{2}	0.004	0.000	-	-	-	-	-	-	-	-	0.000^{12}	3.4
Pre-thicket (M)	61	P	Log	^{2}	0.000^{1}	-	-	0.018	0.006	-	-	-	-	-	-	0.033^{12}	-
Pre-thicket (M & F)	90	P	Log	-	0.000	-	-	-	-	0.011^{1}	0.009^{2}	0.004	0.000^{3}	0.0414	0.0015	0.037^{1}-5	3.7 – 3.9

Notes: Numbers below variables are the P values for significant terms; M = Map data only; M & F = Map and field data combined (note that field data (F) incorporates more data – this is explained further in section 3.2.3.; P = Poisson; B = Binomial; Superscript numbers indicate the terms which interact.

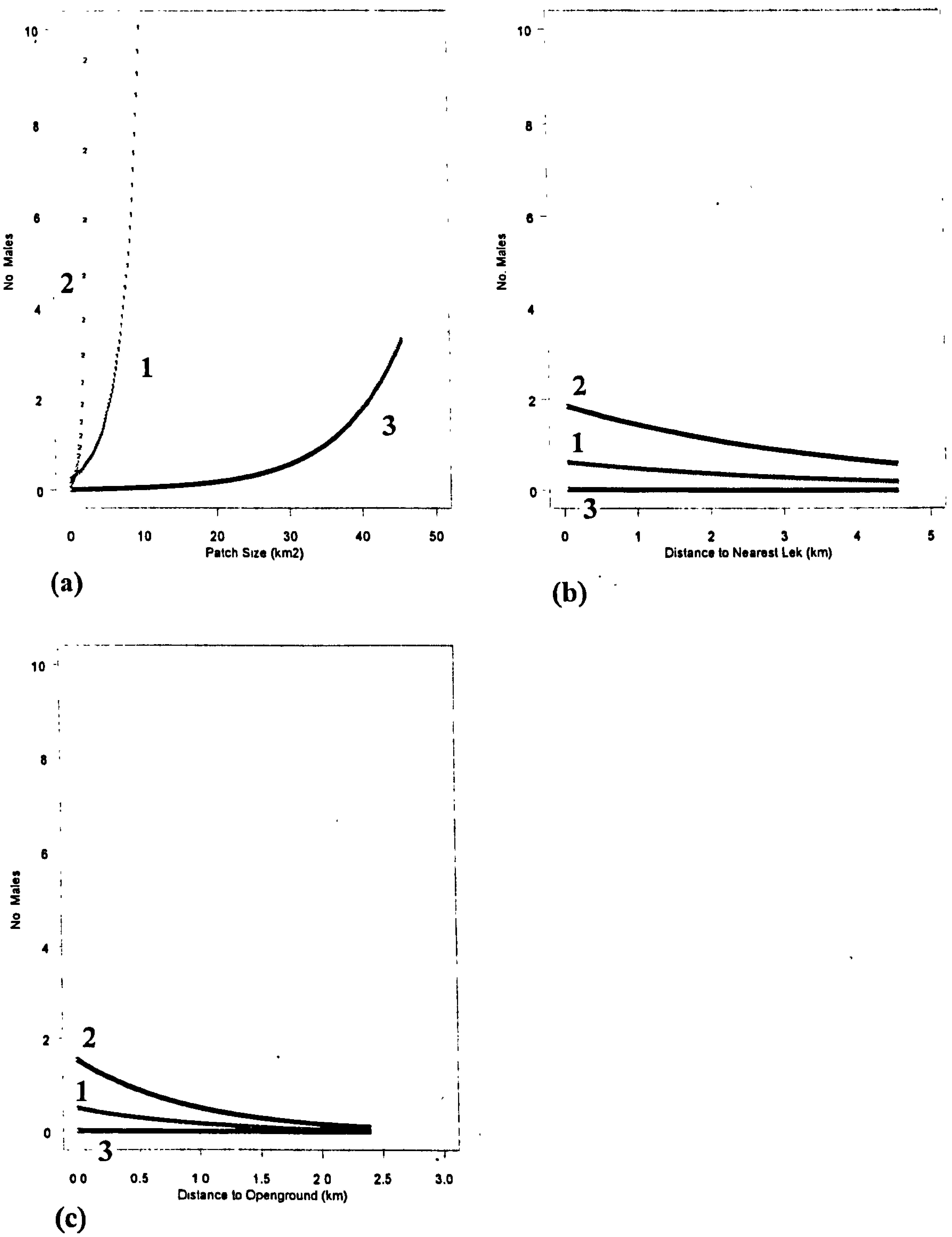


Figure 3.4. Fitted log model of the number of males in a patch predicted for forest habitats using a range of (a) patch sizes, (b) distances to the nearest lek, and (c) distances to the nearest open ground.

3.3.2.3 Pre-thicket Habitats

As with the previous dataset, the mean tree age and its standard deviation were included in the analyses. However, here each analysis was performed once only as 'habitat' merely differentiated between 1st and 2nd rotation pre-thicket patches and did not cause pseudoreplication. The minimal models were generated to explain the presence of a lek in a pre-thicket patch, the number of leks and the total number of males in a patch (Tables 3.1, 3.4 and 3.2). Graphs illustrating these are not shown as superior models were developed and are presented below. Note that the limitations noted earlier in this chapter concerning the reliability of the models at the extremes of the range of x-variables applies particularly here. For example, the models involving canopy cover are plotted for the whole observed range of canopy cover (i.e. 0 to 100 %) but in the pre-thicket patches sampled the average canopy cover was 24 ± 26 (SD) %. Predictions beyond regularly observed habitat values should therefore be treated with caution, however the approximate values and trends exhibited by the model in the mid-range are valid. The figures to which this limitation applies are highlighted in the legend.

The minimal model generated to explain the presence of a lek in a pre-thicket patch when singletons were included explained just 30% of the variation present in the dataset. This was considered to be inadequate. Consequently in 1998 habitat field-data were collected with the aim and effect of improving the fit of the models (Tables 3.1, 3.2, 3.3 & 3.4).

Probability of occupation increased with canopy cover (Figure 3.5a) and grass ground cover (Figure 3.5c). In both, the probability increased to an asymptote. A similar pattern was shown for the density of vegetation in the 0 – 0.5 m height band (VPA; Figure 3.5d). The reverse trend was shown with average height of the crop trees (Figure 3.5c). The average height of the crop trees increased as the probability of occupation dropped (reaching zero when the trees were 6 m tall).

Note that the model shown in Figure 3.5 was constructed from pre-thicket data only thus the model breaks down where canopy cover or tree height values fall beyond those commonly observed in pre-thicket stands. The average canopy cover recorded in the field was 24 % ± 26 % and 2.8 m ± 1.6 m in the case of tree height. However, the general trends shown within Figure 3.5.a & b are applicable.

A notable feature of this model was that none of the habitat variables extracted from the maps (for example: patch size; variability in tree age; distance to nearest lek;) were included despite the fact that they were significant in earlier analyses. Patch size did, however, feature as a significant term in the minimal model generated to explain the number of leks in a patch (Table 3.4 & Figure 3.6.c).

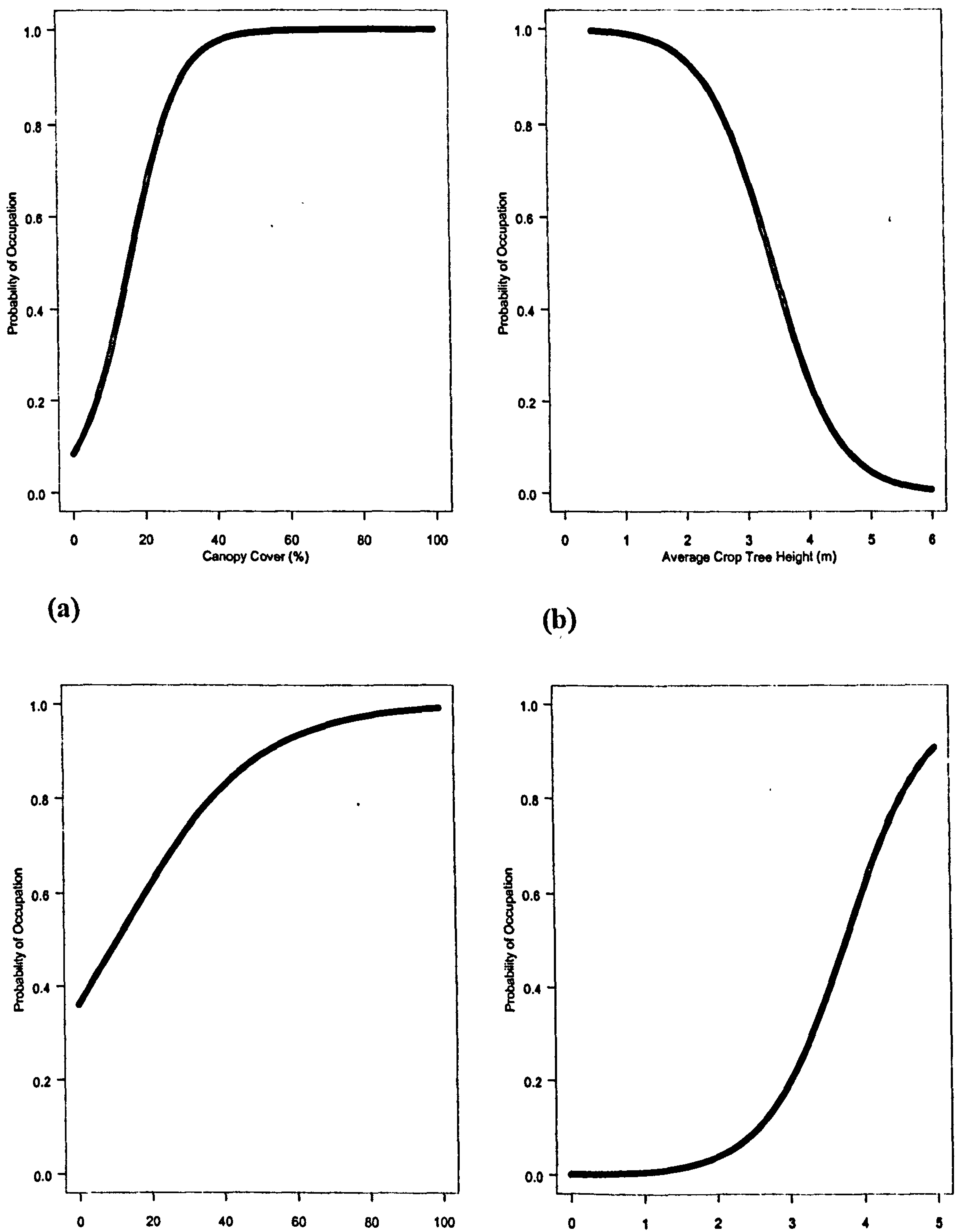
Table 3.3. Summary of minimal models generated to predict the mean lek size in a patch from patch analysis.

Habitat used in Model	R² (%)	GLM Error Structure	Link Function	Patch Size	Canopy Cover	Average Crop Tree Height	Percentage of pine in stand	Heather ground cover	Grass ground cover	Vegetation Profile 0 – 0.5 m (VPA)	Notes	Figures in text
Forest	-	-	-	-	-	-	-	-	-	-	Not possible	-
Pre-thicket (M)	-	-	-	-	-	-	-	-	-	-	Not possible	-
Pre-thicket (M & F)	86	Q	Log	0.000	0.011	0.000	0.000	0.052	0.000	0.000	-	3.6

Table 3.4. Summary of minimal models generated to predict the number of leks in a patch from patch analysis.

Habitat used in Model	R² (%)	GLM Error Structure	Link Function	Patch Size	Variability in Tree Age	Average Crop Tree Height	Vegetation Profile 0 – 0.5 m (VPA)	Interactions	Notes	Figures in text
Forest	-	-	-	-	-	-	-	-	Not possible	-
Pre-thicket (M)	49 (45)	P	Log	0.000^{1}	0.007^{2}	-	-	0.059^{12}	-	-
Pre-thicket (M & F)	54	P	Log	0.002	-	0.005	0.016	-	-	3.10 – 3.11

Notes: Numbers below variables are the P values for significant terms; M = Map data only; M & F = Map and field data combined; P = Poisson; Q = Quasi; Superscript numbers indicate the terms which interact.



(a) (b)

(c) (d)

Figure 3.5. Fitted logit model of the probability of occupation predicted for pre-thicket habitats (map and field data combined) and a range of (a) canopy cover (b) crop tree heights (c) ground cover by grasses (d) vegetation densities in the 0 – 0.5 m height band. Note that model limitations discussed in 3.2.4 apply to (a) and (b).

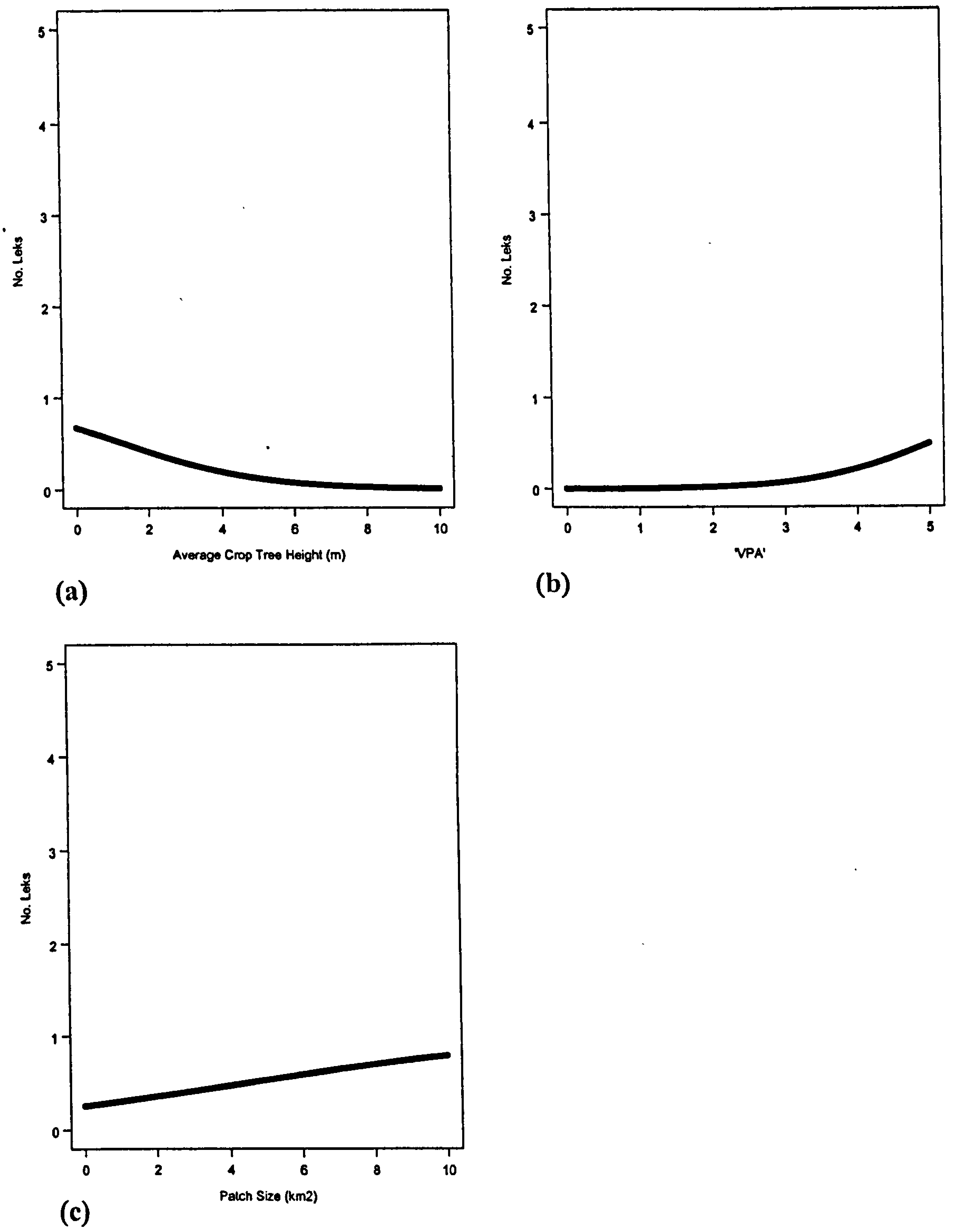
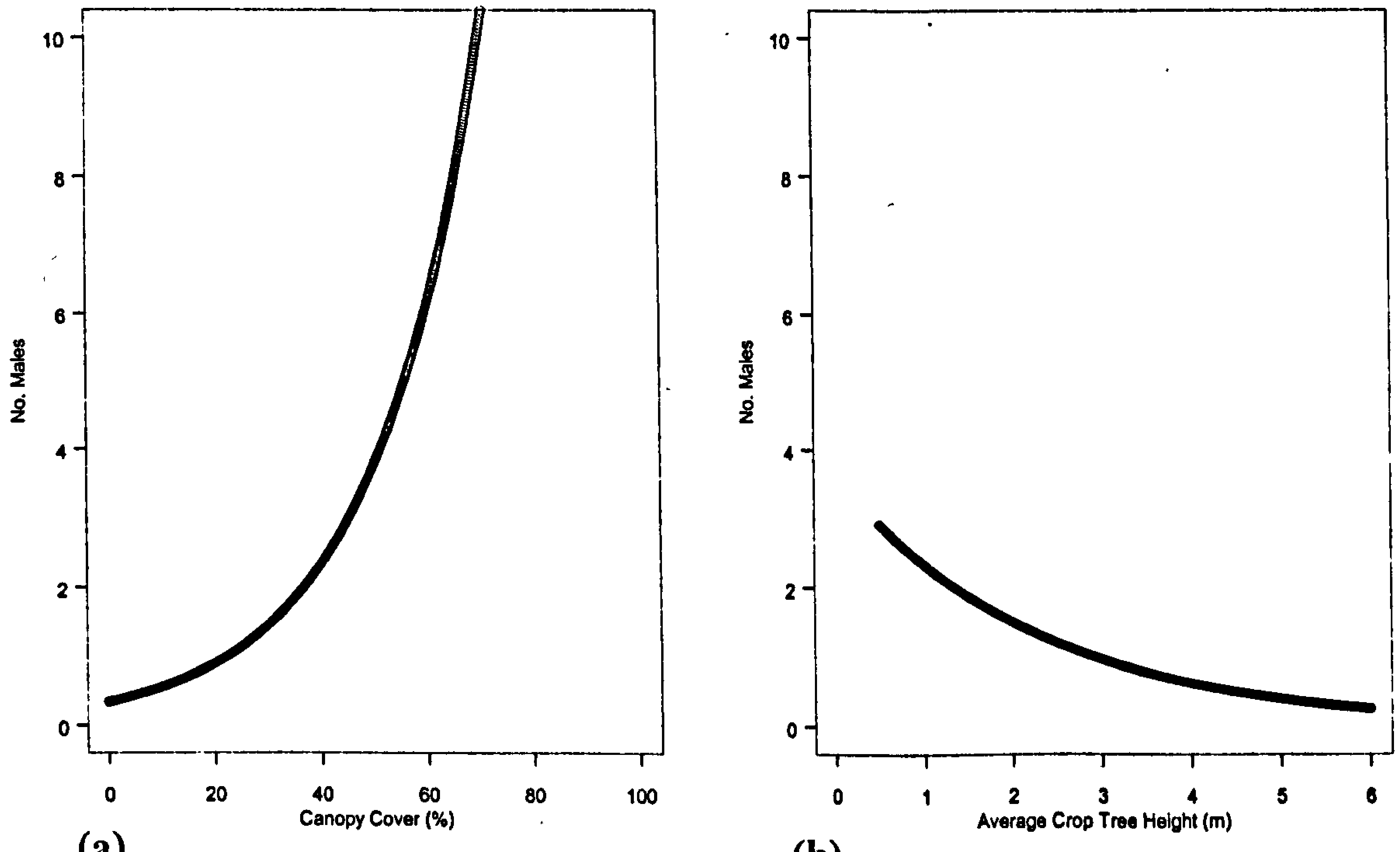


Figure 3.6. Fitted log model of the number of leks in a patch predicted for pre-thicket habitats (map and field data combined) and a range of (a) crop tree heights, (b) vegetation densities in the 0 – 0.5 m height band (VPA), (c) patch sizes. Note that model limitations discussed in 3.2.4 apply to (a) and (c).

The negative relationship between the average height of the crop trees and the number of leks in a patch (Figure 3.6a) concurred with that found for the probability of occupation (Figure 3.5b). There was a gradual increase in the number of leks in a patch with increasing vegetation density in the 0.0 - 0.5 m height band (VPA) (Figure 3.6b). This relationship seemed greatest once the vegetation density exceeded 40 % (this pattern was also shown in Figure 3.5d). The number of leks present in a patch increased with increasing patch size (Figure 3.6c). Note that the model shown in Figure 3.6 was constructed from pre-thicket data only thus the model breaks down where patch size values fall beyond those commonly observed in pre-thicket stands (average patch size recorded in the field was 1.9 km^2 ± 2.3 km^2). However, the general trend shown within the Figure 3.6.c is applicable.

Patch size again features as a significant explanatory variable in the minimal model generated to explain the total number of males in a patch (Table 3.2 & Figure 3.8.b).



(a) (b)

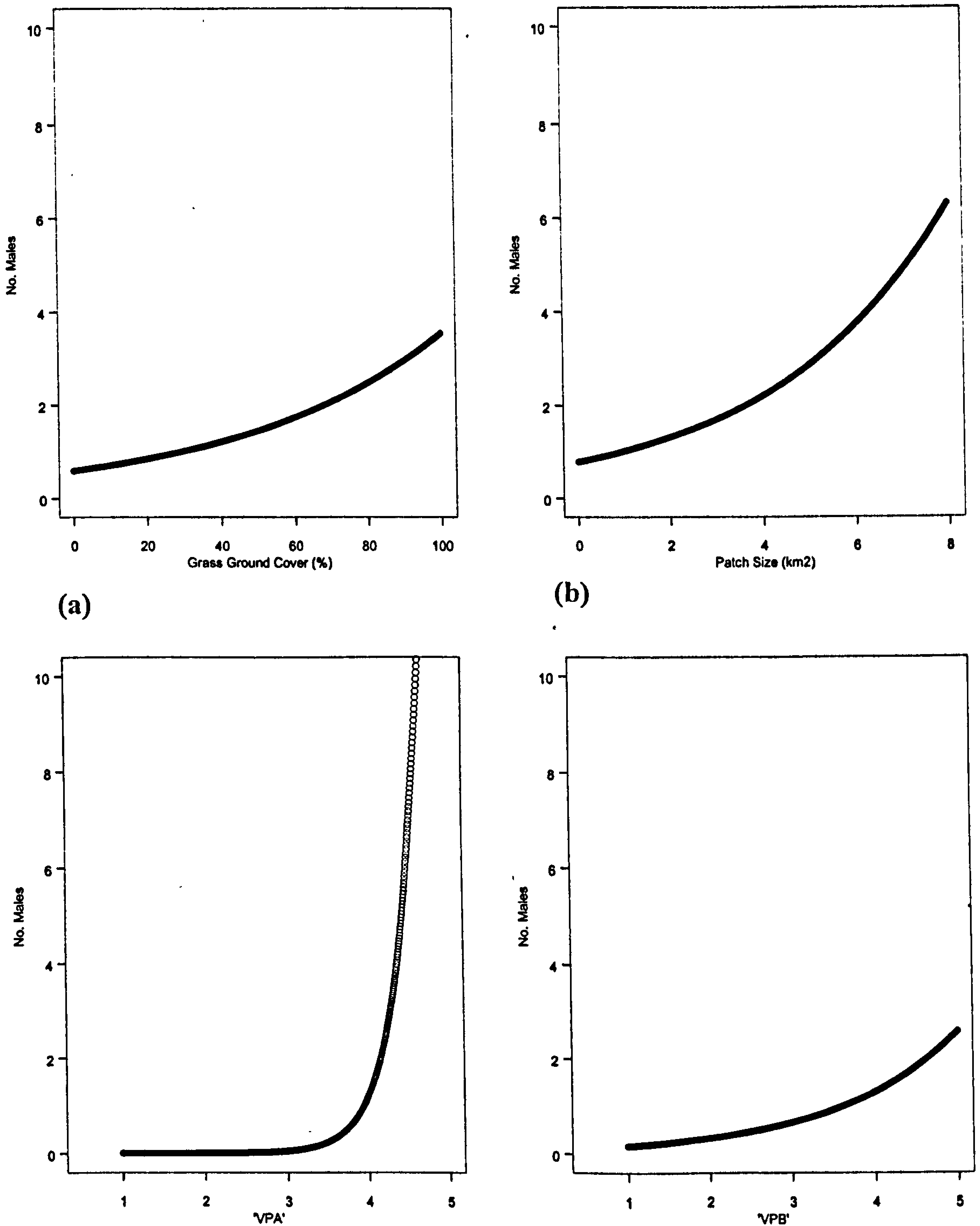
Figure 3.7. Fitted log model of the number of males in a patch predicted for pre-thicket habitats (map and field data combined) and a range of (a) canopy cover, (b) crop tree heights. Note that model limitations discussed in 3.2.4 apply to both (a) and (b).

Positive relationships were shown between the number of males in a patch and canopy cover (Figure 3.7a), grass ground cover (Figure 3.8a), patch size (Figure 3.8b) and the vegetation densities in the 0 – 0.5 m (Figure 3.8c) and 0.5 - 1 m (Figure 3.8d) height bands.

Negative relationships, however, were found between the number of males in a patch and the average height of the crop trees (Figure 3.7b), and the vegetation density in the 1 – 1.5 m height band (Figure 3.9).

In the minimal model generated to identify the habitat features significantly associated with the mean lek size (Table 3.3) positive relationships were shown between the mean lek size and canopy cover (Figure 3.10a), grass ground cover (Figure 3.10c), patch size (Figure 3.10d), heather ground cover (Figure 3.11b) and the vegetation density in the 0 – 0.5 m (Figure 3.11a).

Negative relationships, however, were found between the mean lek size and the average height of the crop trees (Figure 3.10b), and pine canopy cover (Figure 3.11a). Note that this model was constructed from pre-thicket data only thus the model breaks down where pine canopy cover or heather ground cover values fall beyond those commonly observed in pre-thicket stands. The average pine canopy cover recorded in the field was 3 % ± 9 % and 16.5 % ± 15.4 % in the case of heather ground cover. However, the general trends shown within Figure 3.11.a & b are applicable.



(a) (b)

(c) (d)

Figure 3.8. Fitted log model of the number of males in a patch predicted for pre-thicket habitats (map and field data combined) and a range of (a) ground cover by grasses, (b) patch sizes (c) 0 – 0.5 m height band, (d) 0.5 - 1 m height band. Note that model limitations discussed in 3.2.4 apply to (b).

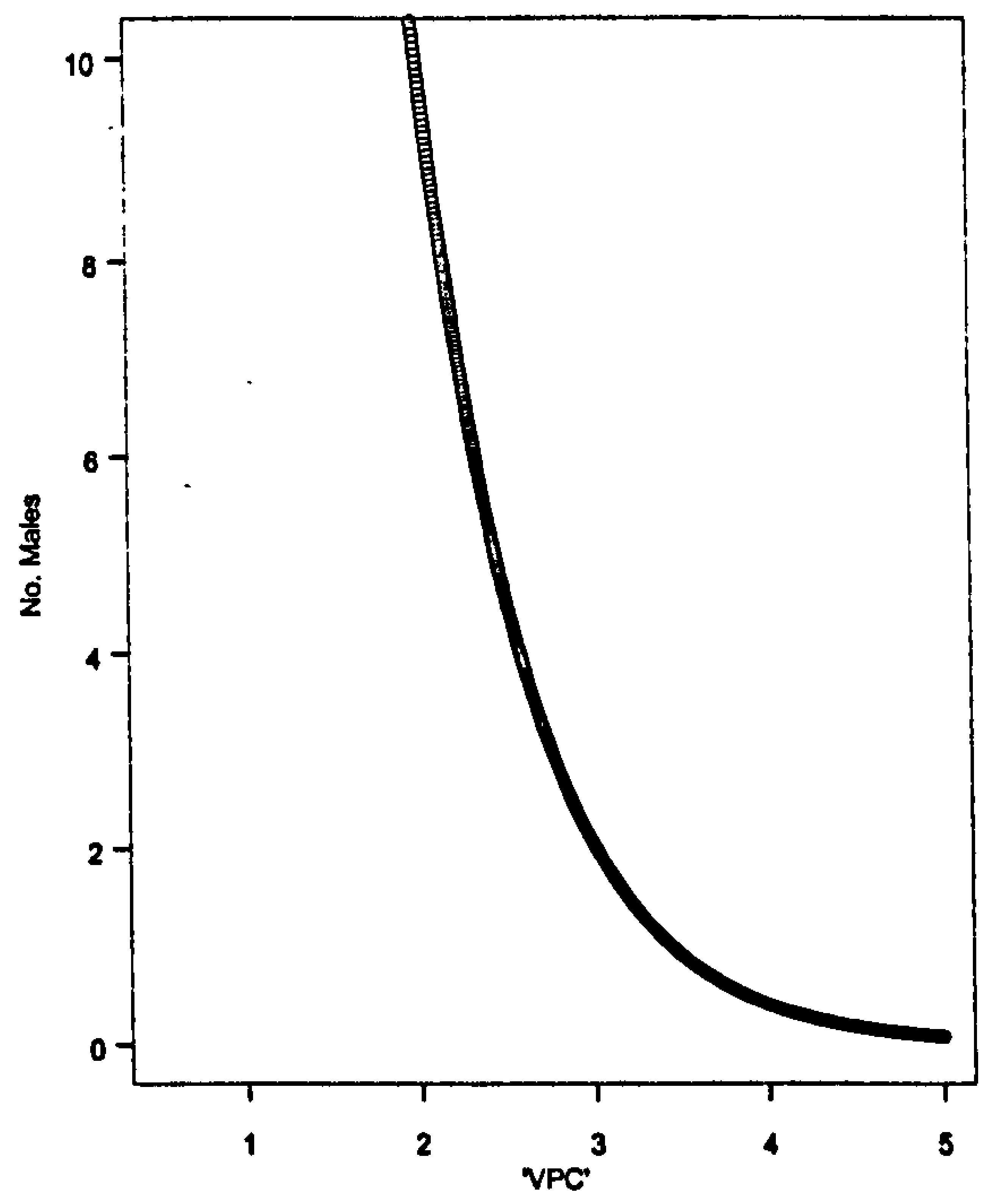


Figure 3.9. Fitted log model of the number of males in a patch predicted for pre-thicket habitats (map and field data combined) and a range of vegetation densities in the 1 – 1.5 m height band.

To summarise the results of the analysis of pre-thicket map and habitat data combined, there was no significant difference between rotations when looking at any of the dependent variables (probability of occupation; number of leks; number of males; mean lek size). There were positive relationships between the patch size and mean lek size, and the number of leks and males in them.

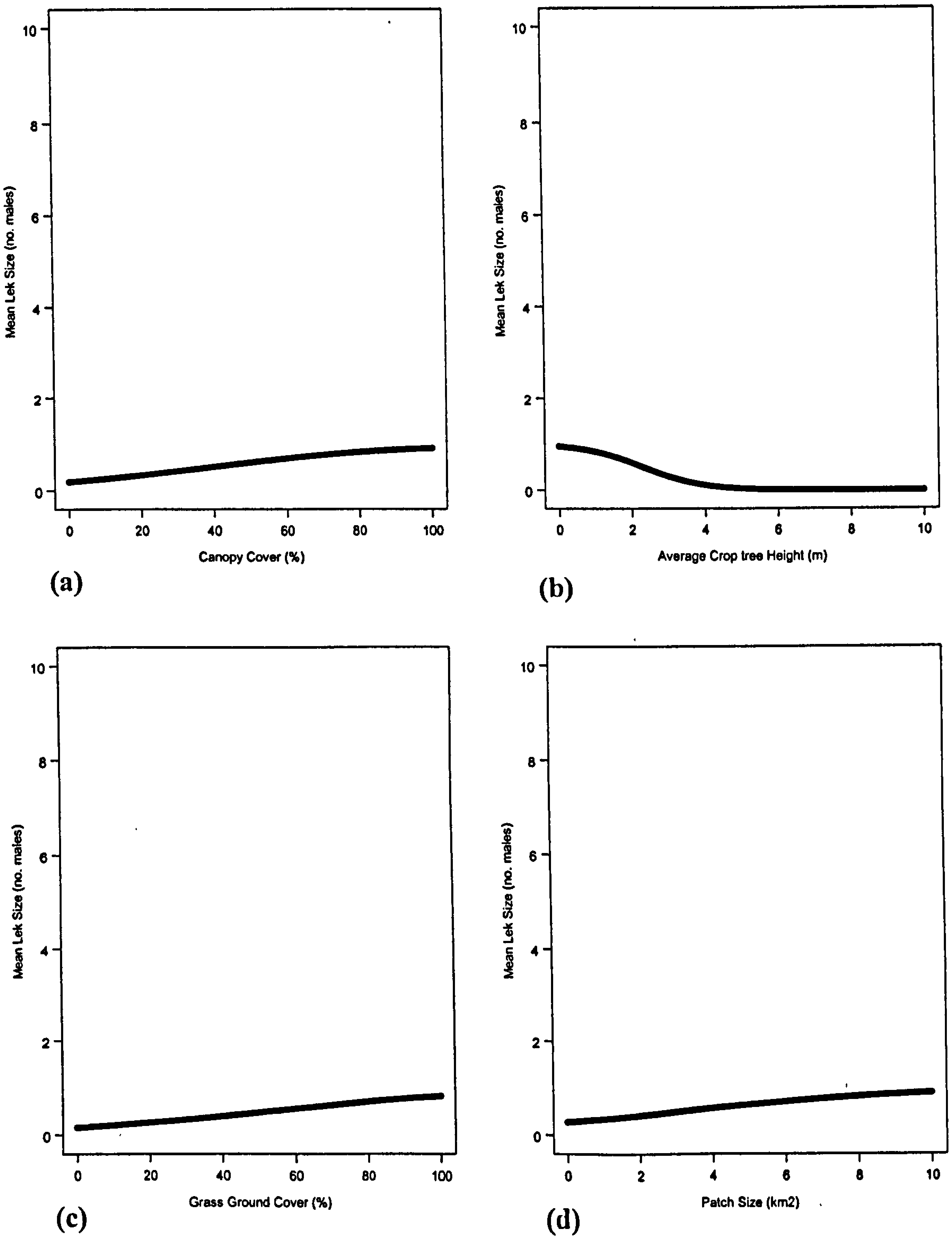


Figure 3.10. Fitted log model of the mean lek size predicted for pre-thicket habitats (map and field data combined) and a range of (a) canopy cover, (b) crop tree heights, (c) ground cover by grasses, (d) patch sizes. Note that model limitations discussed in 3.2.4 apply to (a), (b) and (d).

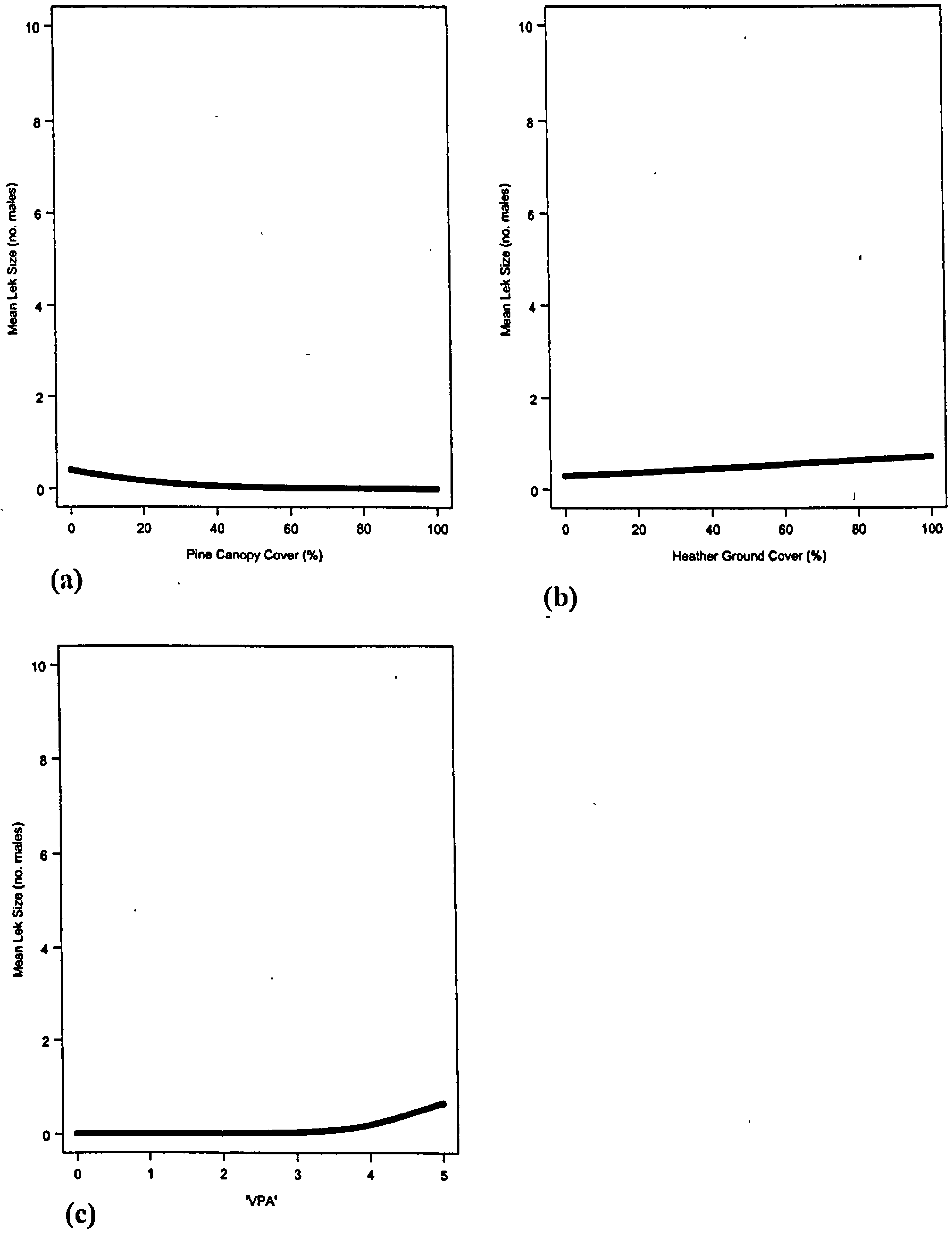


Figure 3.11. Fitted log model of the mean lek size predicted for pre-thicket habitats (map and field data combined) and a range of (a) the percentage of pine in the stand, (b) heather ground cover, (c) vegetation densities in the 0 – 0.5 m height band (VPA). Note that model limitations discussed in 3.2.4 apply to (a) and (b).

3.4 Discussion

This chapter addressed the question: was the presence of a lek associated with habitat features at the 'patch' scale?

The concise answer to this question was yes – the presence of a lek and the number of males attending it, etc. was associated with features at the patch scale. This result will be discussed in greater detail below.

3.4.1 Predicting the probability of occupation of a patch (Table 3.1).

The probability of a lek being present in a patch was strongly correlated with both habitat and patch size. Second and 1st rotation pre-thicket habitats were the most likely to be occupied. Probability increased with patch size to an asymptote. This type of incidence function with a species present in virtually all patches above a certain size but occurring much less frequently in smaller patches is common in fragmented landscapes (Wiens 1994). The distance to the nearest lek was negatively correlated with probability of occupation.

The probability of black grouse occupation was not different for 1st and 2nd pre-thicket habitats. Similar results have been found for other species including nightjar (*Caprimulgus europaeus*) and short-eared owl. Nightjars show no difference in occupation rates of new plantations and restocks (2nd rotation stock) in fact restocked sites now form their largest habitat for in Britain (Gribble 1983 and Leslie 1984 cited in Petty & Avery 1990d). Short-eared owls also breed in replanted forests provided the patch size exceeds a minimum threshold (Shaw 1995). This would suggest that these birds either do not perceive any difference between 1st and 2nd rotation pre-thicket patches or the differences have no significant relevance to their ecology. However, this does not seem to be the case for communities of birds; restock sites have been found to have a different species composition and higher total densities and numbers of species than 1st rotation sites with similar growth stage and tree species (Currie & Bamford 1981; Currie 1983) although Patterson and co-workers (1995) thought rotation had little detectable effect. Currie (1983) speculated that his result was probably due to greater structural diversity being present in restock sites. Structural diversity is a well-known predictor of bird species diversity and, to a lesser extent, density (Currie & Bamford 1981).

In pre-thicket patches the sole variables significantly correlated with occupation when map data alone were examined were patch size and the variability of tree age, a positive relationship in both cases. This association with the variability in tree age was probably due to the structural diversity generated by a variable tree age composition. A diverse physical structure within a pre-thicket patch is likely to provide adequate cover in addition to food plants. Neither of these variables were significant, however, when the map and field data were combined; instead, there were significant associations with the amount of canopy cover, crop tree height, ground cover by grasses and the density of vegetation in the first half metre above the ground. These results fit the habitat preferences reported by previous workers, i.e. a preference for: forest stands of 0 – 20 years old (Swenson & Angelstam 1993); conifer plantations of height 3 – 8 m, (Kolstad *et al.* 1985); stands of 5 – 8 m tall trees (Marcström *et al.* 1982); and an avoidance of open clearcut areas, preferring older felled areas with trees taller than 0.5 m (Marcström *et al.* 1982). Cayford and co-workers found that black grouse preferred young stands with tree canopy cover of 15 – 40 % and ground vegetation of greater than 15 % bilberry (*Vaccinium myrtilis*), 25 – 40 % heather, less than 15 % rushes and less than 5 % grasses (Cayford 1990; Cayford *et al.* 1989). These preferences are thought to have evolved as the optimum combination of vertical and horizontal cover.

The loss of a patch size effect, and others, on inclusion of the field data may have been due to low variation in these previously significant variables in the field-sampled patches (Table 3.5).

Table 3.5. Summary statistics for the sub-sample of pre-thicket patches used for the collection of field data, showing low variation in several previously significant variables.

Variable	Min.	Mean	Max.	N	Variance	SD
Mean age (years)	5.00	10.05	14.00	45	6.65	2.58
Variability in tree age (years)	0.00	1.92	9.60	45	6.29	2.51
Patch Size (km^2)	0.25	1.86	7.90	45	5.25	2.29
Distance to nearest lek (km)	0.05	0.84	4.00	45	0.74	0.86

The finding that black grouse leks are more likely to be located in pre-thicket habitats than others agrees with a number of previous studies (e.g. Angelstam 1984a; Baines 1993a; Kolstad *et al.* 1985; Marcström *et al.* 1982; Swenson & Angelstam 1993; Cayford *et al.* 1989; Cayford 1990b & 1993). The fact that a few leks were found in sites designated as post-thicket habitat may be due to one or more potential factors. These include mapping errors, slow tree growth leading to a pre-thicket structure occurring after more than 15 years of growth (Ratcliffe 1987), or perhaps the low density planting and high rates of tree death present in compartments where trees were planted between 1971 and 1981 (Kenny Hay pers. comm. 1999).

The lack of a significant difference between 1st and 2nd rotation pre-thicket patches in terms of the probability of occupation was surprising. Second rotation patches had been expected to be less suitable for black grouse and therefore avoided. This prediction was made on the basis that the ground flora of 2nd rotation patches often has to develop from a bare layer of conifer needles the previous vegetation having declined as the forest crop developed (Sakura *et al.* 1985; Welch & Scott 1997). The 12 – 15 years between planting and canopy closure in the 2nd rotation was suspected to be insufficient for the development of a ground layer adequate to fulfil the dietary and cover requirements of black grouse (Cayford 1993). This concern appears to have been unfounded in the Cowal study area, perhaps because of the reported increase in intrusion of broad-leaved trees in the 2nd rotation leading to increased diversity in tree species and structure, and lush ground vegetation. Other potential factors include the fact that compartments often lay unplanted for some years after felling, giving time for ground flora re-establishment and frequently, a lack of ground preparation (Hibberd 1991), and thus reduced disturbance to existing ground flora caused slow growth of the crop trees (K. Hay pers. comm. 1999). All of these may have been beneficial to black grouse and other woodland edge wildlife.

This speculation would accord with the results of the analysis of the combined map and field data from the sub-sample of pre-thicket patches visited. In this study the probability of occupation increased with canopy cover (Figure 3.5a) yet declined with increasing crop tree height (Figure 3.5b) and this fits previous workers' findings (e.g. Kolstad *et al.* 1985; Marcström *et al.* 1982; Swenson & Angelstam 1993; Cayford *et al.* 1989; Cayford 1990b). Perhaps the increased canopy cover coming from broad-leaved trees rather than the crop could account for the apparent contradiction between these variables. It is current practice for broadleaves to be left growing *in situ* when crop trees are harvested resulting in varying degrees of canopy cover with small restock crop heights.

3.4.2 Predicting the number of leks in a patch (Table 3.4).

The highly aggregated distribution of the number of leks in a patch restricted this analysis to pre-thicket habitats. Patch size and the variability in tree age (and the interaction between them) were positively correlated with the number of leks when just the map data were analysed. However, when the map and field data were combined, patch size was still significant (but so were average crop tree height and vegetation density in the first half metre above the ground). The correlations were the same as those described and discussed for the probability of occupation above, that is, negatively with crop tree height (Figure 3.6a) but positively with patch size (Figure 3.6c) and vegetation density in the first half metre above the ground (Figure 3.6b).

The positive relationships between patch size and occupation of a patch and the number of leks in a patch were similar to the findings of Angelstam's (1984 & 1990) studies in Sweden. He found that the size and position of preferred habitat patches, which he considered to be seedling and young stands, determined the local and regional distribution of breeding black grouse males (Angelstam 1990). Leks were found only in what he considered to be large patches of preferred habitat these had a mean patch size of 1.6 km^2 (range 0.9 – 3.4 km^2) (Angelstam 1984a). This was close to the mean occupied pre-thicket patch size of this study: 1.85 km^2 (range 0.25 – 7.9

km²). With singletons excluded, as they were in Angelstam's work, these figures became 1.63 km² (range 0.25 – 7.9 km²).

3.4.3 Predicting the number of males in a patch (Table 3.2).

In common with the probability of occupation of a patch, the number of males in a patch was strongly correlated with habitat type and patch size. Second and 1st rotation pre-thicket habitats held the most males and the number of males increased with patch size. This result agrees with Angelstam (1984a). The distances to the nearest lek and to the nearest open ground were negatively correlated with the number of males in most cases, i.e. fewer males were found in isolated patches. Interestingly, this conforms to the fundamental assumptions of the theory of island biogeography (MacArthur & Wilson 1967). In contrast, Angelstam (1984a) found no effect of isolation despite a maximum distance of 6 km between occupied patches.

There was a significant difference between rotations in the number of males, with 2nd holding more than 1st rotation pre-thicket. This was found when the map data for pre-thicket habitats were analysed alone. The other variables that were significantly correlated were patch size, variability of tree age (both positively) and the number of males at the nearest lek (negatively). Of these only patch size was significant (positively correlated), however, when the map and field data were combined. The relationships between the number of males in a pre-thicket patch and the canopy cover, crop tree height, amount of grass and vegetation density follow the patterns found and discussed for probability of occupation.

3.4.4 Predicting the mean lek size in a patch (Table 3.3).

Under-dispersion of mean lek size data restricted analysis to the combined map and field data for prethicket habitats. Eighty-six percent of the variation in mean lek size was explained by patch size (a positive correlation, Figure 3.8) plus six other variables and can be explained by the habitat preferences reported by previous workers.

The findings from this chapter are combined with those from the 'home range' analysis (Chapter 4) and discussed in terms of the implications for forest management and suggestions for further work at the end of Chapter 4.

Chapter 4 The distribution of lekking black grouse in plantation forests: II. Home Range Analysis

4.1 Introduction

According to 'female choice', 'black hole' and 'hotspot' models of lek formation and many empirical studies (e.g. Wegge & Rolstad 1986, Bradbury *et al.* 1989; Gibson 1996) leks tend to be evenly distributed since they are constrained by the distance that females can move (Stillman *et al.* 1996). Consequently, points where leks are expected but are absent presumably occur because habitat is not suitable[8]. This logic can be extended to identify the habitat requirements of a lekking species. This study applied this approach to black grouse inhabiting commercially afforested areas.

The aim of this work was to determine black grouse habitat and area requirements and the relative importance of first and second rotation components of forest structure. Two complimentary approaches were used: first, patch analysis as developed in Chapter 3 found that the presence of a lek (and the number of males attending it) was associated with features at the patch scale; and second, home range analysis which is described here. In home range analysis the habitat features within an area of ground roughly equivalent to the size of a male black grouse's home range were investigated. The home range approach was clearly linked to the scale of male black grouse movements as the home range is the area traversed by an individual in its normal activities of food

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[8] Assuming that the landscape is full; if not, then one would assume that the best areas for the species would be occupied first and/or abandoned last.

gathering, roosting, mating, etc. (White & Garrott 1990c; Wray *et al.* 1992). Unfortunately 'normal' is difficult to define (Robertson *et al.* 1998) and the home range estimate calculated varies according to the analytical technique and software package used (Boulanger & White 1990; Gallerani Lawson & Rodgers 1997). Despite this the home range concept is a useful tool in that it allows us to look at a landscape from the study organism's perspective.

The previous chapter focussed on patch characteristics investigating whether the presence or number of displaying males was related in some way to the habitat features of the habitat patch immediately surrounding the lek. Patches were identified as definable areas of homogeneous habitat structure in terms that on the basis of previous studies were thought to be perceived by black grouse. These same terms were used in this chapter however the scale of the unit investigated was expanded from the patch to the home range. One can see the patch scale as being defined by the landscape but the animal defines the home range scale.

It is advisable to use multiple spatial scales since the same factors can play a different role according to scale (Angelstam 1990; Angelstam & Martinsson 1990; Bland 1997). For example, Illera (2001) found that at the landscape scale (larger than the home range scale here) slopes with high shrub coverage were the best predictors of presence of the Canary Islands stonechat (*Saxicola dacotiae*) whilst at the microhabitat scale (my patch scale) slopes with large boulders were selected. It seems reasonable to assume that all the habitats critical to an animal's existence would be present within its home range whereas they need not be present within a single patch. Densities and dynamics of various organisms often cannot be understood from the processes occurring within separate habitat patches, a landscape perspective has to be used (Hansson 1992).

In this chapter the following broad question was addressed: is the presence of a lek associated with habitat features at the 'home range' scale? In particular the following specific questions were addressed:

- First, was the presence or absence of a lek associated with habitat features within a home range area?

- Second, where a lek was present, was the number of males attending the lek (lek size) associated with habitat features at the home range scale?

An understanding of how these variables are associated with habitat features, if at all, may help to explain the distribution of lekking black grouse within the landscape. For example, Wegge and Rolstad (1986) applied an approach similar to home range analysis and found that the number of resident male capercaillie at leks increased with the amount of mature forest within a 1 km radius of a lek centre. This explained an observed increase in the lek spacing in an intensively logged forest. Kurki and co-workers' (1997) study on woodland grouse also found that the probability of an observed hen being with a brood was positively associated with the proportion of closed canopy forest in the landscape. Similarly, Kumpu and co-workers (1997) found that the proportion of prime hazel grouse (*Bonasa bonasia*) habitat in the landscape was positively correlated with the density at which this species occurred.

4.2 Methods

The data used in this chapter were collected from the Cowal study area in Argyll (for further details see Chapter 2, section 2.2). Although the Cowal study area was surveyed in consecutive years (1996, 1997, 1998) not all of the study area was covered each year (see section 3.2.1.). Full analysis comparing years was therefore not possible, however, the number of leks with two or males present in 1998 was not significantly different to that found in the 1996/7 ($\chi^2 = 7.05$, 6 d.f., $P > 0.05$).

For each site an average of the peak number of males observed each year was taken resulting in a single dataset. Thus this dataset was considered representative of the three years of study.

4.2.1 Lek Survey and Habitat Mapping

Section 3.2.1. (Chapter 3) provides details of the lek survey and habitat mapping methods used. The results of these were reported in Chapter 3 and were also used in the analysis for this chapter.

4.2.2 Home Range Analysis

A circle of radius equivalent to 1 km was defined (on 1:10,000 scale maps) around each lek location (n = 60) and an equal number of random points (n = 60) generated over the study area (excluding water bodies and residential areas). A circle of this size approximates to the average home range area of male black grouse in woodland environments (Table 4.1). Attributes of the habitat mosaic found within this 'home range' were measured and recorded:

i) presence or absence of a lek (1,0);
ii) number of males at the lek, if present;
iii) habitat of the central or 'lek' patch (one of the six categories described in 3.2.1.);
iv) size of the central/lek patch (converted into the proportion of the total home range area);
v) total number of patches;
vi) number of patches of each habitat type (excluding central/lek patch);
vii) an index of habitat diversity (the number of patch boundaries crossed by the diameter of the circle);
viii) length of open-ground boundary (km; synonymous with moorland edge);
ix) size of each patch (ha);
x) area covered by each habitat type (ha; converted into the proportion of the home range area excluding the central/lek patch).

To investigate whether the presence of a lek was significantly associated with habitat features at the 'home range' scale these were analysed using generalised linear modelling (GLM). The error structure of the model (normal, Poisson, binomial or negative binomial) was selected such that it matched the error structure of the dependent variable. The link function used was the default option (often referred to as the canonical link functions) for the given error structure:

Error Structure	Link
Normal	Identity
Poisson	Log
Binomial	Logit
Negative Binomial	Reciprocal

The maximal model comprised all the habitat variables (iii – x) as explanatory variables and 'occupation' - the presence or absence of a real lek at the centre of the 'home range' (i) or the total number of males attending the lek (ii) as the dependent variable. Step-wise elimination of insignificant terms produced the minimal model and the 'occupation' analyses were performed twice, first including lekking singletons, then excluding them. However, the results from the former only are presented as these generally explained a higher proportion of the variation in the dataset and can be considered real leks on the basis of repeated observations and represent a large proportion of the total population of lekking males.

Data analysis was conducted using S-PLUS 4.5 for Windows (MathSoft 1998). To ensure that appropriate models were fitted the residuals were checked for normality and constant variance. A significance level of $P \leq 0.05$ was adopted throughout.

4.2.3 Graph Plotting

Raw data are not shown in this chapter as a modeling approach was taken and the results of the models are shown instead. The modeling process described in 4.2.2 was used to generate models (and their R^2 values) from real data collected as described.

These models were then used to predict occupancy or the number of males at a lek keeping all explanatory variables except one constant (varying more than one variable at a time was beyond the available statistical advice) at the mean value recorded in the study area. The results were plotted in graphs made up of 1000 calculations from the varied explanatory variable that ranged between the minimum and maximum values observed in the study area. The outputs from this process are fitted curves of the dependent variable.

The mean values of the other variables in the model should be borne in mind when looking at the absolute values plotted. In addition, the relative lack of data points at the extremes of the x-variables ranges (in particular at the upper limits) make the models less robust in these areas. The patterns and trends shown within the graphs are more generally relevant. Raw data were not plotted on these graphs since the data have a non-normal error structure and would not show how good a fit the fitted curves represent. The R^2 value indicates what percentage of the variation in the dataset the model explains and this is the best available measure of the 'goodness of fit'.

Table 4.1. Summary of black grouse home range estimates from the literature.

Reference	Study Area	Habitat	Time of Year	Home Range (H.R.) Estimate (ha)	H.R. Radius Estimate (km)	Notes
Robinson *et al.* (1993)	Perthshire	Mostly moorland	Not known	320 per lekking group	1	Extrapolated from inter-lek distance
Johnstone 1969 cited in Cayford (1993)	NE Scotland	Not known	Not known	500 per lekking group	1.26	-
Cayford (1990b)	Wales	Coniferous plantations	Not known	325 ± 71 (male H.R.)	1.02	Implied that 500 – 700 ha suitable habitat needed
Cayford & Hope Jones (1989)	Wales	Forests	Not known	-	-	"Rarely travel > 1.5 km from the lek"
Cayford *et al.* (1989)	Wales	Conifer forests	Not known	Male 338.9 ± 82.3 SD Female 60.2 ± 52.6 SD	1.04 0.44	-
Ellison *et al.* (1989)	French Alps	Larch & pine forests	Autumn Winter	15 – 312 2 – 30	0.22 – 1 0.08 – 0.31	Also suggests that habitat within 10 km of lek is important
De Franceschi & Mattedi (1995)	Italian Alps	Not known	Summer - Winter	51 - 66	0.40 – 0.46	Average of 3 males, yearling H.R. 2.5 – 5 times larger
Kolstad *et al.* (1985)	E. Norway	Conifer plantations & natural regeneration	Mid May – late August	24	0.28	No significant difference between sexes. A tendency for larger H.R. among yearlings
Picozzi & Hepburn (1984)	North East Scotland	Not known	Not known	Male 355 ± 177.6 SD Female 74.5 ± 34.4 SD	1.06 0.49	Average of 3 males for 119 – 340 days Average of 17 females for 91 – 374 days
Robel (1969a)	Scotland	Moorland & forest	Not known	458 ± 126 SD Conc. Use 48.2 – 151.1	1.21	Average of 7 males (1 juvenile) 75% of locations

4.3 Results

4.3.1 The probability of occupation of a 'home range'.

The minimal model generated to identify the habitat features significantly associated with the presence of a real lek in a 'home range' (Table 4.2) showed that the probability of occupation was greatest when the 'lek patch' was 1st rotation pre-thicket (Figures 4.1 a – c). Each line represented the predicted relationship between the dependent and independent variables for a different 'lek patch' habitat (1 = 1st pre-thicket, 2 = 2nd pre-thicket, 3 = post-thicket, 4 = open ground, 5 = agriculture).

The probability of occupation increased with increasing amount of 1st rotation pre-thicket habitat in the 'home range' (expressed as the proportion of the 'home range') (Figure 4.1a). This positive relationship existed irrespective of the habitat of the 'lek patch'. The distribution of the 1st rotation pre-thicket habitat was also important (Figure 4.1b) – as the number of patches increased the probability of occupation decreased, that is, fragmentation of the preferred habitat reduced the probability of occupation of a 'home range'. Note that the model shown in Figure 4.1 breaks down where the amount of 1st rotation pre-thicket and the number of 1st rotation pre-thicket patches fall beyond those commonly observed. The mean amount of 1st rotation pre-thicket and number of 1st rotation pre-thicket patches recorded in the field was 0.16 ± 0.23 (SD) and 0.75 ± 0.95 respectively. However, the general trends shown within the Figures 4.1./4.2. a & b are applicable.

Key to symbols used in Chapter 4 graphs:

1 = 1st rotation pre-thicket 2 = 2nd rotation pre-thicket 3 = post-thicket 4 = open ground 5 = agriculture

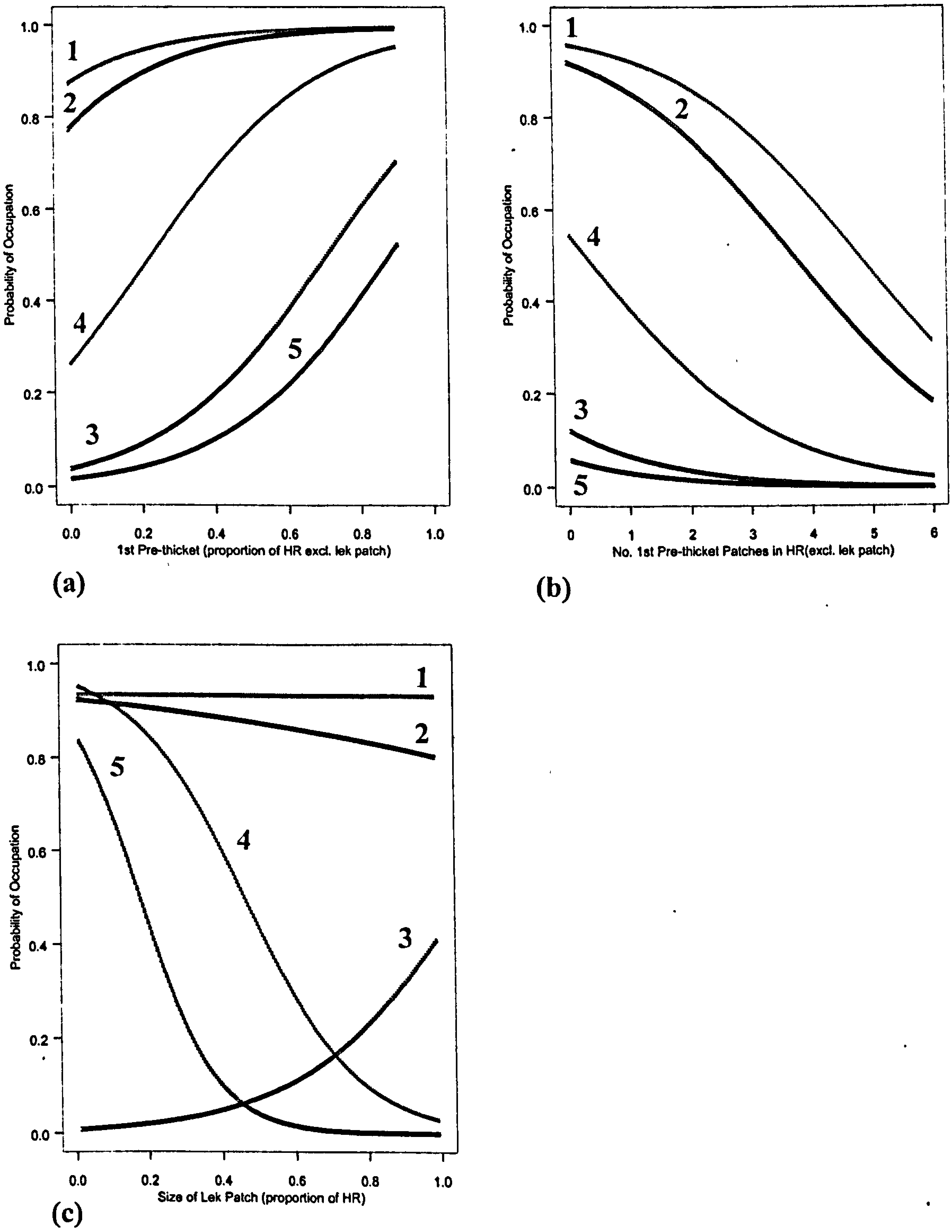


Figure 4.1. Fitted logit model of the probability of a real lek being present in a 'home range' predicted from (a) the amount of 1st rotation pre-thicket excluding the lek patch, (b) the number of 1st rotation pre-thicket patches (excluding the lek patch), (c) the size of the lek patch. Note that model limitations discussed in 4.2.3 apply to (a) and (b).

The size of the 'lek patch' (expressed as the proportion of the 'home range) had a relatively small effect on the probability of occupation when the 'lek patch' was either 1st or 2nd rotation pre-thicket (Figure 4.1c). However, when the 'lek patch' was open ground (4) or agriculture (5) the probability dropped as the size of the lek patch increased. It dropped to near zero and zero respectively indicating that it was very unlikely that a home range sized area of either of these habitats could hold a real lek. As the size of a post-thicket 'lek patch' increased the probability of occupation increased, this was surprising but the probability of occupation did not exceed 0.4 even when the entire 'home range' was covered by the 'lek patch'.

Table 4.2. Summary of minimal models generated by home range analysis.

Dependent variable	Habitat used in Model	R^2 (%)	GLM Error Structure	Link Function	Habitat of Lek Patch	Size of Lek Patch*	Amount of 1st rotation pre-thicket**	No. of 1st rotation pre-thicket patches**	Interactions	Figure Nos. in text
Probability of occupation	1st rotation pre-thicket	61	B	Logit	0.000^1	0.007^2	0.000	0.017	0.002^{12}	4.1
Probability of occupation	2nd rotation pre-thicket	53	B	Logit	0.000^1	0.012^2			0.001^{12}	4.1
Probability of occupation	Pre-thicket (1st & 2nd rotations lumped)	57	B	Logit	0.000^1	0.016^2			0.001^{12}	4.1
No. of Males	1st rotation pre-thicket	64	P	Log	0.000^1	0.037^2	0.003	0.015	0.000^{12}	4.2

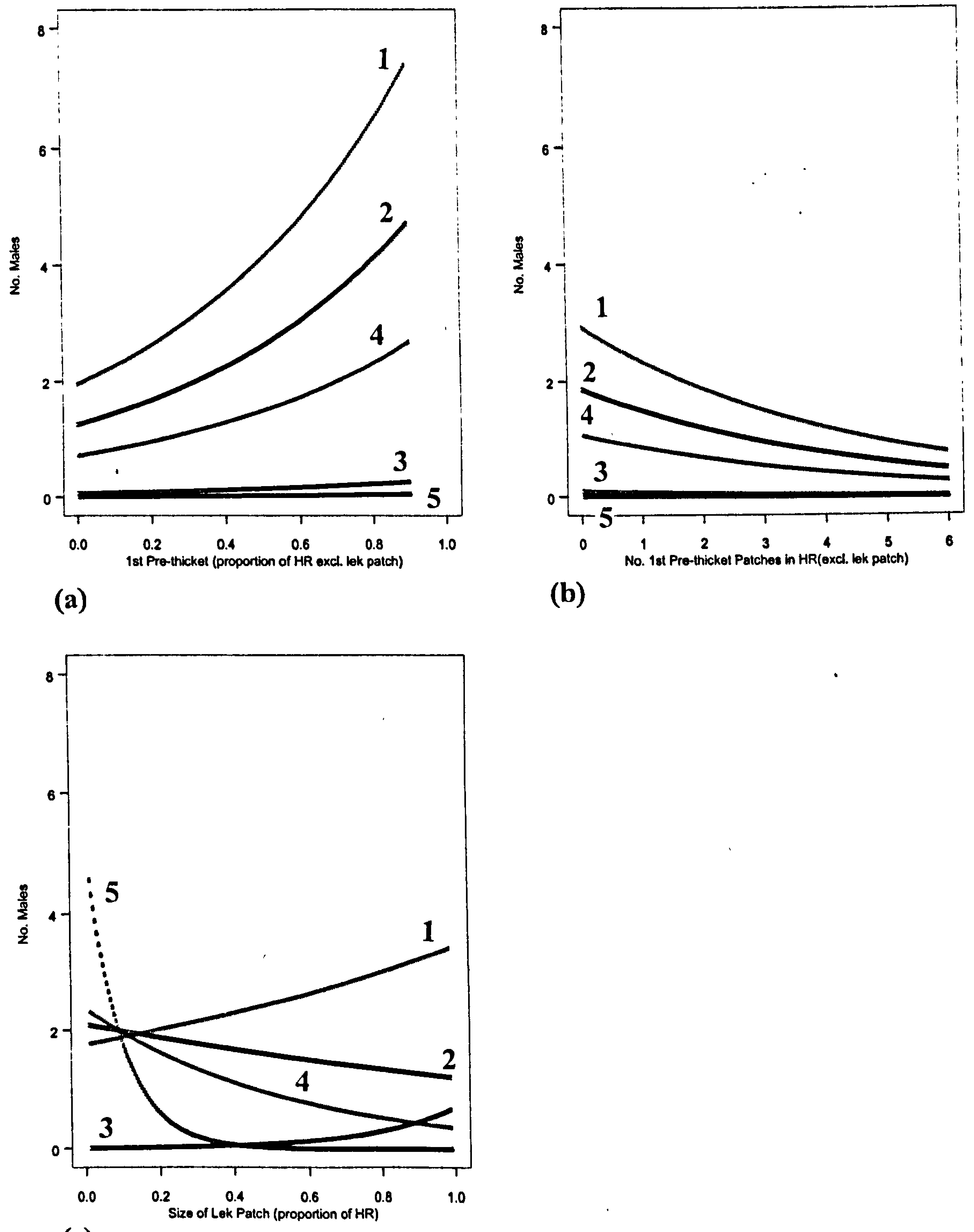
Notes: Numbers below variables are the P values for significant terms; B = Binomial; P = Poisson; Superscript numbers indicate the terms which interact; * expressed as the proportion of the 'home range'; ** excluding lek patch, expressed as the proportion of the 'home range'.

4.3.2 The number of males in a 'home range'.

The minimal model generated to explain the total number of males attending a lek contained the same explanatory variables as the previous model (Table 4.2). The number of males attending the lek was greatest when the 'lek patch' was 1st rotation pre-thicket (Figures 4.2 a – c).

The number of males attending the lek increased with increasing amount of 1st rotation pre-thicket habitat in the 'home range' (expressed as a proportion of the 'home range') (Figure 4.2a). This positive relationship existed irrespective of the habitat of the 'lek patch'. The distribution of the 1st rotation pre-thicket habitat was important (Figure 4.2b) – as the number of patches increased the number of males decreased, that is, fragmentation of the preferred habitat reduced the number of males attending the lek. These patterns echo those shown for the probability of occupation (Figures 4.1 a and b).

There was a positive relationship between the number of males and the size of 'lek patch' only when it was 1st rotation pre-thicket (1) or post-thicket (3), otherwise the relationship was negative (Figure 4.2c).



(a) (b) (c)

Figure 4.2. Fitted log model of the total number of males attending a lek predicted from (a) the amount of 1st rotation pre-thicket excluding the lek patch, (b) the number of 1st rotation pre-thicket patches (excluding the lek patch). Fitted log model of the total number of males attending a lek predicted from (c) the size of the lek patch. Note that model limitations discussed in 4.2.3 apply to (a) and (b).

4.4 Discussion

This chapter addressed the question: was the presence of a lek associated with habitat features at the 'home range' scale?

The concise answer to this question was yes – the presence of a lek and the number of males attending it was associated with features at the home range scale. This result will be discussed in greater detail below.

4.4.1 Predicting the probability of occupation of a 'home range' (Table 4.2).

The probability of a lek being present in a home range area of land was strongly correlated with the habitat and size of the central or 'lek patch'. Also important were the total amount of 1st rotation pre-thicket habitat in the home range and its level of fragmentation. Garson & Starling (1990) reported similar results, leks only persisted where appreciable areas of open ground or young plantations were found in the vicinity of leks. These authors also used a lek survey and habitat mapping technique in their analysis although their habitat categories (heather moor, sheepwalk, improved grasslands, mixed, open forest and closed forest) differed from those used here.

Similar models resulted when 2nd rotation pre-thicket habitat or pre-thicket (rotation ignored) habitat was used as the mosaic descriptor instead of 1st rotation pre-thicket. In these, the diversity of the mosaic within the home range was significantly related to the probability of occupation. However, none explained a higher proportion of the variation in the occupation data than the original model. As black grouse do not differentiate between 1st and 2nd rotation pre-thicket patches it would be valuable to repeat this analysis without differentiating between the two.

4.4.2 Predicting the number of males in a 'home range' (Table 4.2).

The number of males attending the lek increased with increasing amount of 1st rotation pre-thicket in the home range of 1 km radius. Similarly, Cayford (1993) found that the number of males at a lek reflected the availability of preferred habitats within a radius of approximately 2 km of the lek. Angelstam and co-workers (1987) were less specific: "the amount of acceptable habitat and the habitat quality influenced the mean density within an area". In my study, the distribution of 1st rotation pre-thicket habitat was important with a decrease in the number of males accompanying increased fragmentation. Relationships between the number of males and the amount and distribution of 2nd rotation pre-thicket or pre-thicket (rotation ignored) habitat were not investigated.

The negative impacts of increased habitat fragmentation due to human activity, be it the industrialisation of forestry or intensification of agriculture, have been reported for black grouse (e.g. Angelstam 1984a; Kurki & Lindén 1995; Swenson & Angelstam 1993; Cayford 1993) and many other species including helmeted honeyeater (*Lichenostomus melanops cassidix*) (Akçakaya *et al.* 1995), capercaillie (Ims *et al.* 1993), tawny owl (*Strix aluco*) (Redpath 1995) and small mammal communities (Kozakiewicz 1993). The proximate causes of these detrimental effects include: the increase in small and medium-sized predators (Andrén *et al.* 1985; Andrén 1992; Bauer & Kalchreuter 1984; Swenson & Angelstam 1993); lower quality habitat in terms of abundance of food plants and cover; and the isolation of small groups of birds leading to extinction through stochastic effects (Opdam 1990; Simberloff 1994; Swenson & Angelstam 1993; Wiens 1997). In addition, individuals from a number of grouse species are known to collide, often with fatal results (Baines & Summers 1997; Catt *et al.* 1994; Andrew & Baines 1997), with deer fences that are commonly erected around artificial forests (Summers 1998). This work has identified acceptable habitat specific patch sizes but not the degree of isolation or specifically looked at the role of dispersal. Female (the dispersing sex) dispersal is likely to be very important in determining colonisation rates and the stability of metapopulation structure, if a metapopulation exists.

In contrast, a few studies have identified positive effects of fragmentation. Robertson (1994) found that pheasants were a species associated with the intimate interspersion of habitat types, whilst Patterson and co-workers (1995) showed that the number of birds was higher at the edge of woodlots than at the centre. However, generally the effects of habitat loss far outweigh those of fragmentation no matter the arrangement of remaining fragments the negative effects of habitat loss will not be mitigated (Fahrig 1997). Worse still, habitat fragmentation generally occurs as a consequence of habitat loss so both processes must be considered concurrently (Wiens 1990).

The results discussed are somewhat limited by the assumptions that had to be made for the analyses to be performed. A circular 'home range' of 1 km radius is a crude approximation to a real male black grouse home range. Ideally, a sample of male and female black grouse would have been radio-tracked. This would have permitted more accurate estimations of home ranges to be made and would also have allowed direct observation of habitat selection and dispersal. Unfortunately, this was not feasible within the constraints of this project. An alternative approach would be to use a geographic information system (GIS) that would permit repetition of the analyses at a range of 'home range' radii. Such analyses would help to identify the scale at which habitat selection would tend to operate, an approach used by Kurki and co-workers (1997). It is also important to remember that a single species may exhibit different home range sizes in different regions (Wiens 1994) and studies need to consider variations within and between populations.

4.4.3 Implications for forest management with the aim of conserving black grouse.

The implications of the patch and home range analyses results (Chapters 3 and 4 combined) for black grouse 'friendly' forest management are that a substantial proportion of the forest mosaic should be composed of pre-thicket stage stands, ideally grown in large blocks with a variable age structure within them. This necessarily means, however, that when the pre-thicket stands mature they will become large blocks of unsuitable habitat. To combat this, the forest must be designed to ensure that as one block becomes unsuitable another suitable patch within black grouse foraging distance becomes available. Radio-tracking studies are required to establish the length of these foraging distances and trials must be put in place to establish the sustainable ratio of suitable to unsuitable habitat that fulfils black grouse habitat requirements. Unfortunately, the need for large roughly even-aged blocks of trees can be undesirable for other species, for example French and co-workers (1986) stated that uniform, even-age blocks greater than 5 hectares should be avoided when managing woods for songbirds. However, retaining standing trees and shrubs in restock sites may help to mitigate this effect (Currie 1983). The challenge for forest planners will be to find an appropriate grain size such that in the same 'patch' a black grouse 'perceives' one large patch whilst small passerines perceive lots of small patches with lots of edges, their preferred habitat type (Currie & Bamford 1981; Patterson *et al.* 1995; Sankey 1995).

In natural conditions black grouse inhabit the early successional stages of forest so this species could be considered to be pre-adapted to the modern system of clearcut forest management (Baines 1993a; Swenson & Angelstam 1993). However, clearfelling should not be seen as a substitute for providing permanent black grouse habitats within forests. Diversifying the age structure (e.g. Blyth 1993) of a forest at the end of the first rotation by patchwork clearfelling will improve the area for black grouse providing heather is allowed to regenerate on restocked sites (Cayford 1993). To this end, post-felling treatment e.g. drainage, slashburning, scarification, mounding and biocide treatment (Hibberd 1991) should be minimised (Boag & Rolstad 1991; Parr & Watson 1988). Petty & Avery (1990d) broadened this recommendation to other wildlife by advising that areas within commercial forests should be devoted to permanent conservation features and that these should be designed to form an interlinking network using roads and watercourses. Cayford (1993) proposed targeting black grouse management improvements within a 1.5 km radius of known leks (plus specific management of lek sites, young plantations, forest edge, riparian zones, etc.). This, however, may not be economically feasible and many of his management recommendations seem to be on far too small a scale to have any significant lasting benefit. Finally, metapopulation theory suggests that it is very important to conserve all patches of suitable habitat even if they are unoccupied (Angelstam & Martinsson 1990; Hanski 1997; Opdam 1990). Wider countryside measures (Baillie *et al.* 2000) are also needed to maintain and enhance the habitat suitability in the matrix surrounding suitable patches (Hansson 1992; Andrén 1994).

4.4.4 Suggestions for further work.

Despite the limitations discussed above, the correlations found do give an important insight into black grouse habitat and area requirements. Future work could test these findings by establishing experimental plots in commercial plantations and monitoring black grouse habitat use and productivity (Bowers *et al.* 1996). Collaborative forest research is being performed in Scandinavia (Boag & Rolstad 1991) and increasingly so in Britain, e.g. a recent collaboration between the Royal Society for the Protection of Birds (RSPB) and FC in Wales. This sort of initiative is urgently needed and must be continued. Research should be implemented to assess how applicable the findings from Cowal are to other geographical areas. This is a standard requirement for all studies but particularly important in this case as Cowal, at 31.2% (Petty & Avery 1990d), has one of the highest proportions of non-forest land within its total forest area in Britain. Although Cowal has such a high proportion of non-forest land within the forest boundary the actual forest cover is fairly continuous so one might expect the relationships observed here to be more extreme in a more fragmented forest (Wiens 1990) such as Glentrool forest in Dumfries.

Results from the patch analysis in Chapter 3 indicated that black grouse do not differentiate between 1st and 2nd rotation pre-thicket patches. Therefore the obvious next step is to reanalyse the data without differentiating between the two. Also, now that the elements of a 'suitable' patch have been identified another variable, distance to nearest suitable patch, could be included in the maximal model. Time constraints did not permit the performance of these analyses.

This study used the distribution of leks to indicate general habitat selection, i.e. specific requirements such as nest sites, brood habitat (see Chapter 6), lek arenas, etc. were not investigated. Once coarse habitat requirements are understood it is advisable to address these specific areas in detail so that fine-scale requirements can be identified and managed for.

One important issue that was outwith the scope of this study is that of predation. Increased numbers of predators (Gregory & Marchant 1995; Tapper & France 1992) in the wider countryside are thought to be linked with the changes in land management and gamekeeping practices (Holloway 1996a; Tapper & France 1992; Tapper 1992; Reynolds & Tapper 1996). The increase in corvids and other small and medium-sized predators associated with forest fragmentation and modern forestry is well documented (Andrén *et al.* 1985; Andrén 1992; Hansson 1992; Storaas & Wegge 1984; Storaas & Wegge 1987; Swenson & Angelstam 1993). Studies of black grouse in non-forest habitats have shown that in poor breeding years predator control may be important (Baines 1991), especially in poor quality habitat (Baines 1992; Baines 1996). Consequently, another important area of investigation should be on the effects of predation within a modern forest environment; perhaps the habitat quality will be sufficient to counter the impact of increased predator density but this remains to be seen.

Chapter 5 The distribution of lekking black grouse in highland Perthshire 1990 - 1998

5.1 Introduction

Black grouse are frequently described as a 'woodland' species (Kurki *et al.* 2000) and are regarded as birds of early stage succession forest (Baines 1993a; Swenson & Angelstam 1993) yet they exhibit wide-ranging habitat associations. In Britain, notably northern England, they utilise moorland, improved fields and rough grazings (Baines 1990 & 1994; Garson & Starling 1990) as well as plantation forestry (Cayford & Hope Jones 1989; Grove *et al.* 1988; Cayford 1988). In Fennoscandia and other boreal regions they are birds of the forest edge, particularly favouring a deciduous mix (Helle *et al.* 1987), whilst in Britain significant use of native woodlands tends to only feature in northern England and north-east Scotland (Picozzi & Hepburn 1984; Picozzi 1986a; Hancock *et al.* 1999).

Plantation forestry is increasingly recognised as an important habitat in the UK (Baines & Hudson 1995) but its relative importance within a more mixed landscape mosaic has not yet been evaluated. In this chapter, the spatial and temporal distribution of lekking black grouse in relation to habitat features was investigated within the mixed landscape of highland Perthshire. Within the context of the United Kingdom Perthshire represents a major stronghold of the black grouse (Baines 1990 & 1993b; Robinson *et al.* 1993; Tapper 1992). Nevertheless the population there has not been immune from the general decline, indeed the population of displaying males is estimated to have halved in the period 1992 to 1996 (Hancock pers. comm.).

The specific aim of the work described was to determine their associations with, and the relative importance of moorland and forest components of the landscape mosaic, and identify the important features within each habitat type. The Perthshire study area was considered to provide a contrasting landscape pattern to Cowal; Cowal can be seen as a 'sea' of forestry with 'islands' of open-ground and Perthshire the opposite.

To meet this aim, two spatial scales were used for analysis - the lek scale (roughly equivalent to the 'home range' scale in Chapter 4) and the block scale (roughly equivalent to the 'patch' scale in Chapter 3). These spatial scales are not directly equivalent to those used in Cowal as the landscape pattern in Perthshire has a coarser grain size – there are larger blocks of similar habitat within the landscape. Thus, the Cowal study area suited a more intensive approach with habitat variables measured in the field. Nine continuous years of lek surveys in Perthshire enabled two temporal scales (the absolute number of males and the change in number of males) to be nested within each spatial scale.

The importance of using multiple spatial scales has been illustrated (e.g. Angelstam 1990; Angelstam & Martinsson 1990; Bland 1997) and discussed in previous chapters where it was shown that the importance of independent variables can vary with the scale of investigation. The same principle applies to temporal scales. This is now widely recognised but, partly due to short-term funding and lack of long-term datasets, fewer studies have looked at multiple temporal (e.g. Welander 2000) than spatial scales. Angelstam (1990) showed that different factors affected the distribution and abundance of black grouse at different spatial scales but in addition to this he found that given a sufficiently long time series the effects of the habitat patch dynamics overruled other effects. This may be a widespread phenomenon since the temporal distribution of many animals' activity in space reflects the interactions between their needs and the spatio-temporal dynamics of resources (Kozakiewicz 1995). In contrast Saari and co-workers (1998) studied hazel grouse over a period of 21 years and found that occupancy (a static variable) and colonisation and extinction (dynamic variables) probabilities were all affected by the size of suitable habitat patches.

Wiens (1990) emphasised the need for long-term experimental studies counselling that time lags in a species' response to environmental changes could lead to them being overlooked if an inadequate temporal scale is used. This point is neatly illustrated by the results of Rolstad and co-workers' (1997) 17 year study of capercaillie leks in fragmented forests. In the first seven years after the forest was logged densities of male capercaillie remained unchanged but in the second period of seven years they declined. Logging clearly affected the distribution and size of capercaillie leks but this would not have been the recognised after only seven years of study.

In this chapter the following questions were specifically addressed: was the absolute number or the change in number of lekking males associated with habitat features at the scale of the lek or the scale of the habitat block?

5.2 Methods

The data used in this chapter were collected from the 800 km² Perthshire study area (for further details see Chapter 2, section 2.4.). Members of the Perthshire Black Grouse Study Group (PBGSG) and Game Conservancy Trust (GCT) staff generously provided the lek survey data they collected during that period. In addition, David Baines made GCT questionnaire results available to me.

5.2.1 Lek Surveys

Members of the Perthshire Black Grouse Study Group (PBGSG) (700 km²) (Robinson *et al.* 1993) and Game Conservancy Trust (GCT) staff (100 km²) surveyed lekking males in the nine years 1990 to 1998. The whole of the study area, excluding some montane ground, was searched for displaying males. The location, date, time, and number of males attending each lek between early April and late May (the peak lekking season) were recorded each year. Lekking singletons and the number of females attending leks were also recorded but these data are not analysed here. Although Robinson and co-workers (1993) reported that all grouse were recorded it was thought that singletons might have been under-reported. As a consequence singletons in this dataset were excluded from the analysis. Leks were visited and the males counted from first light up to 1.5 hours after dawn. This time period was restricted to reduce the variation in numbers of males since numbers are known to vary both throughout the season and the day (Baines 1995; Cayford & Walker 1991). Ideally, each lek should have been visited twice each year during the survey period but this was not always feasible; where more than one lek visit was made per year the maximum number of males recorded attending the lek that year was used in subsequent analyses. This is a repeat of the methodology used in Chapter 3.

The change in the number of lekking males between 1990 and 1998 was calculated in the same way for both spatial scales: the difference in the number of lekking males from year to year was calculated and from this the average change for the period 1990 – 1998 was derived. The methods used for calculating the 'total' number of lekking males differed, however, between the spatial scales. At the block scale, the total number of lekking males in 1998 was used. At the lek scale, the average number of males attending the lek from 1996 to 1998 was used (to allow comparison with the Cowal 'home range' analysis results, see Chapter 4). These figures were used as the dependent variables in the analyses described below.

5.2.2 Habitat Mapping

One hundred and forty-nine leks were surveyed in the period 1990 to 1998. All lek locations were plotted on 1:50,000 scale Ordnance Survey 'Landranger' maps (last updated in the mid-1990s). These maps clearly show the location of woodland (both broad-leaved and coniferous) as well as other landscape features, e.g. lochs, roads, settlements, etc. Additional data for woodland areas (e.g. tree species composition, tree age, rotation, amount of open-ground within a forest, etc.) were extracted from Forestry Commission stock maps and the Forestry Commission database where appropriate and available.

5.2.2.1 Lek Scale

The four 1 km squares (or tetrad, totalling 400 ha) surrounding each lek were considered analogous to the home range of a black grouse in a similar way to the 1 km radius circle used in Chapter 4. The nearest grid intersection to the lek was taken as the middle of the tetrad. This limitation was necessary due to the data extraction limitations of the Countryside Information System (CIS). The habitat composition of each tetrad was extracted from the Land Cover Map of Great Britain using CIS version 5.23 a geographical database application developed by the Department of the Environment. The Land Cover Map of Great Britain shows land cover subdivided into 17 classes and was produced by a semi-automated computer classification of images made by the Thematic Mapper sensor on board the Landsat satellite.

5.2.2.2 Block Scale

Landownership/estate boundaries (which generally follow physical landscape features) were plotted on the same 1:50,000 scale Ordnance Survey 'Landranger' maps as the lek locations. The 200 and 550 m a.s.l. contour lines were highlighted and areas below the lower or above the upper contour were excluded from block scale analyses. This stratification follows from the results of an earlier survey of the area (Robinson *et al.* 1993) which found that "displaying cocks were found within a distinct altitudinal band, at 230 – 470 m", thus land outside this band was considered unsuitable for black grouse. Moorland and forest 'blocks' were then identified using the following rules:

Moorland Blocks – All non-forest areas excluding lochs, settlements and roads. Block boundaries followed landownership/estate boundaries. Patches of woodland smaller than 25 ha were considered to be scattered woodland or scrub within the moorland block. Moorland enclosed by forest was only considered to be a moorland block if the forest edges were separated by a minimum of 500 m.

Forest Blocks – All forest areas excluding lochs, settlements and roads. Block boundaries followed forest edges. Patches of woodland had to exceed 25 ha to be considered a forest block.

In both cases, the study area boundaries were ignored if the block continued beyond them as the block boundaries were more biologically meaningful than those of the study area as a whole. Once the blocks had been identified, the area of each one was measured by tracing the block outline onto paper and weighing each paper 'block'. In the absence of electronic data mapping facilities this proven method was considered suitable.

5.2.3 Lek Scale Analysis

In total, 149 leks and their associated tetrads were identified. For each lek/tetrad the following attributes were measured and recorded:

i) the change in the number of lekking males 1990 - 1998;

ii) the average number of males lekking 1996 - 1998;

iii) lek class, expressed as one of three categories – forest (1), moorland (2), or marginal – on moorland but within 500 m of a forest boundary (3) this category was included because birds inhabiting forest blocks have been observed lekking up to 500 m from the forest edge (D. Baines pers. comm.);

iv) forest area (ha) – this included both deciduous and coniferous woodland land classes;

v) average age of trees where present (years);

vi) rotational stage of trees where present, expressed as one of five categories – first (1), second (2), mixed first and second (3), historical woodland (4), mixture of first four categories (5);

vii) moorland/bog area (ha) – this included 'heath grass', 'open shrub heath', 'dense shrub heath' and 'bog' land classes;

viii) area of other potential black grouse habitat (ha) - this included 'managed grassland', 'rough grass' and 'bracken' land classes;

ix) distance to the nearest lek (km);

x) change in the number of lekking males at the nearest lek;

xi) the ratio of the length of forest edge: forest area.

To investigate whether the numbers of lekking black grouse were significantly associated with habitat features at the lek scale the data were analysed using generalised linear modelling. The maximal model comprised all the habitat variables (iii – xi) as explanatory variables and 'lek change' - the mean annual change in the number of lekking males 1990 - 1998 (i) or 'mean lek' - the average number of males lekking 1996 - 1998 (ii) as the dependent variable. Step-wise elimination of insignificant terms produced the minimal model.

5.2.4 Block Scale Analysis – Moorland Blocks

In total, 21 moorland blocks that contained leks were identified. For each block the following attributes were measured and recorded:

i) the change in the number of lekking males 1990 - 1998;
ii) the total number of lekking males in 1998;
iii) the number of small (<25 ha) patches of woodland/scrub present, expressed as one of three categories – none (0), up to 5 patches (1), more than 5 patches (2);
iv) the level of moorland management present (data source: GCT questionnaire), expressed as one of three categories – no gamekeeper (0), part-time gamekeeper (1), full-time gamekeeper (2);
v) the block area (ha);
vi) the ratio of the length of moorland edge: block area.

To investigate whether the numbers of lekking black grouse were significantly associated with habitat features at the block scale the data were analysed using generalised linear modelling. The maximal model comprised all the habitat variables (iii – vi) as explanatory variables and 'lek change' - the mean annual change in the number of lekking males 1990 - 1998 (i) or 'total males' - the total number of lekking males in 1998 (ii) as the dependent variable. Step-wise elimination of insignificant terms produced the minimal model.

5.2.5 Block Scale Analysis – Forest Blocks

In total, 40 forest blocks that contained leks were identified. For each block where the data were available (tree species, age, rotation, etc. data were unavailable for some blocks) the following attributes were measured and recorded:

i) the change in the number of lekking males 1990 - 1998;
ii) the total number of lekking males in 1998;
iii) the block area (ha);
iv) the ratio of the length of forest edge: block area;
v) mean age of the trees (years);
vi) percentage of first rotation stock within the block;
vii) percentage of pre-thicket stock (taken to be trees planted since 1983) within the block;
viii) percentage of unplanted (open) ground within the block;
ix) the tree species composition within the block , expressed as one of four categories – Sitka spruce (*Picea sitchensis*) (1), mixed conifers (2), broadleaves (3) or mixed conifers and broadleaves (4).

To investigate whether the numbers of lekking black grouse were significantly associated with habitat features at the block scale the data were analysed using generalised linear modelling. The maximal model comprised all the habitat variables (iii – ix) as explanatory variables and 'lek change' - the mean annual change in the number of lekking males 1990 - 1998 (i) or 'total males' - the total number of lekking males in 1998 (ii) as the dependent variable. Step-wise elimination of insignificant terms produced the minimal model.

5.3 Results

5.3.1 Lek Survey Results

Mean lek size 1996 – 1998 was 4.49 ± 3.47 (1 S.D.) males per lek. Density of males was 0.50 per km^2. The frequency distributions of leks and males are shown in Figures 5.1 and 5.2 below.

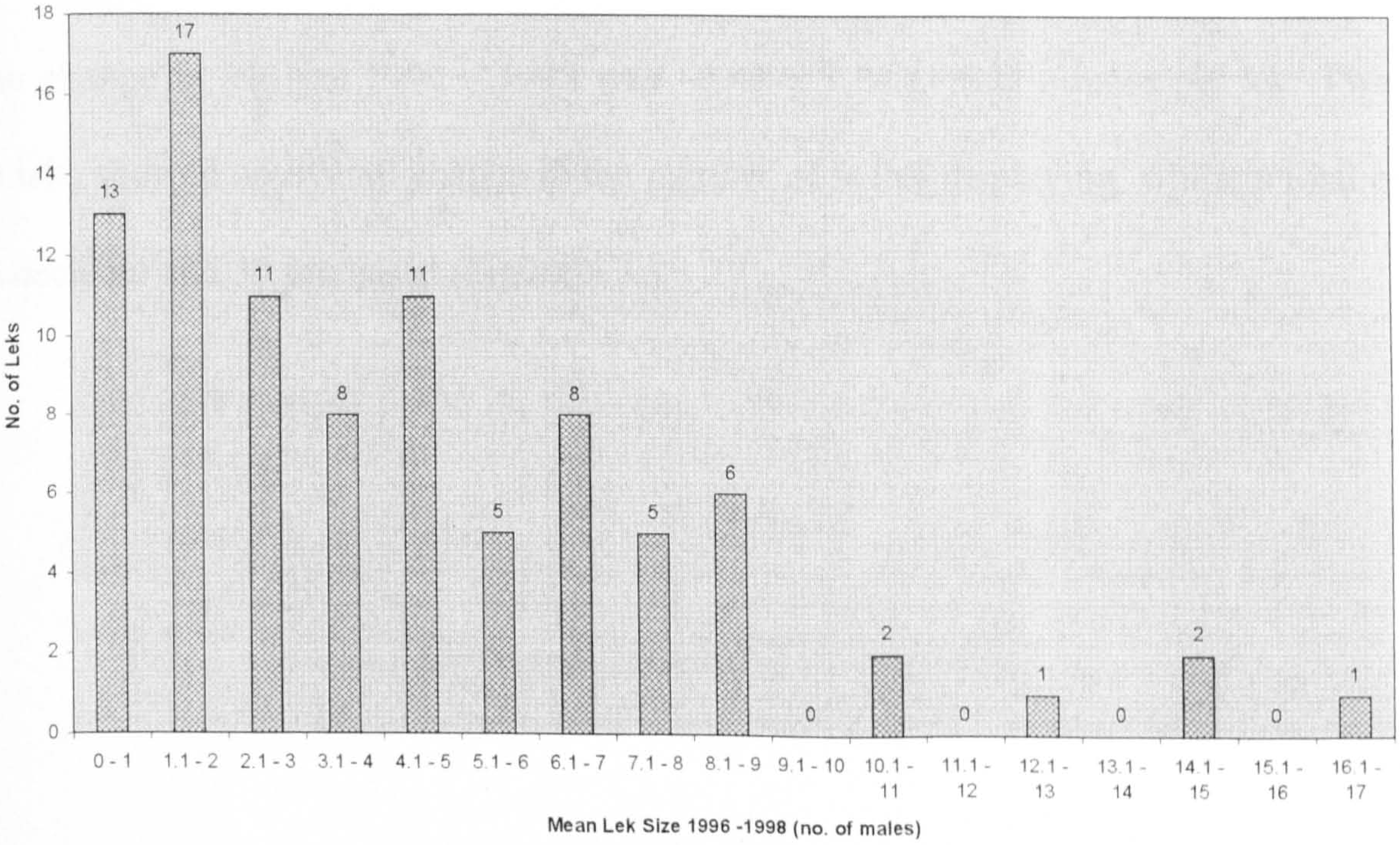


Figure 5.1. Frequency distribution of mean lek size 1996 -1998 in Perthshire study area.

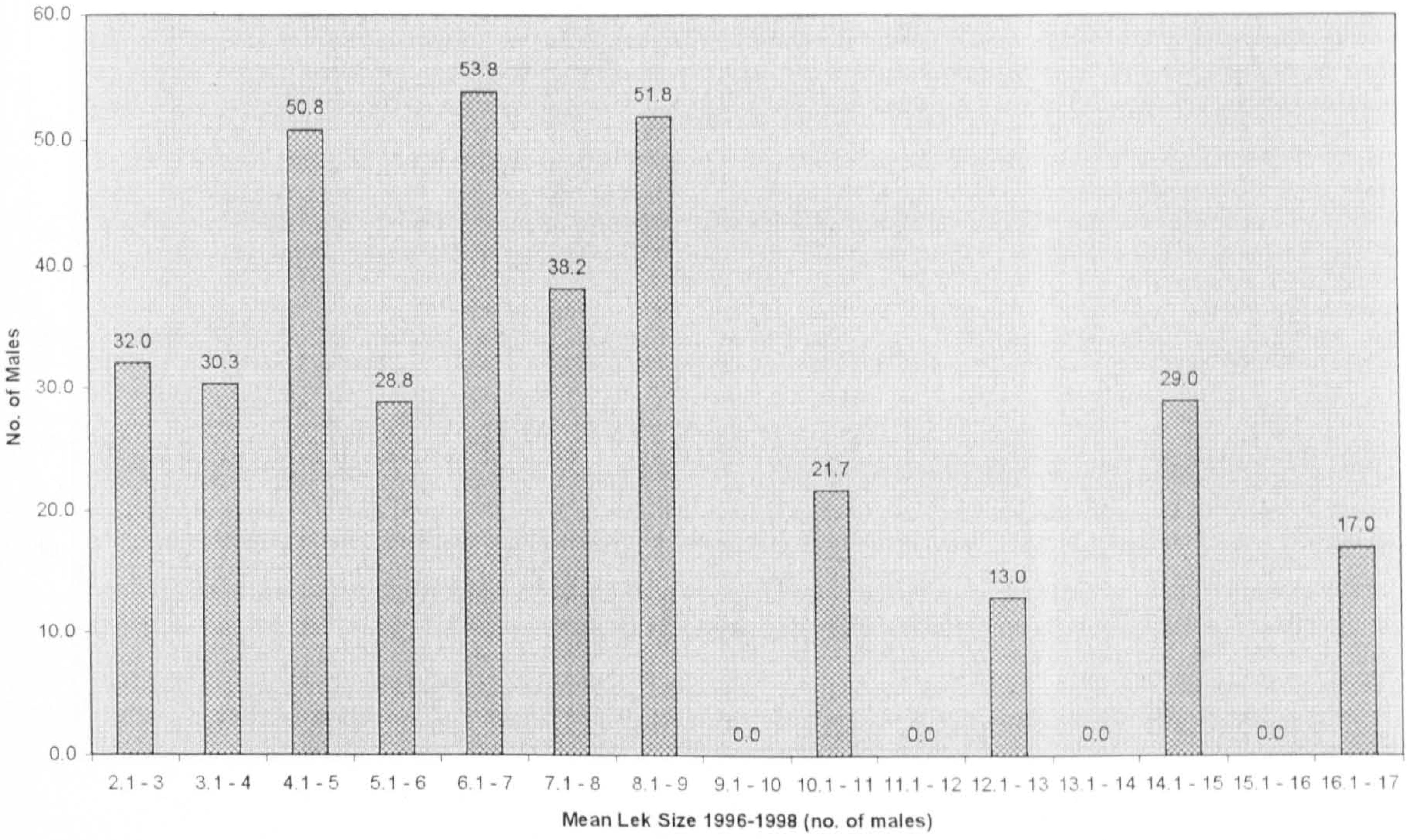


Figure 5.2. The total number of individual males observed attending leks of different mean size (1996 –1998, Perthshire study area).

Mean change in lek size 1990 – 1998 was –0.43 ± 1.24 (1 S.D.) males per lek. Twenty-nine leks showed no overall change in the number of males displaying, whilst a total of 33 leks declined and 30 increased (Figure 5.3.)

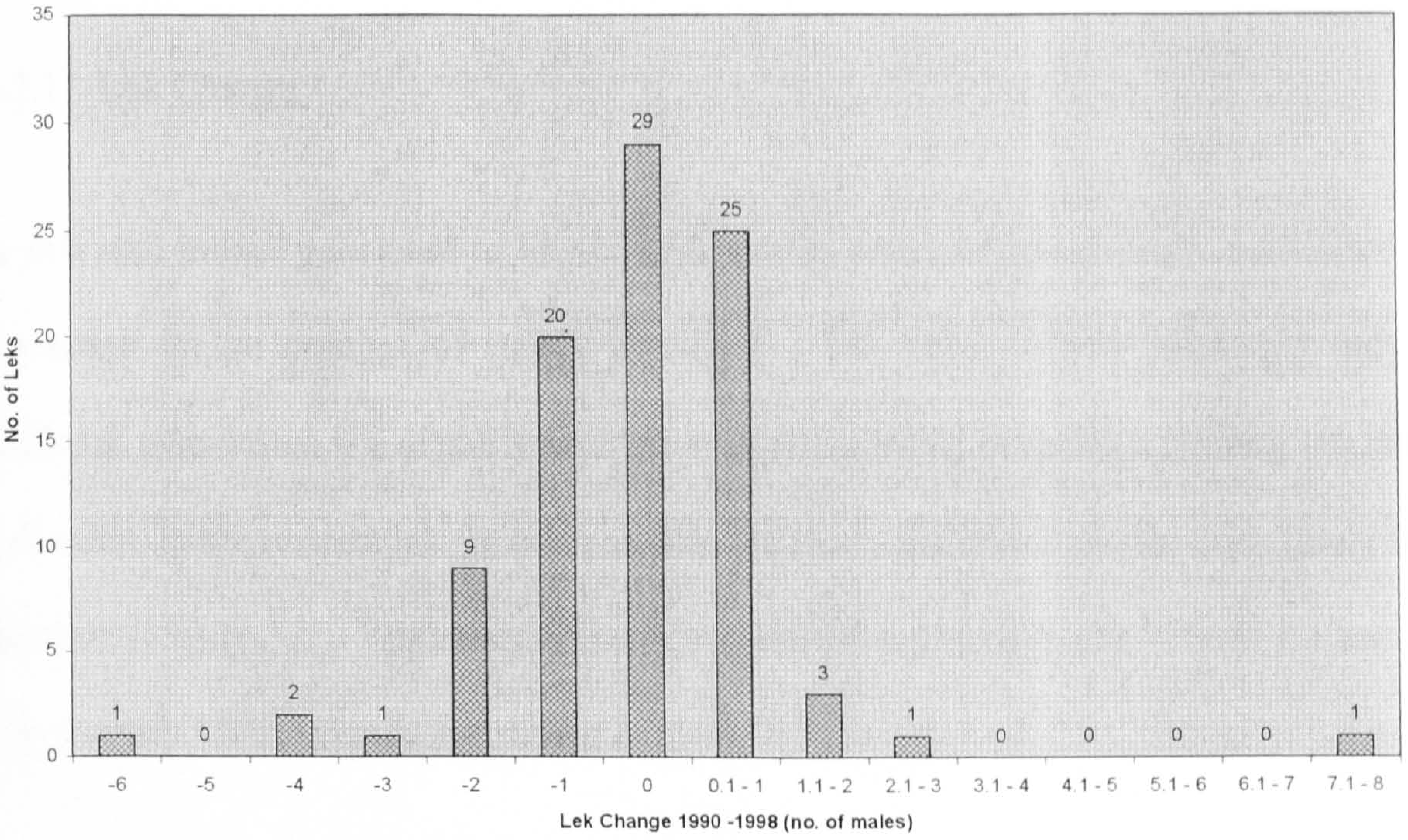


Figure 5.3. Frequency distribution of change in number of males attending leks 1990 – 1998 in Perthshire study area.

Mean distance to the nearest lek was 1.00 ± 0.49 (1 S.D.) km.

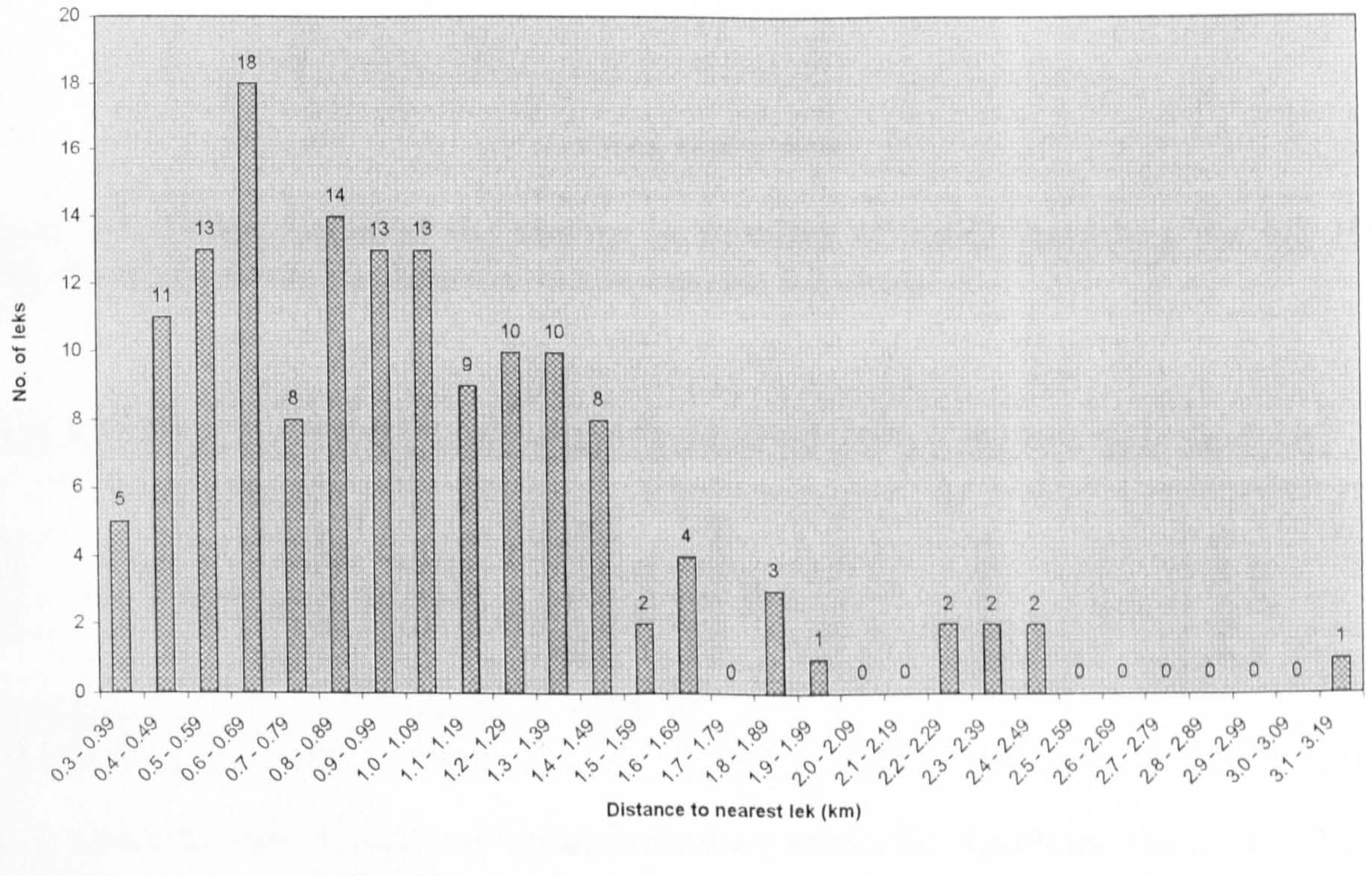


Figure 5.4. Frequency distribution of distance to nearest lek in Perthshire study area.

5.3.2 Lek Scale Analysis Results

5.3.2.1 Lek Change

The minimal model generated to identify the habitat features significantly associated with the change in the number of males attending a lek 1990 – 1998 identified only one significant association – a negative one between the number of males attending the lek and the distance to the nearest lek. In other words, the more isolated a lek the more likely it was to decline (Figure 5.5). Whilst significant, this model only explained 7 % of the variation in the dataset. Model details are shown in Table 5.1.

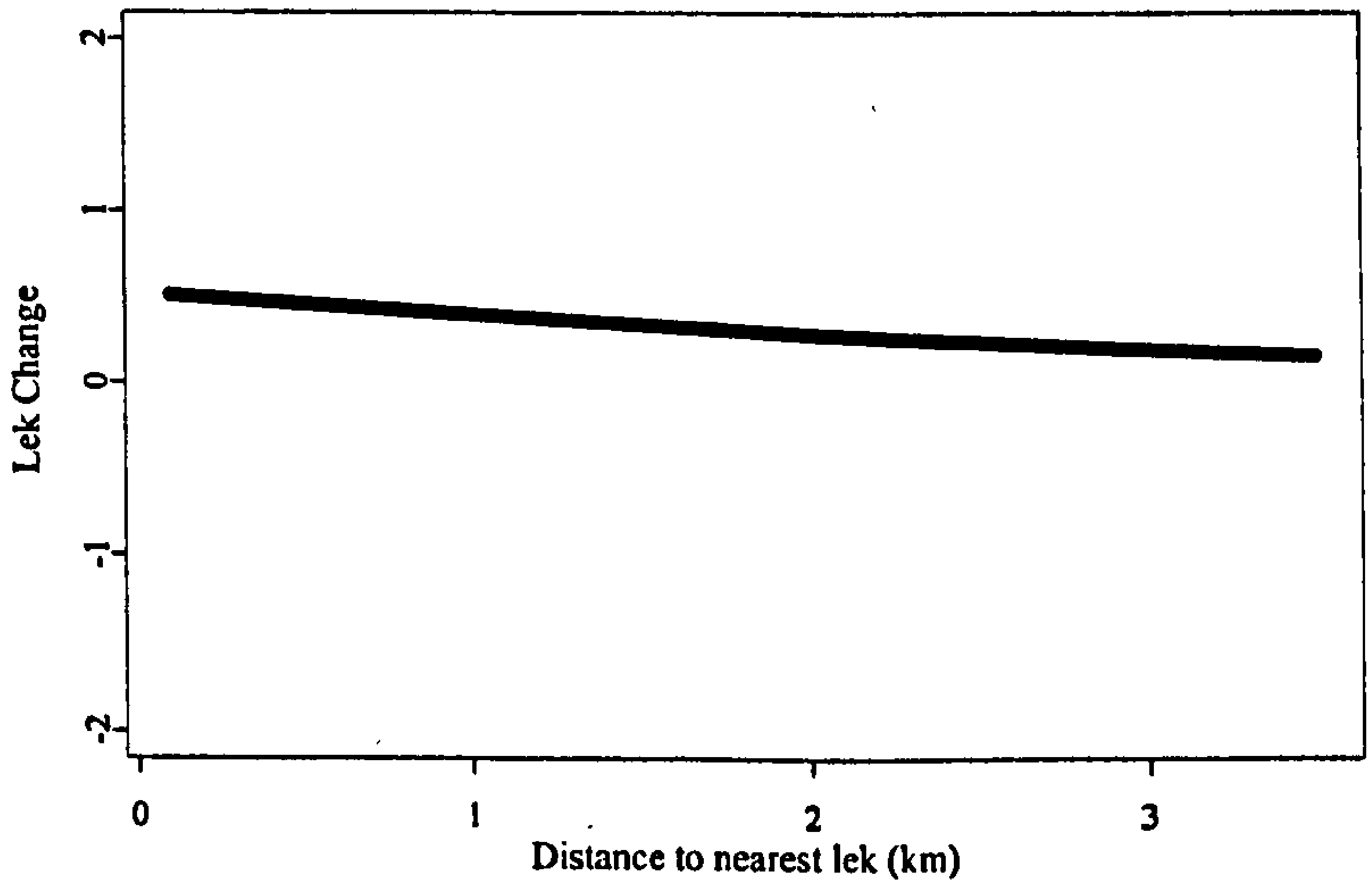


Figure 5.5. Fitted model of the change in number of males attending the lek 1990 – 1998 predicted from the distance to the nearest lek (km).

Table 5.1. Summary of minimal models generated during the lek scale analysis.

Dependant Variable	R^2 (%)	GLM Error Structure	Link Function	Distance to nearest lek (km)	Forest Area (ha)	Mean Age of trees (years)	Rotation	Lek class	Figures in Text
Lek Change	7	G	Identity	0.004	-	-	-	-	5.5.
Mean Lek Size	70	NB	Log	-	0.001	0.005	0.017	0.019	5.6. & 5.7a & b

Notes: Numbers below explanatory variables are the P values for significant terms; NB = Negative Binomial.

5.3.2.2 Mean Lek Size

The minimal model generated to identify the habitat features significantly associated with the mean lek size 1996 – 1998 identified four variables, two continuous and two categorical, explaining 70 % of the variation in the dataset. The effects of these variables are shown in the following two figures. The two continuous variables are shown in Figure 5.6., the forest area in the tetrad showed a positive correlation (Figure 5.6.a) and tree age showed a negative correlation (Figure 5.6.b).

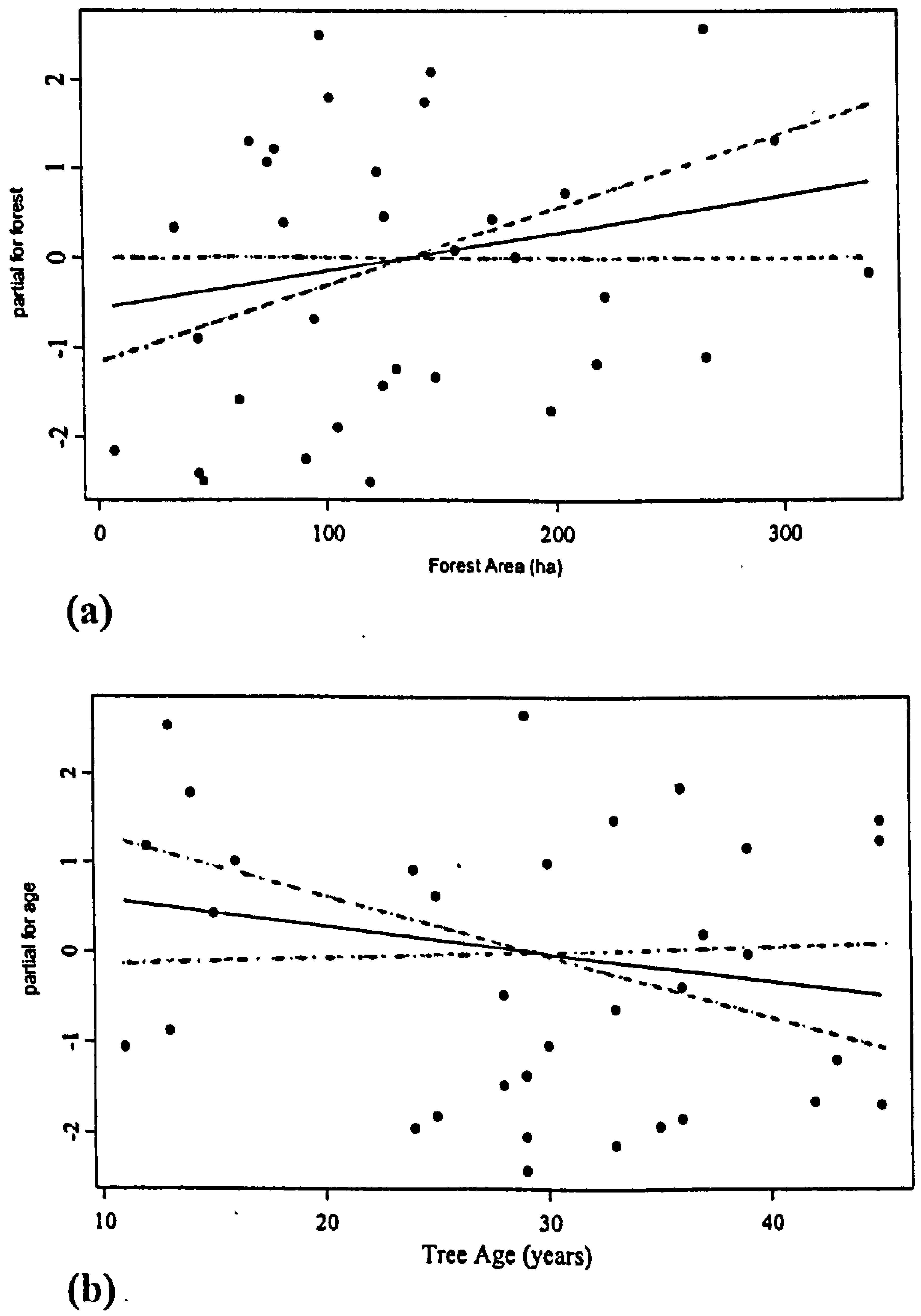


Figure 5.6. Plot showing the adjusted fit (solid line) with partial residuals for each data point (dots) and S.E.s (dashed lines) overlaid for (a) forest area (ha) and (b) tree age (years). See Table 5.1. for model details.

The two categorical variables were the rotational stage of the trees and the lek class, these are shown in Figure 5.7.

Tetrads containing first rotation trees (1) and first and second rotation mixed (3) supported larger leks than tetrads containing woodland of other rotational stages including historic woodland (5) (Figure 5.7.a).

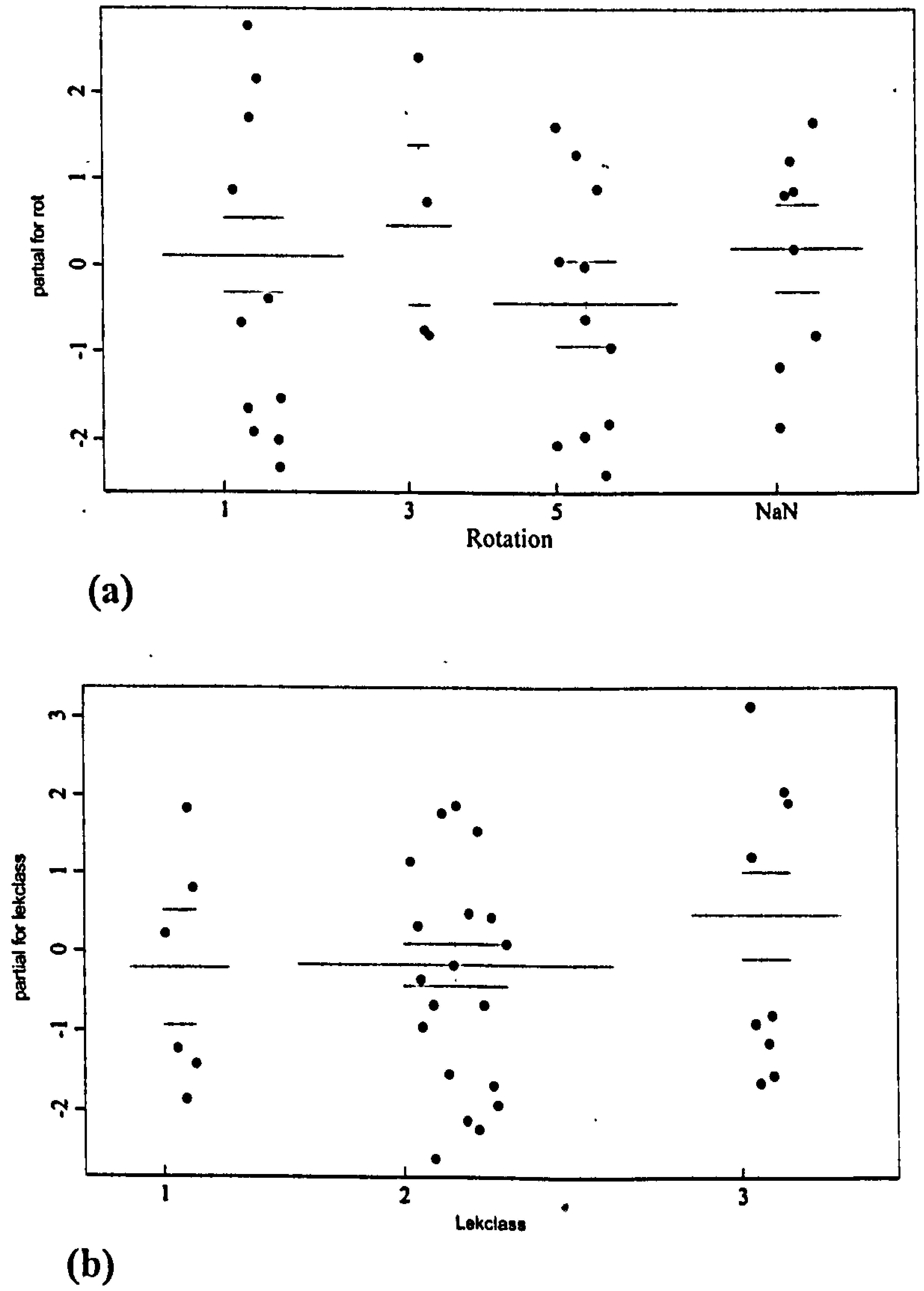


Figure 5.7. Plot showing the adjusted fit with partial residuals (dots) and medians (middle line, outer lines indicate quartiles) overlaid for (a) rotational stage and (b) lek class. In (a) NaN indicates that the rotational stage of the trees was not known.

Marginal leks (3), that is those located on moorland but within 500 m of a forest edge, tended to be larger than either forest (1) or moorland (2) leks (Figure 5.7.b).

To summarise the results of the lek scale analysis, the change in the number of males attending a lek showed a very weak ($R^2 = 7$ %) but significant negative correlation with the distance to the nearest lek. A large proportion (70%) of the variation in mean lek size was explained by a positive correlation with the forest area within the tetrad, a negative correlation with tree age and variation with the rotational stage of the trees and the lek class.

5.3.3 Block Scale Analysis Results

5.3.3.1 Change in the number of lekking males 1990 – 1998

There was no significant correlation between the change in number of lekking males in a block (all blocks lumped with block type as a factor, or moorland and forest blocks split) and any of the habitat variables. Model details are shown in Table 5.2.

5.3.3.2 Total number of lekking males in 1998

<u>All Blocks</u>

When all blocks were lumped together with block type as a factor, the minimal model generated to identify habitat features significantly associated with the number of males displaying in a block identified only one, nearly significant, variable – block area. This showed a very weak ($R^2 = 8$ %) positive correlation with the number of males displaying in a block (Figure 5.8.).

Table 5.2. Summary of minimal models generated during the block scale analysis.

Habitat used in model	R² (%)	GLM Error Structure	Link Function	Dependant Variable	Block Area (ha)	Amount (%) of pre-thicket stock within block	Notes	Figures in Text
All Blocks	-	-	-	Change in no. of lekking males	-	-	No significant correlation	-
All Blocks	8	NB	Log	Total no. males	0.070	-	-	5.8.
Moorland Blocks	22	NB	Log	Total no. males	0.057	-	-	5.9.
Forest Blocks	87	Q	Log	Total no. males	-	0.000	Var. = mu	5.10.

Notes: Numbers below explanatory variables are the P values for significant terms; NB = Negative Binomial; Q = Quasi.

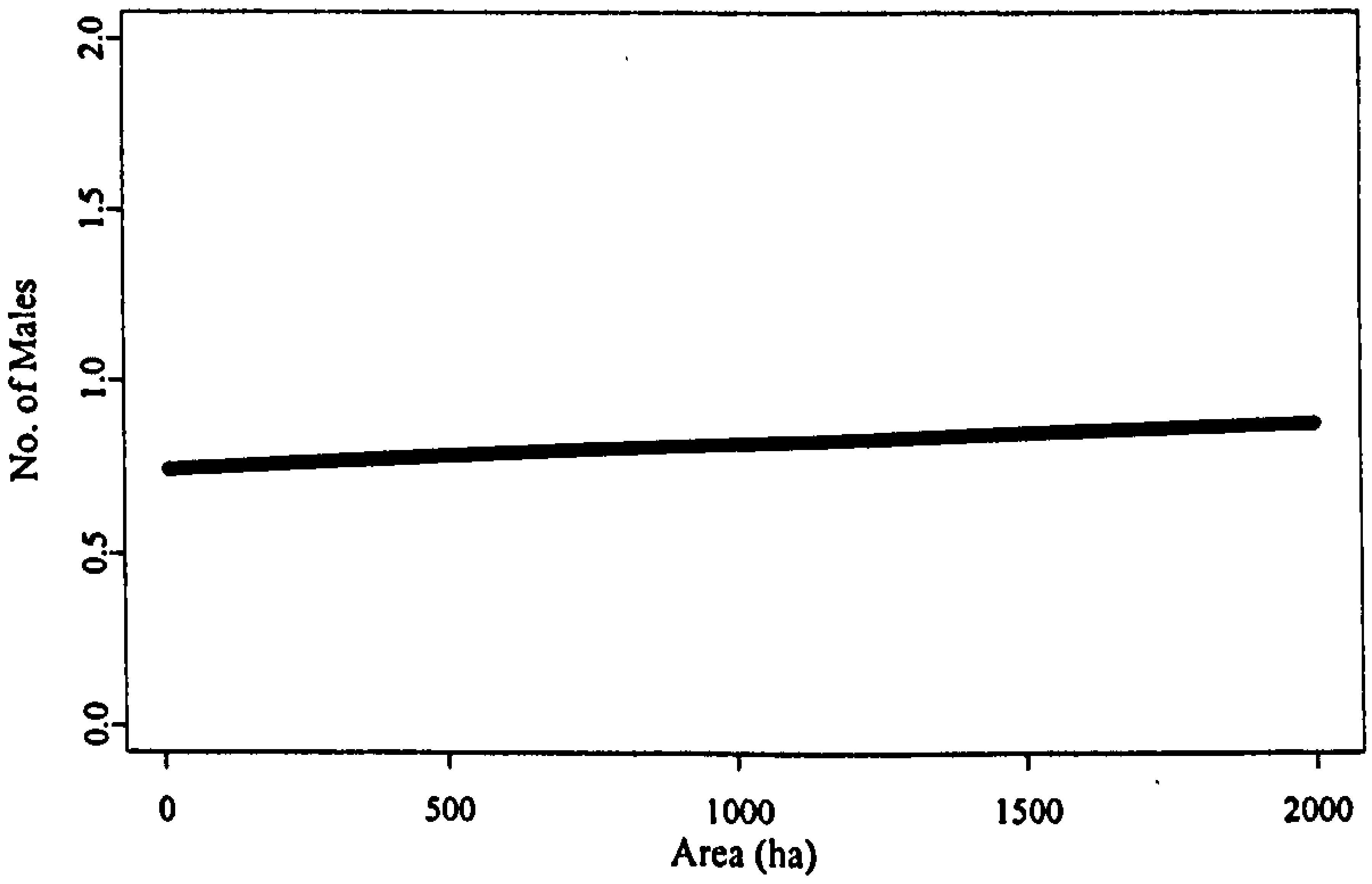


Figure 5.8. Fitted log model of number of males in a block in 1998 predicted from the area of the block (ha).

Moorland Blocks

The same minimal model fitted moorland blocks only and explained a greater proportion (22 %) of the variation in the dataset (Figure 5.9.).

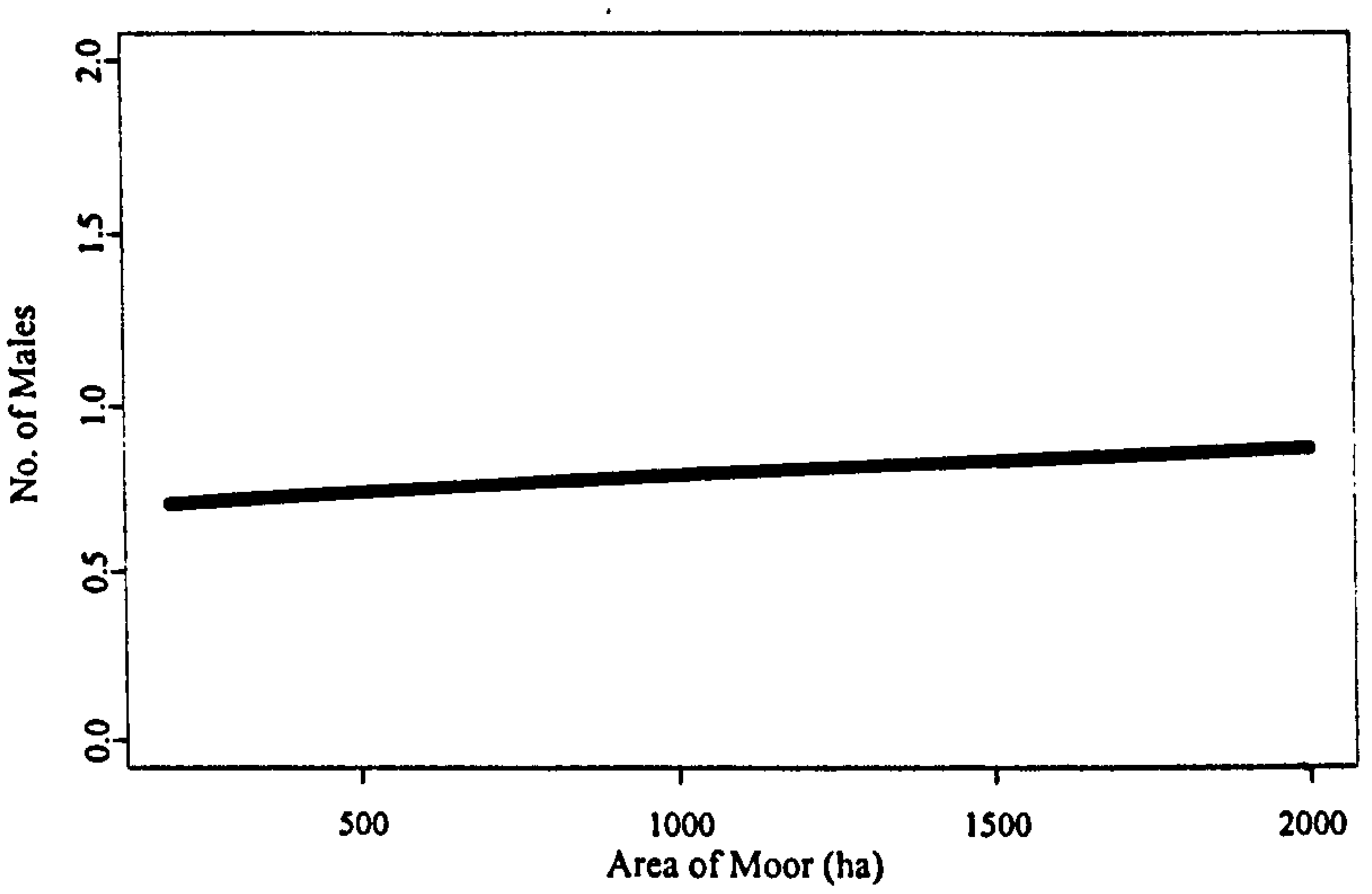


Figure 5.9. Fitted log model of number of males in a moorland block in 1998 predicted from the area of the moorland block (ha).

Forest Blocks

Block area was not, however, significantly associated with the number of males displaying in a forest block. The minimal model contained only one variable – the amount (%) of prethicket stage stock within the forest block and this positive correlation explained a very high (87%) proportion of the variation in the dataset (Figure 5.10.).

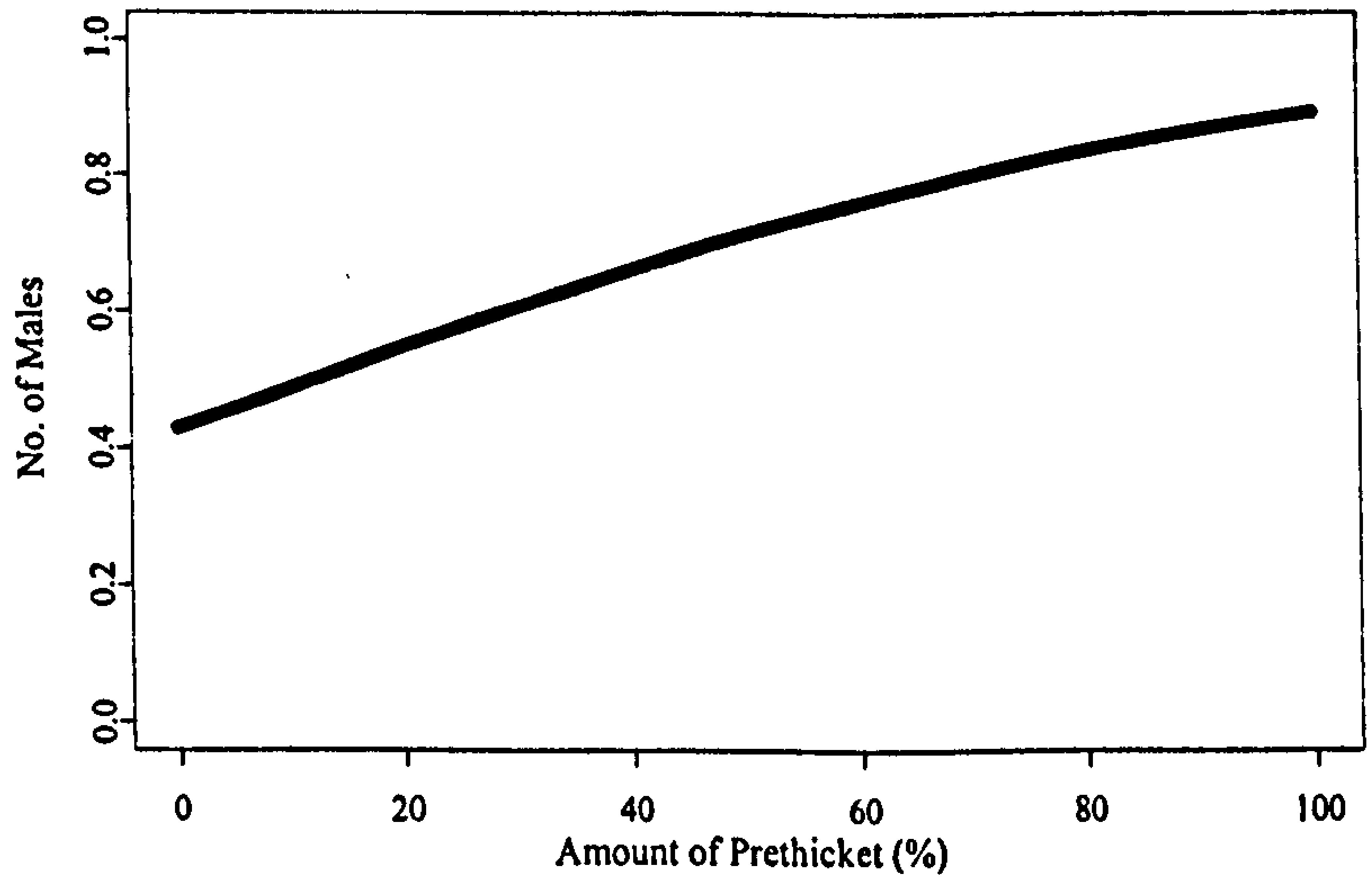


Figure 5.10. Fitted log model of number of males in a forest block in 1998 predicted from the amount of prethicket stock in the forest block (%).

To summarise the results of the block scale analysis, the change in the number of males displaying in a block showed no correlation with any of the habitat variables investigated. The total number of males displaying in moorland blocks or all blocks lumped together was positively correlated with the block area. In forest blocks however, there was a very strong (R^2 = 87%) positive correlation with the amount of prethicket stock within the block.

5.4 Discussion

In this chapter the following questions were specifically addressed: was the absolute number or the change in number of lekking males associated with habitat features at the scale of the lek or the scale of the habitat block?

The concise answer to these questions was yes, except the change in number of displaying males showed no correlation with any of the variables investigated at the block scale and only a very weak correlation at the lek scale. These results are discussed in greater detail below.

5.4.1 Lek Scale Analysis

5.4.1.1 Predicting the change in the number of males attending a lek 1990 – 1998 (Table 5.1.).

There was no correlation between the change in the number of males attending a lek and any measure of the habitat 'quality' (e.g. amount of forest, moorland/bog or other suitable habitat, forest edge to area ratio, tree age or rotation) within the tetrad. The only significant correlation was with the distance to the nearest lek. As leks became more isolated the more likely they were to decline. Whilst this relationship fits with the expectation that isolated groups are more likely to decline through demographic or environmental stochastic effects (Opdam 1990; Simberloff 1994; Swenson & Angelstam 1993; Wiens 1997), with the theory of island biogeography (MacArthur & Wilson 1967) and the results of studies on similar species (e.g. Saari *et al.* 1998) it only explained 7% of the variation in the dataset, i.e. it was not a strong relationship. Were it not for the supporting evidence from the other studies mentioned a correlation this weak would probably be dismissed as biologically insignificant.

5.4.1.2 Predicting the number of males attending a lek (mean lek size 1996 - 1998) (Table 5.1.).

A large proportion (70%) of the variation in mean lek size was explained by a positive correlation with the forest area within the tetrad, a negative correlation with tree age and variation with the rotational stage of the trees and the lek class.

It is interesting that, even in a landscape characterised as a 'sea' of open-ground with 'islands' of forestry, it was the quantity of forestry <u>not</u> moorland/bog or other suitable habitats that was positively correlated with the number of males attending a lek. This partially accords with results from Garson & Starling's (1990) work in that they found that leks only persisted where 'appreciable' areas of young plantations were found in the vicinity of leks but they found that appreciable areas of open-ground could also maintain leks. Andrén (1994), in his review of empirical studies of the effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat, concluded that in landscapes where more than 30 % of suitable habitat remained then the total area of the suitable habitat was the best predictor of the abundance and distribution of organisms. This certainly seems to be the case for black grouse in Perthshire if forestry is considered to be the 'suitable habitat'.

Characteristics of the forestry were also important. Mean lek size declined with tree age, which fits with the findings of many authors (e.g. Baines & Hudson 1995) and was lower where historic woodland was present. It would have been interesting to examine whether there was a significant difference between first and second rotation forestry but no purely second rotation stands were present.

Despite the prevailing importance of the forestry component in the tetrads, marginal leks (i.e. those located on moorland but within 500 m of forest edge) tended to be larger than either forest or moorland leks. This seems to hint at the importance of forest edge, as believed by many authors (e.g. Hudson 1990). However, the ratio of forest edge to forest area was eliminated from the model due to its lack of significance. This is likely to be because the forest edge data was pooled from all forests (thus covering a range of ages), and the less-suitable habitat of the older forest edges may have 'masked' the significance of the younger forest edge-habitat. A useful follow-on to this analysis would be to stratify the forests by age and repeat the analysis, however this was not possible with the dataset used in this study as forest age was in many cases unknown.

5.4.1.3 Limitations of the lek scale analysis.

The results discussed must be seen within the framework of assumptions that were made to allow the analyses to be performed. A tetrad of 400 ha centred on a lek is a very crude approximation to a real male black grouse home range. This approximation had to be used because of the nature of the data available and the methods of data storage/extraction used in CIS. The recommendation, first made in section 4.4.1.2., for a sample of male and female black grouse to be radio-tracked in order to estimate their home ranges and assess habitat selection directly is equally fitting here. Indeed, such a study might reveal the movement of birds between leks that decline or increase over time.

Another limitation of the habitat data was that whilst yearly counts of the leks were made from 1990 to 1998, the change in lek attendance was compared with a single snapshot of the landscape mosaic and habitat features within it. Thus, a dynamic variable was compared with a static one, which probably limits the utility of the analysis and the results. Ideally, the year to year change in black grouse numbers should be compared with year to year habitat changes. The practicalities of this, the difficulty of observing year to year habitat changes and the immense workload involved in collecting, processing and storing the data, may be overwhelming in which case breaking the nine year span into three groups of three years may be adequate. Any future development of this work would, however, necessitate the development of a geographic information system on which to pursue the work.

More fundamentally, the accuracy of the Landsat data should be thoroughly tested and if found to be inadequate the work should be repeated using ground-truthed habitat variables. Despite the CIS developers' claim that the 'minimum consistently mappable area' was between 0.125 and 5 ha false results were sometimes generated, notably a lack of differentiation between pre-thicket forestry and moorland. The 'User's Guide' also warns that:

> " CIS allows individual 1 km squares to be selected and predictions to be made for different sampled features. The values are however flagged with 'Unreliable total' rather than presenting

error terms. Error terms are only produced when the number of sample squares in the area for prediction reach 5000. Even at that limit, results should be handled with care – greater confidence can be placed the larger the region for which the prediction is made."

Only four sample squares were used for each tetrad.

5.4.2 Block Scale Analysis

5.4.2.1 Predicting the change in the number of lekking males in a block (Table 5.2.).

There was no significant correlation between the change in number of lekking males in a block (all blocks lumped with block type as a factor, or moorland and forest blocks split) and any of the habitat variables. This may be taken at face value but there are alternative conclusions. Cayford & Walker (1991) found that leks in forests in north Wales declined more between 1986 and 1988 than those in moorland but they did not give details of the age of the trees in question. In this study it is possible that within blocks some leks declined whilst others grew and lumping them together would have masked these changes. This may be justified by behaviour if the birds move between leks within a block but a radio-tracking or other marking study would be needed to assess this. This was outwith the scope of this project but would be a useful follow-on study. Alternatively, the lack of any correlation between the change in number of males displaying in a block and any aspect of that block may be a direct result of comparing a dynamic variable with a single snapshot of the habitat characteristics.

5.4.2.2 Predicting the total number of lekking males in a block (Table 5.2.).

The total number of males displaying in moorland blocks or all blocks lumped together was positively correlated with the block area. This is not surprising as one would expect to include more leks and thus more males as block size increased (Åberg *et al.* 2000) but the correlation was very weak ($R^2 = 8\ \%$). The biological significance of such a weak correlation would be questionable had Angelstam (1990) not also found that the distribution of breeding male black grouse was determined by the size of preferred habitat patches. It is, however, the insignificant variables that are of interest here – block type and any measure of habitat 'quality' did not show significant association with the total number of males displaying in a block. In particular, the level of moorland management did not feature in the model despite Baines' (1991) finding that juvenile production was three times lower where predator control was not practised on moorland. Later work by the same author (Baines 1992) may explain this apparent contradiction. He concluded that good quality habitat, i.e. not over-grazed (Cadbury 1993; Ellison & Magnani 1984), probably compensates for high numbers of predators. The moorland blocks in Perthshire are primarily managed as traditional grouse moor (Robinson *et al.* 1993) and thus are unlikely to be as overgrazed as moors in other parts of Britain such as the Peak District (Anderson & Yalden 1981).

In forest blocks there was a very strong ($R^2 = 87\%$) positive correlation with the amount of prethicket stock within the block. Again, the variables that were eliminated from the model due to lack of significance are of interest here – block area does not feature, nor does the ratio of forest edge to block area, the amount of open ground within the forest, nor the rotation nor species of the trees. These last four variables have all been put forward as being important for maintaining numbers of black grouse in forests (Baines & Hudson

1995; Cayford & Hope Jones 1989; Hudson 1990; Klaus 1991; Parr & Watson 1988; Cayford 1990b), yet this does not seem to be the case here although tree age and rotation were significant when examined at the lek scale. The lack of significance of the length of forest edge may be due to the tendency for conifer edges to be sharp with no ecotone of intermediate habitat, e.g. Currie (1983) observed a decreased passerine density within 30 m of conifer edges but no decrease adjacent to other types of edges.

Results from this chapter will be compared with those from Cowal described in Chapters 3 (patch analysis) & 4 (home range analysis) in Chapter 7 (general discussion).

5.4.3 Implications for forest management with the aim of conserving black grouse.

It has become clear that even in a landscape that is not dominated by forestry, sympathetic forest management may be crucial to the maintenance of black grouse populations in some parts of Britain.

On the block scale, if forestry is not present then large areas of moorland should be maintained. Contrary to expectation, moorland gamekeepering was not found to be significant in this study. When looking at forest blocks, it is again the amount of prethicket forestry present that is positively correlated with the number of males displaying in a block.

Thus, the implication is that to maintain black grouse populations a large proportion of the landscape mosaic should be forestry, and within that forestry, a large proportion should be prethicket stage stock. This becomes a problem when one considers that the trees will mature to thicket stage and beyond, as Angelstam (1990) observed, given a sufficiently long time series the effects of the habitat patch dynamics in landscapes overrule other effects. However, as Kozakiewicz (1995) pointed out, most habitats are not permanently of the same quality for a given species they are usually better or worse temporally. Thus, it might be supposed that many animal species, e.g. Bachman's sparrow (Pulliam *et al.* 1994), are able to follow these temporal changes by temporarily selecting different patches of habitat. A balance must be found wherein as prethicket forestry matures young forestry, second rotation in effect, must become available nearby. The next challenge is to quantify how this balance can be achieved.

5.4.4 Suggestions for further work.

It would be interesting and desirable for management purposes to establish whether the correlation between the change in number of males attending a lek and the distance to the nearest lek (discussed in section 5.4.1) was biologically significant or merely a chance result. However, an experimental approach using direct manipulation of distances between leks would be difficult and unacceptable in a species of such conservation concern.

In addition to the improvements suggested throughout the chapter, the results discussed should be tested. This should be done on two levels – the manipulation of experimental plots and simultaneous monitoring of leks and black grouse habitat use, and testing the models using independent data. Lek surveys have been performed in Tayside and Angus by the Game Conservancy Trust over a similar period of time and it would be valuable to see how well the Perthshire models fit these data. Unfortunately, if a poor fit is found it may equally be due to differences in geography, geology, land management and weather as to model inadequacy. Testing is essential. Models based on patch area and home range size have been found to grossly over-predict the number of occupied patches and total abundance (Lindenmayer *et al.* 2000) since the effects of habitat quality and matrix conditions were omitted.

Once tested, if models were found to be adequate and applicable to other areas, they could be used to predict the potential impact of different forest plans on black grouse numbers.

Chapter 6 Black grouse broods in plantation forests – are they selective?

6.1 Introduction

> “ Individuals should preferentially select portions of the landscape that enhance their survival and reproduction” (Pulliam 1988 cited in Chamberlain & Leopold 2000).

Once these ‘survival and reproduction enhancing’ habitats have been identified active conservation can begin with the setting aside or management of adequate areas of these habitats. One objective of species specific studies in conservation science is to identify an organism’s habitat selection of ‘suitable’ and ‘preferred’ habitat types. This was the objective of this study.

Habitat selection can be seen as falling into four hierarchical classes:

i) first order selection – the geographical distribution of a species;
ii) second order selection – the home ranges/sites within the first class;
iii) third order selection – the habitat use within the home range;
iv) fourth order selection – the food items taken at a foraging site.

Johnson (1980) first put forward this formal classification in 1980, since when it has been adopted as standard by many ecologists studying resource availability and use (e.g. Aebischer & Robertson 1992; Taborsky & Taborsky 1995; Mannan & Boal 2000; Blakesley *et al.* 1992).

Habitat selection in black grouse has been well studied. Indeed, there have been numerous studies that have examined habitat selection by adult birds in various parts of their global range (Baines 1990, 1993a & 1994; Keller & Pauli 1978; Marti 1982; Málková 1996; Símová 1996; Zettel 1974). Many studies (e.g. Angelstam 1984b; Brittas & Willebrand 1991; De Franceschi & Mattedi 1995; Kolstad *et al.* 1985; Willebrand 1988) have made use of radio-tracking techniques since these are ideally suited to locating visually obscured individuals without disturbance (Bibby *et al.* 1992). Habitat selection is then usually investigated by comparing the amount of use of a habitat as indicated by the number or radio-telemetric registrations with the availability of that habitat (see for example Aebischer *et al.* 1993; Hill 1985). This analytical technique was not used in this study since it relies heavily on home range estimation the accuracy of which is heavily constrained by small sample sizes.

The details of second to fourth order habitat selection by black grouse broods are not well understood (Baines *et al.* 1996; Kastdalen & Wegge 1984; Robel 1969b; Cayford 1990b). Chick survival is an important factor determining autumn population size and population change of many galliformes (Kenward *et al.* 1993; Southwood & Cross 1969). Habitat type and structure will influence the availability of cover and insects and other food. Consequently it will have a direct influence on survival.

Whilst the analysis of habitat use from radio-tracking studies is a common technique it has seldom been applied to chicks (Bergmann & Kenward 1987). This may be because until recently sufficiently small tags were unavailable although Willebrand (1983) instrumented woodland grouse chicks as far back as 1980. A number of studies have tracked broods in order to identify habitat selection (e.g. Barikmo *et al.* 1984; Cayford 1990; Cayford *et al.*

1989; Harnies *et al.* 1996; Kolstad *et al.* 1985) but in all of these cases it was the hen that bore the tag not the chicks. In addition to the unavailability of small tags it may have been perceived that tagging the hen might have been a less risky strategy than tagging the chicks. This is not necessarily a safe assumption since tagging hens during the chick-rearing period has been shown to be linked with high levels of mortality (Herzog 1979; Caizergues & Ellison unpublished). In this study chicks were equipped with tags (following Kenward *et al.* 1993) as it was not possible to capture hens and then tracked directly to reveal their habitat use.

This chapter investigates black grouse brood habitat use by looking at second and third order habitat selection. The aim is to identify whether black grouse brood ranges are randomly located within the study area or selected and if the latter, what forms the basis of this habitat selection. At the next order, the aim is to identify any habitat selection within the brood range.

To meet these aims, two specific questions were addressed:

i) Is the habitat in a brood home range different to that found throughout the entire study area? In other words, do broods exhibit habitat selection within the study area and if so, how?

ii) Is the habitat that is used in a brood home range different to that found throughout the home range? In other words, do broods exhibit habitat selection within the home range and if so, how?

An important consideration in habitat preference work is to ensure the data are not biased For example, Beyer & Haufler (1994) found that elk (*Cervus elaphus*) habitat use throughout the entire 24 hour period was significantly different from that during diurnal hours. To avoid such problems differences between black grouse brood foraging (diurnal) and roosting (nocturnal) habitats were investigated by asking:

iii) Is the habitat at roost sites different to all other brood locations?

6.2 Methods

6.2.1 Brood location, capture and handling

In 1997 and 1998 an intensive radio-tracking study of broods was undertaken in the Trinafour study area in north Perthshire (see Chapter 2, section 2.3 for details). Fences surrounding the plantations were used as the study area boundaries as they clearly demarcated moorland and forest, changes in study area boundaries have been shown to affect the statistical indication of habitat use (Porter & Church 1987). Black grouse broods of 7 - 10 days old were caught by using pointer dogs to locate a brood, flush the hen, and locate individual chicks (following Baines *et al.* 1996).

All the chicks in a brood were caught whenever possible in order to obtain a comprehensive set of biometrics and demographic data from each brood. Mass of each chick was recorded using a 100 g pesola; wing, head and beak lengths were measured to provide an estimate of age. Every chick caught was given an individually marked patagial tag (Baines *et al.* 1996). Any faeces produced by chicks during handling were collected for faecal analysis (see 6.2.6.). In each brood, two chicks (later three chicks when it became apparent how few broods would be caught and how frequently tags were lost) were randomly selected and equipped with radio-transmitters as described under 6.2.2.

The entire brood was released as close to the capture location as possible, after both dogs and dog-handlers had withdrawn. The capture location was marked in the field. Back-bearings to landmarks were taken using a sighting compass and the precise location calculated and marked on a map of the fieldsite (developed from an Ordnance Survey 1: 10,000 scale map showing forestry compartments, crop species and year of planting, see Chapter 2 figures 2.3 & 2.4).

6.2.2 Radio telemetry

BD-2 transmitters from Holohil Systems Ltd. were fitted to chicks. The mass of a transmitter was 1.2 g which, on average, represented 2.2 % ± 1.0 % (1 S.D.) of the chick biomass. The dimensions were 16 x 8 x 4 mm thick with a whip antenna of stranded stainless steel wire covered with black nylon coating and reinforced at the base with shrinkable tubing. Pulse width was 20 ms ± 10 % within the frequency range 172.506 – 173.021 MHz with a battery life of more than 9 weeks. The transmitters were the smallest transmitter package available that would meet the requirements of this study and were painted black to be as inconspicuous as possible (following White & Garrott 1990a).

The transmitters were attached to the chicks using ‘Saltair Ostomy Adhesive Solution’, a latex-based adhesive that forms a flexible bond and is less of an irritant to skin than Superglue. Transmitters were attached to a small area of down on the back between the wings clipped to reveal skin following the methods of Kenward and co-workers (1993) and Whittingham (1996). A blob of glue was placed on the skin and underside of the transmitter, the transmitter placed on the glue covered skin, the down/feathers pressed gently onto the transmitter and glue to improve adhesion (Figure 6.1.). Finally the transmitter was held in place for one minute whilst the glue set.

The broods were tracked using a Telonics TR-2 receiver, a 3-element foldable Yagi aerial (Mariner Radar) and headphones (8 ohm, Electromail). Each brood was located at least once per day where possible. The thermoregulation of galliform chicks is believed to be poorly developed in their first few days of life so during cold and wet weather hens brood the chicks up to 90% of the time (Aulie & Moen 1975 and Rajala 1974 cited in Erikstad 1979; Cramp & Simmons 1980). No fieldwork was carried out in the vicinity of broods on rainy days (following Børset & Krafft 1973).

Radio-tracking in dense woodland is not easy since the signal suffers diffraction, reflection and interference caused by the trees reducing accuracy to an unacceptable level. Kenward (1987) recommended taking bearings for triangulation in woodland from beyond the Fresnel Zone, i.e. further than 20 wavelengths, in this instance equivalent to a distance of 35 m away from the woodland boundary. However, use of this method did not give satisfactory results, possibly due to additional interference coming from the 2 m high wire-mesh deer-fence that bounded the woodland.

Figure 6.1. Transmitter being glued to a black grouse chick as a glue-mounted backpack (following Kenward *et al*. 1993).

Trials in the field revealed that the tagged bird could effectively be stalked by the observer walking in the direction of the strongest signal until the signal could only just be heard (through headphones) at '2½ gain' at which point the source tag would be approximately 5 m away (after Kenward 1987). Approaching the tags this closely gave a very precise location but was not so close as to cause the hen and brood to flush from cover. Due to the nature of the forest habitat, it was not possible to observe the effects of the radio-tracker approaching the brood. Although the hen and brood may have been seeking what cover they could without flushing, it is not thought that the hen and brood moved greatly from their undisturbed position. The precision of this technique was tested during the development of the field protocol and at the end of each field season (after White & Garrott 1990b) and is given in the results (see 6.3.).

Back-bearings were taken (see 6.2.1.) but, where this was impossible due to topography or tree height/density, the site was marked using a spare radio-transmitter. The site was later re-located after the brood had moved away and habitat variables were recorded and position confirmed using a global positioning system (Eagle Explorer GPS).

The order in which the broods were tracked each day was varied so that each brood was not located at the same time every day. Diurnal radio tracking took place any time between dawn and dusk.

In the first three weeks after capture two broods per dry night were tracked in order to locate the roost site. Roost sites were confirmed on the subsequent daylight visit by easily identifiable hen and chick droppings, thus validating the assumption that these points were roost sites. In 1997 this was performed in the hour before dawn but at this time some broods had a tendency to flush from distances greater than 5 m. In 1998, nocturnal radio tracking was performed from 02:00 hours and this proved more successful although progress in the field in the dark was slower.

6.2.3 Study area sampling system

The habitats within the entire study area were sampled by placing a 2 x 2 cm grid (equivalent to 200 x 200 m at a 1:10,000 scale) over maps of the two plantations (Auchleeks 1 and 2). Grid intersections were pinpointed in the field and the full range of habitat variables recorded (see 6.2.5.). This type of systematic sampling was used as it ensured an even coverage of the study areas and the ease of navigation allowed a greater sample size to be used. Habitat variables were recorded from 27 points in Auchleeks 1 and 52 in Auchleeks 2.

Prior to analysis 'fake brood ranges' were generated from the study area habitat data. Comparing habitat data from the entire study area with that found within brood ranges would have been inappropriate, as the data from the larger area of the entire study site was more variable than the data from the inherently smaller brood ranges. To avoid this problem a fake range was generated by randomly selecting (using random number tables) one of the grid intersections and this was treated as the 'capture' location. Fake ranges were paired with real ranges such that there were equal numbers of fake and real ranges in each plantation, and each real range had a fake partner with the same number of 'fixes' (locations where the birds had visited and the habitat recorded). Adopting the nearest grid intersections to the 'capture' location generated fake 'fixes'.

To investigate whether broods exhibited habitat selection within the study area the dataset composed of habitat information from fake and real brood ranges was analysed using general linearised modelling. The maximal model comprised all the habitat variables (see 6.2.5.) as explanatory variables and 'real' (whether the range was real (1) or fake (0)) as the dependent binomial variable. Step-wise elimination of insignificant terms revealed the minimal model.

The method described above differs from those commonly used in the analysis of resource selection, e.g. χ^2 analysis (White & Garrott 1990c), the ranking of resource components by usage and availability (Johnson 1980) or compositional analysis (Aebischer & Robertson 1992; Aebischer *et al.* 1993; Baines *et al.* 1996; Redpath 1995) in that it does not rely on the categorisation and mapping of habitat types nor home range estimation. It was selected in an attempt to avoid the introduction of additional error from mapping (Marcum & Loftsgaarden 1980) and home range estimation methods (White & Garrott 1990c). The error from the latter would have been large due to the small number of 'fixes' achieved for each brood and almost all home range estimation methods are sensitive to sample size (Robertson *et al.* 1998; Boulanger & White 1990). Also, it has been observed that black grouse broods make long daily movements in the first 3 – 4 weeks and do not establish fixed home ranges (Kolstad *et al.* 1985) so using standard home range estimators may be inappropriate (Hjermann 2000). Indeed, the small sample sizes obtained in this study make the use of these estimators impossible.

6.2.4 Brood range sampling system

Every brood location was visited the following day and habitat variables recorded (see 6.2.5.). This was performed immediately after the brood's actual position had been found.

If the previous day's location was very close to the birds, as it frequently was, then habitat sampling was postponed, to minimise disturbance, until the brood had moved on.

To sample locations the birds had not used but were available (i.e. within the brood range) the following procedure was used: on day $t + 1$ the distance (y m) between the real locations on day t and day $t + 1$ was calculated; the observer returned to the day t location and walked y m along a randomly selected compass bearing to the fake day $t + 1$ location and recorded the habitat variables (see 6.2.5.).

To investigate whether broods exhibited habitat selection within the brood range the dataset composed of habitat information from fake and real brood locations within the range was analysed using generalised linear modelling. The maximal model comprised all the habitat variables (see 6.2.5.) as explanatory variables and 'real' (whether the location was real (1) or fake (0)) as the dependent binomial variable. Step-wise elimination of insignificant terms revealed the minimal model.

The same process was used to investigate whether the habitat at roost sites differed from other brood locations. The maximal model comprised all the habitat variables (see 6.2.5.) as explanatory variables and 'roost' (whether the location was a roost (1) or not (0)) as the dependent binomial variable.

6.2.5 Habitat sampling

The following habitat variables were recorded at every grid intersection, brood location and fake location. These variables, although point samples (and in particular based on point locations of each brood), were considered representative of the patch in which they were located.

i) number of broad-leaved trees within a 5 m radius expressed as broad-leaved tree density, stems per ha;

ii) number of coniferous trees within a 5 m radius expressed as coniferous tree density, stems per ha;

iii) canopy cover (%) in a 2 x 2 m quadrat (subjectively estimated to the nearest 5 %);

iv) average crop tree height (m) within a 5 m radius (subjectively estimated to the nearest 0.5 m);

v) species of the nearest tree in each of the four cardinal compass quadrants (expressed as percentage of that species in the stand);

vi) whether the canopy of the nearest tree in each of the four quadrants interlocked with that of another (expressed as percentage of stand with interlocking canopy);

vii) the height at which the canopy of the nearest tree in each of the four quadrants interlocked with that of another (expressed as average canopy interlocking height, m);

viii) ground cover (%) in a 2 x 2 m quadrat (subjectively estimated to the nearest 5 %) of each of the following plant groups: *Calluna vulgaris* and *Vaccinium* species; bog myrtle; grass; bracken; rushes; herbs;

ix) vegetation profile: the density of vegetation in 4 height bands (0 – 0.5, 0.5 – 1, 1 – 1.5, 1.5 – 2 m) recorded as the percentage (0 – 20, 21 – 40, 41 – 60, 61 – 80, 81 – 100 %) of a pole obscured by the vegetation when viewed from 10 m away (north, east, south and west) (after Nudds 1977).

At each location these data were collected from the exact point and also points 5 m to its north, east, south and west. This protocol was adopted to accommodate an anticipated 5 m error between actual brood locations and those indicated by radio telemetry (calculated from field trials before birds were caught – see 6.3. for actual error achieved (after White & Garrott 1990b). An average value for the point location was calculated from the 5 sets of data and this was used in subsequent analyses.

6.2.6 Invertebrate sampling

Invertebrates form the major component of black grouse chick diet in the first three weeks after hatching (Baines 1993a; Baines *et al.* 1994; Baines *et al.* 1996; Hudson 1990; Kastdalen & Wegge 1984; Cayford 1990; Cramp & Simmons 1980) in common with other galliformes (e.g. Savory 1977; Stuen & Spidsø 1988). At each brood location (real and fake) during this period invertebrates were sampled by sweep netting whenever possible (between 10:00 and 16:00 hours when the vegetation was sufficiently dry). In 1997, sweep net samples were taken from the 5 sample points per brood location (i.e. 25 sweeps at each of the centre, north, east, south and west points). Preliminary statistical analysis revealed that the dry weight of the invertebrates from the central sample point was not significantly different from that from the other sample points ($F_{4,25} = 2.24$, $P = 0.070$) hence in 1998 only the centre point was sampled.

Invertebrate samples were stored frozen until sorting, then frozen again until dried and dry weight recorded.

Invertebrate sampling was performed to allow (in conjunction with faecal analysis) analysis of food availability versus use, i.e. to allow the fourth order of habitat selection to be investigated. These data are not presented here since the weather during the sampling period was very wet consequently fewer samples were collected than planned and these were not thought to be representative, and subsequently time did not permit full analysis of the samples.

6.3 Results

In 1997, ten broods of 7 - 10 day old black grouse chicks were caught. Mean brood size was 2.7 chicks (range 1 – 7). A total of 16 chicks were equipped with radio-transmitters; data from two broods were later excluded as they moved from forest to moorland habitat.

In 1998, nine broods were caught, mean brood size was 3.9 chicks (range 2 – 6). A total of 13 chicks were equipped with radio-transmitters; data from three broods were later excluded as they moved from forest to moorland habitat and one further brood was never found again after capture.

Since the primary purpose of this study was to relate brood presence/absence to habitat data rather than to study year-to-year changes 'year' was excluded from the analyses. Preliminary analysis had shown that the strength of 'year' effect masked that of the habitat variables. Analysing the years separately was not an option since the sample sizes were too low: n = 8 in 1997 and n = 5 in 1998. It was not possible to identify individual hens so it was assumed for the purposes of this study that they were different between years, so that the broods were treated as independent. This also makes the reasonable assumption that habitat quality and not individual hen bird preference is the over-riding factor in brood habitat selection. Thus, the data from both years were pooled, and 'year' excluded, giving a total of 13 forest-dwelling broods for subsequent analysis.

The habitat sampling protocol accommodated an approximate 5 m error between actual brood locations and those indicated by radio telemetry. This was found to be adequate as the actual error in 1997 was estimated to be 5.3 m ± 4.4 m (1 S.D.), and in 1998 just 1.72 m ± 1.54 m.

6.3.1 Habitat selection within the study area

The habitat within the home range differed significantly from that found elsewhere in the study area, such that broods appeared to exhibit habitat selection within the study area. Five habitat variables were significantly correlated with the likelihood of the site being within a brood home range: tree density; crop tree height; 1.0 –1.5 m vegetation profile; height at which canopies interlocked; and the percentage ground cover by herbs (see table 6.1 and figures 6.3a & b). All of these variables, with the exception of crop tree height, had a positive relationship with the likelihood of the location being real. The model explained 40% of the variation present in the dataset, fairly typical of regression models for this type of ecological study (Trout *et al.* 2000).

Table 6.1. Summary of minimal binomial models (logit link function) generated to predict the probability of a point location being selected.

Model	**R^2 (%)**	**Total density of trees (stems/ha)**	**Average crop tree height (m)**	**Vegetation Profile 1 – 1.5 m (VPC)**	**Average height at which canopies interlock (m)**	**Ground cover by herbs (%)**	**Amount of spruce in the stand (%)**	**Figures in text**
6.3.1.	40	0.000	0.000	0.039	0.001	0.002	-	6.2 a & b & 6.3 a - c
6.3.2.	7	0.025	-	-	-	0.001	-	6.4 a & b
6.3.3.	34	0.000	-	0.007	-	-	0.010	6.5 a - c

Notes: Numbers below variables are the P values for significant terms.

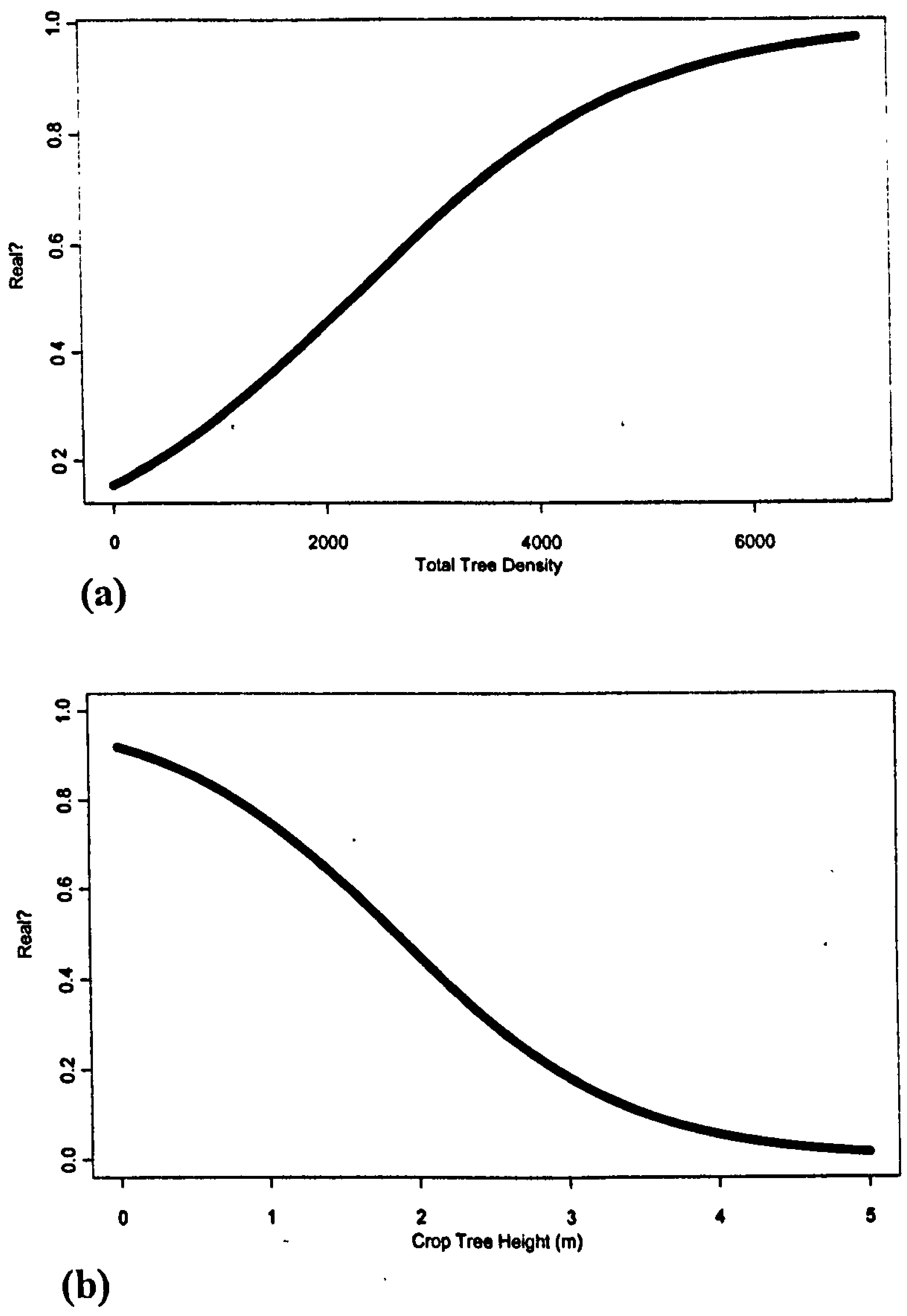


Figure 6.2. Fitted logit model of the probability of a fix within the study area being real predicted using a range of (a) total tree densities (stems per ha) and (b) crop tree heights (m).

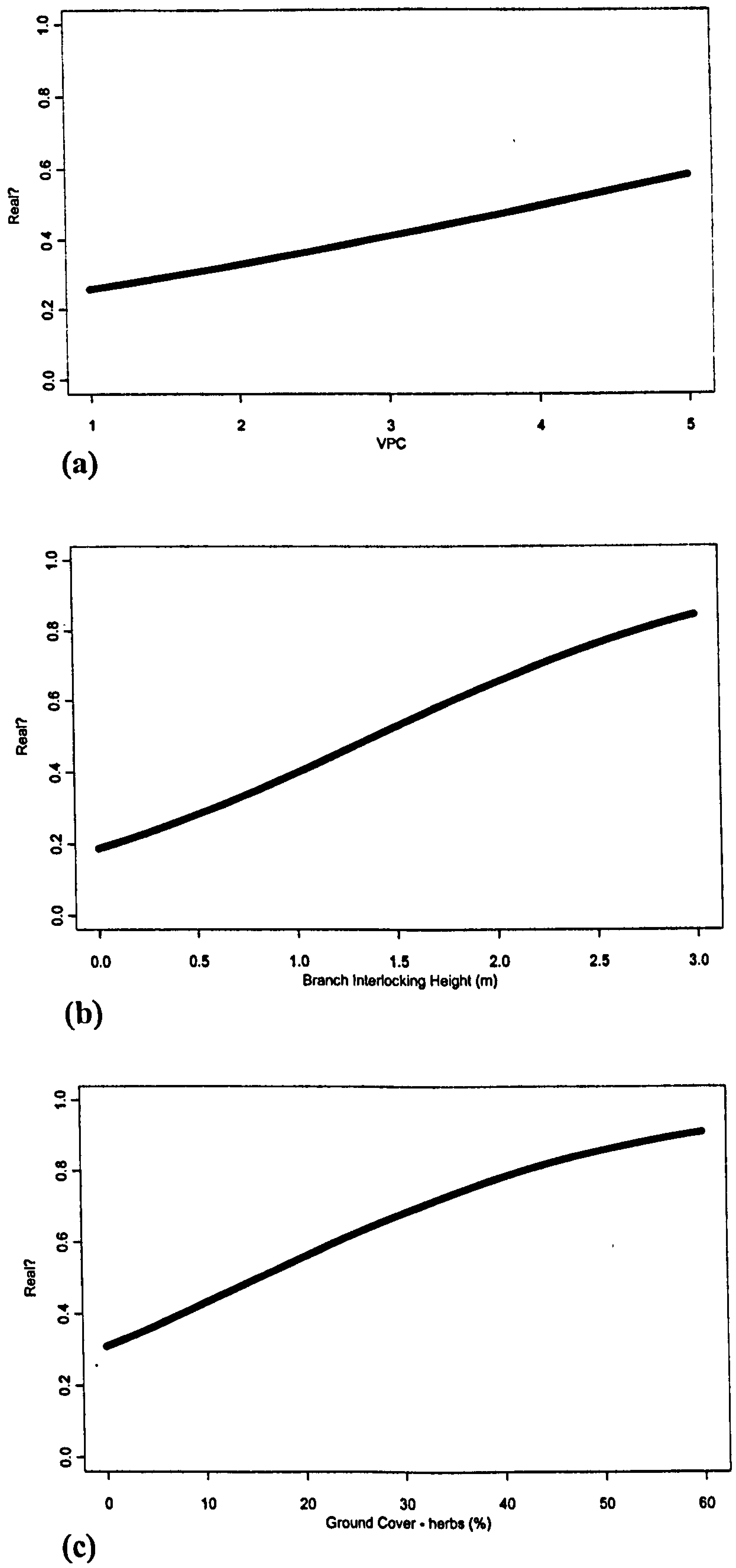


Figure 6.3. Fitted logit model of the probability of a fix within the study area being real predicted using a range of (a) vegetation densities in the 1 – 1.5 m height band ('VPC'), (b) heights at which canopies interlocked (m) and (c) ground cover by herbs (%).

6.3.2 Habitat selection within the brood home range

The habitat used within the brood range also differed significantly from the habitat found within the brood range but not used, i.e. broods did appear to exhibit habitat selection within the range. Only two habitat variables were significantly correlated with the likelihood of a site being used at this scale: tree density and the percentage ground cover by herbs (see table 6.1 and figures 6.4a & b). Both these variables showed a positive relationship with the likelihood of the location being real. However, the biological significance of these findings is weak since this model only explained 7% of the variation present in the dataset.

6.3.3 Roost habitat

The habitats used for roost sites differed significantly from those used for other activities. Three habitat variables were significantly correlated with the likelihood of a site being used for roosting: crop tree height; 1.0 –1.5 m vegetation profile; and the percentage of spruce within the stand (see table 6.1 and figures 6.4a-c). The 1.0 –1.5 m vegetation profile had a positive relationship with the likelihood of the location being real, whilst the other two variables showed negative relationships with the dependent variable. This model explained 34% of the variation present in the dataset.

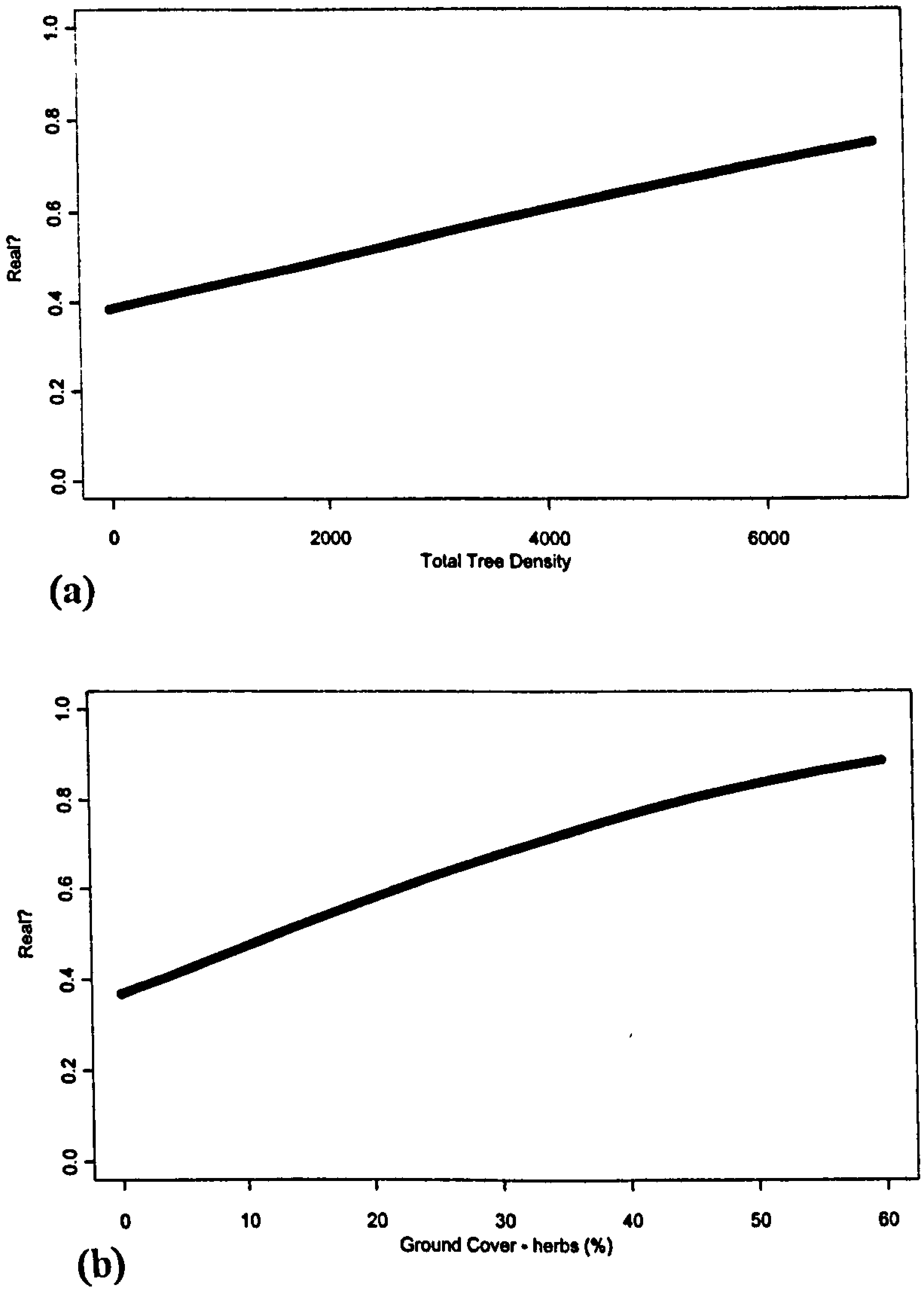


Figure 6.4. Fitted logit model of the probability of a fix within brood home range being real predicted using a range of (a) total tree densities (stems per ha) and (b) ground cover by herbs (%).

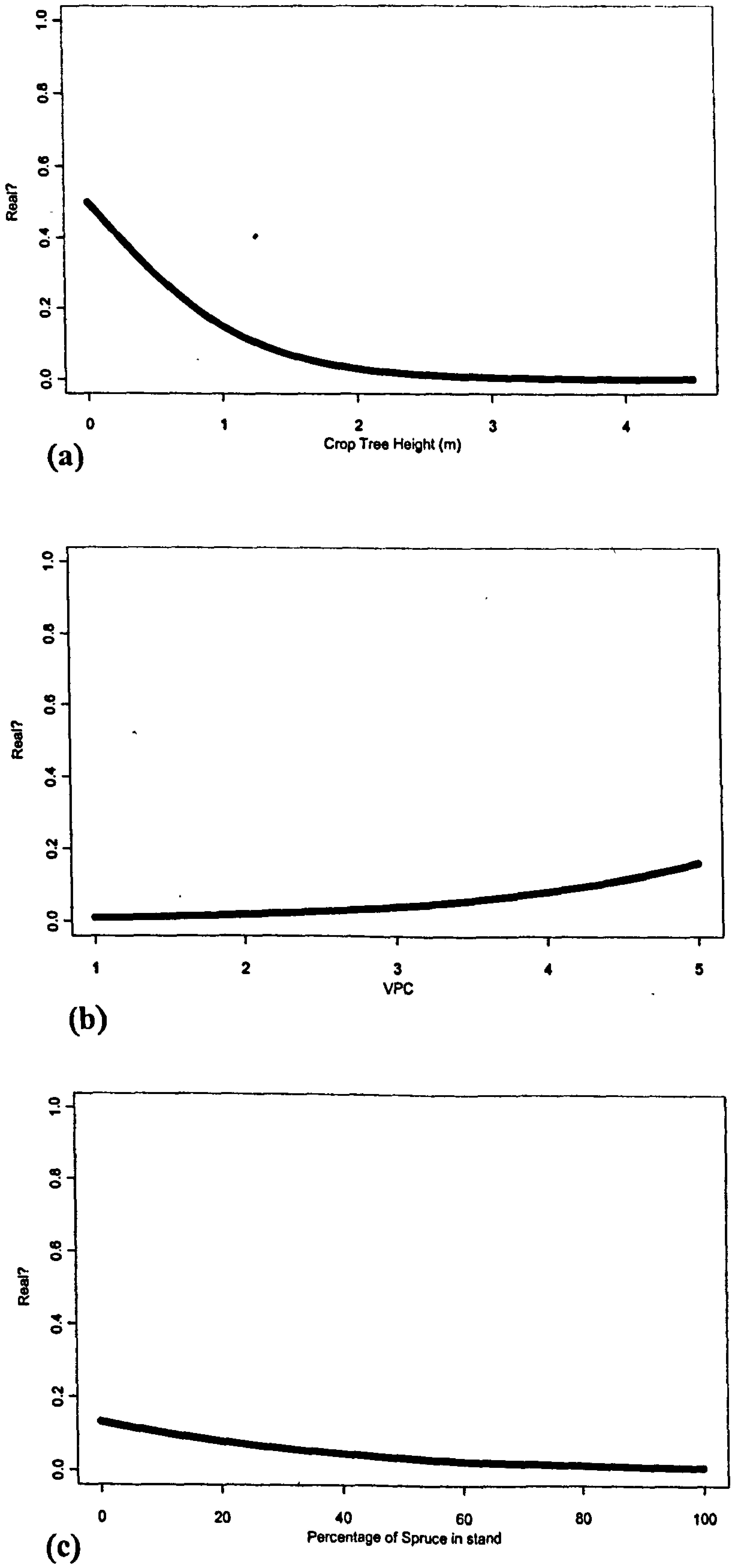


Figure 6.5. Fitted logit model of the probability of a fix being a real roost site predicted using a range of (a) crop tree heights (m), (b) vegetation densities in the 1 – 1.5 m height band ('VPC') and (c) amounts of spruce within the stand (%).

6.4 Discussion

6.4.1 Habitat selection within the study area

In this study, black grouse broods selected habitat within the study area (i.e. second order habitat selection). Habitats found within the brood range differed from those in the remainder of the study area in that locations within brood ranges had more trees per hectare, shorter crop trees (with canopies interlocking at a greater height), thicker vegetation in the 1.0 –1.5 m band and a higher proportion of herbs in the ground layer than did locations elsewhere in the study area (see table 6.1 and figures 6.2a-c & 6.3a & b). This model explained 40 % of the variation present in the dataset. This behaviour contrasts with the preference black grouse broods showed for older moist forest rich in ericaceous shrubs in Norway (Kolstad *et al.* 1985; Wegge 1983; Børset & Krafft 1973) but, to a certain extent, concurs with earlier work undertaken in Perthshire which found that black grouse broods preferred herb-rich grassy flushes with bog myrtle (Baines *et al.* 1996). Cayford (1993) also states that broods in Scottish and Welsh forests favoured stream margins, sunny rides, verges and young plantations supporting a mixture of tall grasses, heather and blaeberry. It is likely that food availability and vulnerability to predators interact and may drive habitat selection. Overall, the broods studied in Trinafour, Perthshire can be interpreted as selecting habitats that were 'open' enough to support a rich ground flora and thus an adequate invertebrate fauna but also 'closed' enough to provide cover, representing a compromise between foraging potential and predation risk. The Norwegian broods may have been doing the same – habitat preferences must be seen within a local context.

It should be noted that tree density in isolation can be a misleading variable. Whilst it specifies the number of trees per unit area it gives no indication of the size, age, or stage of the trees. Therefore, it is not surprising that in the minimal models this variable is generally accompanied by others, such as crop tree height, height of interlocking canopies, vegetation profile or ground cover, which in combination are more informative.

6.4.2 Habitat selection within the brood home range

Whilst habitats used within the brood range differed significantly from those not used it is uncertain whether black grouse broods in this study really selected habitat within the brood home range (i.e. third order habitat selection). Habitats used within the brood range had more trees per hectare and a higher percentage ground cover by herbs than those that were not used (see table 6.1 and figures 6.4a & b). However, this model only explained 7 % of the variation in the dataset which suggests that although habitat selection occurs at both scales, the selection within the brood range could be regarded as 'fine-tuning' if, indeed, it was biologically meaningful. High tree densities have been shown to be associated with high invertebrate larval densities (Baines *et al.* 1994) thus the broods may have been selecting prime feeding areas as almost half of their invertebrate diet has been found to consist of larvae (Kastdalen & Wegge 1984). Without testing the model using an independent dataset it was not possible to ascertain whether this third order selection was merely an artefact or a real effect. Significant positive correlation with invertebrate densities in the field weighted according to importance in black grouse chick diet (Poulin & Lefebvre 1997) would, however, strengthen the argument for third order habitat selection. Many studies (e.g. Green 1984; Hill 1985; Park *et al.* 2001; Southwood & Cross 1969; Niewold 1990) have identified the link between galliform chick survival and the abundance of their arthropod prey.

6.4.3 Roost habitat

In this study, black grouse broods also appeared to select their roost habitats since the habitats used for roost sites differed significantly from those used for other activities. Habitats used for roost sites had shorter trees, a lower proportion of spruce in the stand and greater vegetation density in the 1.0 –1.5 m height band than those that were not (see table 6.1 and figures 6.5a-c). This model explained 34 % of the variation present in the dataset. Little has been written on black grouse brood roost sites although Cayford (1990b) observed that hens with broods often returned to the same general locality to roost each night. This may have been a result of habitat selection.

6.4.4 Limitations of the study

There are several limitations of this study that need to be addressed. First, brood habitat selection is not independent of nest site selection. What is described as brood habitat selection within the study area could be an artefact of the hen selecting a nest location and the brood merely establishing a range in the vicinity of the nest site. Grant and co-workers (1992), for example, found that most whimbrel (*Numenius phaeopus*) broods remained within 400 m of the nest site. Brittas & Willebrand's (1991) study using radio-tracked black grouse hens found a marked preference for nesting in stands of young trees (height 0.5 – 3.0 m) rather than mature and maturing forest stands. Cayford and co-workers (1989) stated that females selected tall vegetation in rides and plantations for nesting but this work was limited by a sample size of four nests. Other studies, however, found no specific preference for nesting habitat (e.g. Wegge 1983). Black grouse broods can and frequently do travel relatively large distances (Robel 1969; Wegge 1983). Cayford and co-workers (1989) recorded average brood movements of 26 – 50 m per 6 hour interval (ranging from

21 – 401 m per 6 hours) although again these measurements came from four broods only and Kolstad and co-workers (1985) observed that black grouse broods left the nesting area shortly after hatching. Given the mobility of the broods it is reasonable to believe that the selection identified was brood habitat selection but this could not be tested in this study due to the limited number of broods available and the sensitivity of this species to the stress that translocation experiments would cause.

Second, statistically significant associations merely indicate which features might be important but they do not necessarily reflect causal relationships (Newton *et al.* 1996). Manipulation experiments should be carried out to test conclusions from correlative studies (Green 1994).

Third, it was assumed that all of the study area constituted 'available' brood habitat, but the perception of an area by black grouse will, almost certainly, be different from an anthropocentric one. The presence of a predator's centre of activity or a high level of disturbance may render an area unavailable yet it would have been included in analyses.

Finally, whilst every effort to minimise any impact of the radio-tracking study on the birds was made, it must be recognised that it is impossible to have no impact whatsoever. This impact should be assessed because of ethical considerations and also to check that the research has not merely recorded the study species' response to tagging. It was not possible to assess the level of impact in this study although Kenward and co-workers (1993) found that glue-mounted radios had no effect on the survival of pheasant (*Phasianus colchicus*) chicks. Also, a behavioural response to tagging would have to be exhibited for the results of this study to be biased. As the tagged chicks continued to stay and move with the untagged members of the brood this is considered unlikely. However, investigators have noted that tagged animals may alter their behaviour for several days after tag attachment (White & Garrott 1990a; Boag 1972; Nenno & Healy 1979) sometimes with a subsequent increase in risk of death (Angelstam 1984b). Consequently most authors exclude the first few days from their analyses. This was not possible in this study given that the chief period of interest was the first 3 weeks after hatching when chick and adult diet differ substantially. No broods within the study area were intentionally left untagged so it was not possible to assess the impact of tagging on chick survival. Comparing chick survival in 1997 and 1998 with previous untagged years was inappropriate as weather is known to have a great impact on chick survival (Ellison & Magnani 1984; Marcström & Engren 1984; Zbinden 1987). 1997 and 1998 were appalling years for chick survival due to prolonged heavy rain and low temperatures despite Moss' (1986) conclusion that rain had no detectable effect on black grouse breeding success in his study.

Cotter & Gratto (1995) found no difference in brood size at fledging or fledging success between rock ptarmigan (*Lagopus mutus*) broods that were visited frequently or infrequently, but they did not compare these with untagged broods. Many authors have stated that their radio-telemetry work had no quantifiable detrimental effect on their study species (e.g. Lance & Watson 1977; Taylor 1991; Esler *et al.* 2000; Thirgood *et al.* 1995) but a recent review suggests that tests of tag effects often lack statistical power (Godfrey & Bryant 2001). It is unlikely that so many would be willing to publish reports of such an effect, although this does occur when new techniques are introduced and best practice is rapidly evolving (e.g. Caizergues & Ellison 1998; Kenward *et al.* 1993; Herzog 1979; Erikstad 1979).

6.4.5 Implications for forest management with the aim of conserving black grouse.

This chapter only looked at black grouse brood habitat selection within plantations but broods have been shown to use young forests disproportionately (Baines *et al.* 1996). Within plantations, broods prefer areas with many short trees, dense vegetation between 1 and 1.5 m high, and a herbaceous ground flora. Knowledge of the preferred habitat types is important for conservation management since they must be identified before they can be maintained. It is not possible to say that this habitat is critical for chick survival without manipulation experiments (White & Garrott 1990c) but it is clearly an important one and should be conserved. Such habitats currently occur within the modern forest environment although clearcutting is thought to markedly reduce larval & invertebrate density (Kastdalen & Wegge 1984; Stuen & Spidsø 1988) but this work compared Norwegian old forest with clearcuts – a situation not entirely comparable with British plantations. In The Netherlands the opposite pattern was found (Angelstam unpublished).

6.4.6 Suggestions for further work

As with the work described in previous chapters, the models discussed here must be tested with independent datasets and also manipulation experiments. Prior to this, further investigation of chick diet via analysis of the faecal and invertebrate samples collected during this study should be performed to see if habitat use within the home range correlates with higher than average densities of food items.

Chick survival in relation to weather, invertebrate supply and predation (and the interactions between these) is another interesting field of investigation and might reveal useful future management techniques (with reference to predators not weather). Analysis of daily movements and home ranges in light of these variables may also be informative.

Chapter 7 General Discussion

7.1 Introduction

The aim of this chapter is to discuss the findings described in the previous chapters, not individually, as this has already been performed at the end of each chapter but by comparing and contrasting the findings from different chapters. The distribution of lekking black grouse in plantation forests in Cowal, Argyll (Chapters 3 and 4) will be examined in the light of their distribution in highland Perthshire (Chapter 5) in section 7.2. Then, in 7.3, adult (Chapters 3, 4 and 5) habitat preferences will be compared with those of broods (Chapter 6).

The broad aim of this research was to identify the habitat and area requirements of black grouse in first and second rotation forestry plantations. Results shared by different study areas and age classes are particularly relevant to the species' conservation, thus the implications of the research findings for forestry management will be summarised in section 7.4. Finally, the suggestions made for further work at the end of Chapters 4, 5 and 6 are summarised in section 7.5.

7.2 The distribution of black grouse in the landscape

Despite distinctly different landscapes, and slightly different scales of analysis, the results of the work in Cowal and Perthshire showed broad agreement. In particular, in Perthshire leks were more likely to decline the more isolated they were whilst in Cowal the probability of a patch holding a lek and the number of males in a patch decreased with increasing distance to the nearest lek.

In Cowal, the probability of a patch holding a lek and the number of leks per patch decreased with increasing tree height, the most rapid decline occurring when the trees exceeded 2 m in height. Similarly, the number of males attending a lek in Perthshire declined as the nearby trees aged, and within forest blocks the number of lekking males increased with increasing proportion of prethicket stock.

In both areas, the more prethicket forestry (of either rotation) available the more likely a lek would be present and the more males attended the lek. In Cowal, fragmentation of the forest was detrimental but this did not appear to be the case in Perthshire.

7.3 Adult and chick habitat preferences

Adult and chick habitat preferences showed some, but not extensive, parallels. Again, the probability of a site being used (both diurnally and nocturnally by chicks) decreased with increasing tree height. However, broods appeared to select sites with higher than average tree densities; this merits further investigation as it may reflect food abundance, provision of cover or may just be an artefact of the study site.

High levels of cover in the first half metre above the ground were important for adults but chicks' preferential use of sites was correlated with the amount of cover 1 –1.5 m above the ground. This distinction may be linked to their relative vulnerability to predation from different sources, mobility or the more herbivorous nature of adult diet.

Dietary needs may also be the key to the discrepancy between the ground flora favoured by adults and chicks. Broods were more likely to use a site (exhibiting both second and third order habitat selection) as the percentage of herbaceous plants in the ground layer increased, but adults were more likely to be found in patches where grasses exceeded 60 % of the ground flora.

7.4 Implications for 'black grouse friendly' forestry

It is within living memory that many foresters considered black grouse to be a pest species because of the damage their feeding could inflict on young plantations (Johnstone 1965, 1966 & 1967; Sharrock 1976). Fortunately, this attitude has changed with the decline of the species and the increasing prevalence of the idea that forests are more than just timber production factories (Bliss 2000). Indeed, foresters and conservationists are now collaborating to conserve many species. Some habitat management prescriptions may have a negative fiscal implication through reduced timber production but given the current conservation climate and availability of grants they may increasingly be considered feasible.

Even in landscapes that are not dominated by forestry, sympathetic forest management may be crucial to the maintenance of black grouse populations in some parts of Britain. Thus the following advice should be borne in mind when developing forest plans and reviewing planning applications. It has been collated from the results of this study (in which case the original section is referenced) and studies by other authors (in which case the relevant publication is referenced).

1. To maintain black grouse populations a large proportion of the landscape mosaic should be forestry (Sections: 4.4.1.1; 4.4.1.2; 4.4.2; and 5.4.1.2).

2. If forestry is not present then large areas of moorland should be maintained (Section 5.4.3).

3. It is important to conserve all patches of suitable habitat even if they are unoccupied (Section 4.4.2; Angelstam & Martinsson 1990; Hanski 1997; Opdam 1990).

4. Wider countryside measures such as controlling grazing pressure are needed to improve, maintain or enhance the habitat suitability in the matrix between suitable habitat patches (Baillie *et al.* 2000; Hansson 1992; Andrén 1994).

5. Within forestry, a large proportion of the crop should be prethicket stage, ideally grown in large stands containing a variable age structure (Sections 3.4.1; 3.4.2; 3.4.3; 4.4.1.1; 4.4.1.2; 4.4.2; 5.4.1.2; 5.4.3). The amount of prethicket forestry within a forest block is positively correlated with the number of males displaying in the block; i.e. the more young forestry the better (Sections 5.4.2.2; 5.4.3).

6. Large stands become a problem when the trees mature beyond the thicket stage. A balance must be found wherein as prethicket forestry matures young forestry, second rotation in effect, must become available within black grouse foraging distance (Sections 4.4.2; 5.4.3).

7. Large even-aged blocks of trees can be undesirable for other species, e.g. songbirds (French *et al.* 1986). An appropriate grain size must be found such that in the same 'patch' a black grouse 'perceives' one large patch whilst small passerines perceive lots of small patches with lots of edges (Section 4.4.2).

8. Using slower growing tree species and planting them further apart can increase the length of the pre-thicket stage (Parr & Watson 1988) and hence extend the 'suitable' period of the stand.

9. Post-felling treatment, e.g. drainage, slashburning, scarification, mounding and biocide treatment, should be minimised in order (Section 4.4.2) to allow the regeneration of the ground flora on restocked sites (Cayford 1993).

10. Leks should not be afforested (Cayford 1993). Cayford also proposed targeting black grouse management improvements within a 1.5 km radius of leks but this may not be economically feasible nor on a sufficiently large scale to have any significant lasting benefit.

11. Deer fences present a collision hazard for woodland grouse (Baines & Summers 1997; Catt *et al.* 1994; Andrew & Baines 1997; Summers 1998). They should be removed or at the very least marked and alternative strategies for safeguarding trees such as deer culling pursued where practicable (Andrew & Baines 1997; Baines & Summers 1997).

12. Broods have been shown to use young forests disproportionately (Baines *et al.* 1996). Within plantations, broods prefer areas with many short trees, dense vegetation

between 1 and 1.5 m high, and a herbaceous ground flora. Such habitats do currently occur within the modern forest environment (Sections 6.4.1; 6.4.5).

7.5 Suggestions for further work

Suggestions for further work, to both address limitations of the work presented and build on it, were made in Chapters 4, 5 and 6. They are listed below:

1. The models should be tested. Statistically significant associations merely indicate which features might be important but they don't necessarily reflect causal relationships (Newton *et al.* 1996). Manipulation experiments should be carried out to test conclusions from correlative studies (Green 1994). This should be done on two levels – the manipulation of experimental plots in commercial plantations and simultaneous monitoring of leks and black grouse habitat use, and testing the models using independent data. For example, the models from Chapters 3 and 4 (Cowal) could be tested with data from Glentrool Forest in Dumfries and Kielder Forest in the Scottish Borders. The models from Chapter 5 (Perthshire) could be tested with data from Tayside and Angus.

2. Once tested, if models were found to be adequate and applicable to other areas, they could be used to predict the potential impact of different forest plans on black grouse numbers.

3. Trials should be put in place to establish the sustainable ratio of suitable: unsuitable habitat that fulfils black grouse habitat requirements.

4. Habitat selection at specific sites, e.g. nests, not investigated in this study need to be identified within the context of British commercial forestry plantations.

5. A sample of male and female black grouse should be radio-tracked in order to estimate their home ranges and assess habitat selection directly. Such a study would allow movements between leks and the length of foraging distances to be investigated.

6. Year to year change in black grouse numbers should be compared with equally dynamic habitat data.

7. Future development of this work should preferably incorporate the use of a geographic information system. Forest Enterprise stock maps for the study areas should now be available in a digitised form.

8. Further investigation of chick diet via faecal analysis should be performed to see if habitat use within the home range correlates with higher availability of food items.

9. Conflicting evidence of the impact of clearcutting on larval & invertebrate density comes from studies in Norway and The Netherlands. The composition and abundance of the invertebrate fauna associated with forest stages and management in Scotland should be investigated.

10. Chick survival in relation to weather, invertebrate supply and predation requires further investigation. Analysis of daily movements and home ranges in light of these variables may also be informative.

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